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Modelling the Effects of Contemporary Climate Change on the Physiology and Distributions of Non-Indigenous Species

by

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Thesis for the degree of Doctor of Philosophy

July 2021

University of Southampton

Abstract

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Contemporary climate change (CCC) and non-indigenous species (NIS) are two of the biggest threats to global biodiversity and together are expected to drive a rapid global redistribution of species by the end of the century. Although understanding the interaction between NIS and CCC is crucial for the management of native ecosystems, forecasting future changes remains a significant challenge. It is thus recognised that understanding the physiological mechanisms that shape distributions and promote NIS spread is necessary to make robust forecasts under CCC. In this thesis, novel experimental and ecological niche modelling (ENM) techniques were combined to explore how the highly successful NIS, the Pacific oyster *Magallana gigas*, may be affected by end-of-the-century environmental conditions. The present research has shown during long-term exposure that *M. gigas* individuals were physiologically tolerant to CCC conditions predicted for the end of the century. It was evident that *M. gigas* has a broad environmental tolerance and have undergone rapid niche shifts during introduction that have likely facilitated its current rapid global spread. In addition, both correlative and mechanistic ENMs predicted that *M. gigas* will undergo a poleward range expansion by the end of the century. Modelling with inter-individual variability showed complex geographical changes in life-history traits in response to CCC. It was apparent that both correlative and mechanistic ENMs can complement each other and provide a unique insight into the predicted changes in species' niches under environmental change.

This thesis presented the first long-term, multi-factor mesocosm study of *M. gigas*, tested the differences between popular niche shift frameworks and presented the first bioenergetic model combining inter-individual variability and environmental variability to predict species responses to CCC across large geographical areas. Taken together, a combination of techniques has produced robust predictions forecasting the continued survival and spread of *M. gigas* under end-of-the-century CCC.

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Academic Thesis: Declaration Of Authorship

I, Kathryn Elizabeth Pack

declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

Title of thesis: Modelling the effects of contemporary climate change on the physiology and distributions of non-indigenous species

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
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    1. Pack, K.E., Rius, M. and Mieszkowska, N. (2021) Long-term environmental tolerance of the non-indigenous Pacific oyster to expected contemporary climate change conditions. *Marine Environmental Research*, 164, p.105226.

Signed: ....

Date: ....

Acknowledgements

Firstly, I would like to thank my supervisors Dr Nova Mieszkowska and Dr Marc Rius for the guidance and support they have provided me during the last 4 years. Nova, since I started with you back in 2016, I have learned so much. I am grateful to have a mentor who has provided me with fantastic opportunities and is always really good laugh, especially on all those long fieldwork days. Marc, it has been great to be part of your lab group for the last two years. I have also very much appreciated your attention to detail, and I have become a better writer because of it.

I want to give a special thank you to Professor Steve Hawkins who without whom I would not be where I am today. I will be forever grateful for your generosity and support over the last five and a half years. I am thankful for all the exciting projects you involved me in and everything you have taught me, it has undoubtably helped progress my career. Assisting you on many a MarClim field trip over the years has been a definite highlight.

I feel very fortunate to have been surrounded by such hard-working and enthusiastic people during my research. To my PhD partner in crime Hannah. Your words of encouragement always got me back on track when times were tough. I am honoured to have had such an amazing friend along this journey. I cannot wait to go on a much-needed nudibranch hunt again soon. I also owe a big thank you to the hard-working interns who I had the pleasure of working with during all those months in the lab.

To my family, you have been a constant source of happiness during my PhD. You really are the best family ever and I am so lucky to have you. Mum, I can’t thank you enough for your continuous love, support and kindness, it has always meant so much to me. Dad, I owe you so much. You have been my biggest supporter and source of encouragement. This PhD is dedicated to you.

Finally, James, my husband. Words cannot describe how much your love and support means to me. You were there during all the highs and mini celebrations (no matter how small) and kept me going during the all the lows. Marrying you during my PhD has made me the happiest person and I can’t wait to spend the rest of my life with you. Thank you for all your love and putting up with me when all I talked about was oysters for the last 4 years (P.S. invertebrates rule).

Definitions and Abbreviations

ANOVA	Analysis of Variance
AUC	Area Under the Curve
BRT	Bootsted Regression Trees
CBD	Convention on Biological Diversity
CCC	Contemporary Climate Change
CMIP5	Coupled Model Intercomparison Project
CO_2	Carbon Dioxide
COUE	Centroid shift, Overlap, Unfilling and Expansion
CR	Clearance Rate
DEB	Dynamic Energy Budget
DMW	Dry Meat Weight
ENM	Ecological Niche Model
EU	European Union
GBIF	Global Biodiversity Information Facility
HADGEM-ES	Hadley Centre Global Environment Model - Earth System
IBM	Individual-Based Model
IPCC	Intergovernmental Panel on Climate Change
MD	Mahalanobis Distance
MODIS	Moderate Resolution Imaging Spectroradiometer
MSDF	Marine Strategy Framework Directive
MSE	Mean Squared Error
NIS	Non-Indigenous Species
PC	Principal Components
PCA	Principal Components Analysis
PLS	Partial Least Squares
POM	Particulate Organic Matter
PPM	Parts Per Million
RCP	Representative Concentration Pathways
RCP4.5	Medium ‘Stabilisation’ Scenario
RCP8.5	High Emission ‘Business as Usual’ Scenario
RM-ANOVA	Repeated Measures Analysis of Variance
ROC	Receiver Operating Characteristic
SDM	Species Distribution Model
SST	Sea Surface Temperature
TSS	True Skill Statistic
WMW	Wet Meat Weight

Chapter 1 Introduction

1.1 Contemporary climate change

The world's climate is changing at an unprecedented rate. Anthropogenic activities such as burning fossil fuels and agriculture have led to an increase in greenhouse gas emissions into the atmosphere over the last 250 years (IPCC, 2014). Concentrations of carbon dioxide (CO_2) in the atmosphere have increased from 280 parts per million (ppm) to more than 410 ppm over the last 200 years, levels which have not occurred for over 800,000 years (Petit *et al.*, 1999; IPCC, 2014). The accumulation of greenhouse gases has led to the increase in global surface temperatures by more than 1°C since pre-industrial times (IPCC, 2018). By the end of the century, it is expected that future climatic states will exist for which there is no current analog, along with the disappearance of some extant climates (Williams *et al.*, 2007).

The effects of warming have been observed in the oceans where more than 90% of world's excess heat is stored, increasing ocean temperatures (Cheng *et al.*, 2019). Global sea surface temperature (SST) has increased by 0.11°C per decade between 1971 and 2010 (Caldeira & Wickett, 2003, 2005; IPCC, 2014) and the five warmest years in the ocean since 1955 have all occurred between 2015 and 2020 (Cheng *et al.*, 2020). If greenhouse gas emissions continue at current levels, global SST is expected to rise further by 3 – 4°C by the end of the century (Caldeira & Wickett, 2005; IPCC, 2014, 2018). In addition, increasing temperatures are expected to alter ocean stratification and circulation, increase the extent of oxygen minimum zones, decrease sea ice extent and lead to a rise in sea levels as a result of thermal expansion (Doney *et al.*, 2012). Changes in temperature also have far-reaching influences on biotic systems due to temperature-dependent physiological processes and hence warming is expected to have a profound individual, population and community-level effects in the future (Doney *et al.*, 2012).

Approximately 30% of anthropogenic carbon dioxide in the atmosphere has been absorbed by the surface ocean (Sabine et al., 2004). Rising CO_2 concentrations in seawater increases the formation of carbonic acid and releases hydrogen ions, which is measured as a reduction in the pH of the water. This decline in ocean pH over an extended period is known as ocean acidification. Average surface ocean pH has decreased by 0.1 units over the last 250 years and is expected to decrease by a further 0.3 – 0.4 and 0.5 – 1.0 units by the years 2100 and 2300, respectively (Sabine *et al.*, 2004; Caldeira & Wickett, 2005; IPCC, 2014, 2018). Ocean acidification leads to excess hydrogen ions in the water binding to carbonate ions, subsequently changing the saturation state of aragonite and calcite. This is expected to severely impact calcifying marine organisms by leading to the net dissolution of carbonate structures such as calcium carbonate shells and skeletons or internal structures such as otoliths (Orr *et al.*, 2005; Hofmann *et al.*, 2010). Equally, ocean acidification can alter other physiological processes and life-history traits such as reproduction, development, growth rates and survival of species (Kroeker *et al.*, 2010; Kroeker *et al.*, 2013).

Rapid environmental changes have already been shown to modified the abundance, distribution and phenology of flora and fauna across terrestrial and marine realms (Parmesan & Yohe, 2003). Hence, contemporary climate change (CCC) is recognised as one of the most significant threats to biodiversity and is expected to cause significant changes to species functioning, distributions and community compositions in the future (Walther *et al.*, 2002; Thomas *et al.*, 2004; Berg *et al.*, 2010).

1.2 Species distributions

Understanding the factors which determine spatial variation in species distributions is a central aim across a range of disciplines in ecology. The realisation that environmental conditions determine species distributions was recognised in the early 1800s (von Humboldt & Bonpland, 1807) and is often recognised in the early literature (Salisbury, 1926; Good, 1947). Large-scale patterns in species distributions and biodiversity with gradients in space or environmental conditions (for example, latitude, altitude, temperature, precipitation) are well documented (Wallace, 1876; Gaston *et al.*, 1995; Gaston, 2000; Willig *et al.*, 2003). In the marine environment, pioneering work correlated biogeographic patterns with temperature (Orton, 1920; Hutchins, 1947). Hutchins (1947) described the role of thermal tolerance in setting range boundaries of coastal species by correlating SST isotherms with the global distributions of mussels and barnacles. Similarly, studies have identified relationships between species distributions and the environment through the mapping of observational data with environmental gradients and laboratory experiments investigating species temperature tolerances (Southward & Crisp, 1954a; Crisp & Southward, 1958; Southward, 1958). Temperature is generally considered one of the main factors determining large-scale patterns in distribution and the range limits of a species (Chen *et al.*, 2011; Stuart-Smith *et al.*, 2017). A recent meta-analysis study by Stuart-Smith *et al.* (2017) showed that the distributions of 1,790 shallow-water marine ectotherms are strongly defined by SST.

A species' niche ultimately determines its biogeographic range limits where environmental conditions outside of the niche are either unsuitable or the species fails to adapt (Wiens, 2011). The 'niche' concept was first described by Grinnell (1917, 1924) but most notably by Hutchinson (1957) who described the niche as a set of abiotic and biotic conditions where a species can persist and sustain a population. The niche of an organism is often separated into the fundamental niche and realised niche (Hutchinson, 1957) and it is important to distinguish between the two when determining species distributions. The fundamental niche encompasses all the areas where the species can exist due to the abiotic conditions and is defined by the physiological tolerance of a species to the environment. In optimal conditions, organisms maximise their biological functioning, leading to growth and reproduction. Outside of the optimum range of conditions functioning can be less efficient and fitness can be negatively impacted (Pörtner & Farrell, 2008). The realised niche, however, is essentially a subset of the fundamental niche and describes all the areas where the species lives due to constraints such as competition, predation, dispersal capabilities. Understanding the processes which determine the realised and fundamental niches of an organism has significant implications for predicting the performance and the biogeographic distributions of species under environmental change.

1.2.1 Redistribution of species

The redistribution of species occurs naturally in line with climate fluctuations in marine and terrestrial environments, for example, changes in glaciation and temperature or carbon dioxide concentrations (Hewitt, 1999; Graham *et al.*, 2010). In response to these environmental changes, species must tolerate or adapt to new conditions, shift their geographical distributions or face extinction (Berg *et al.*, 2010; Wiens, 2016). Over long and short time scales, changes in climate have been recognised to drive shifts in species distributions and abundances (Southward & Crisp, 1954b, 1956; Southward, 1991; Southward *et al.*, 1995). Anthropogenic activities are one of the main causes for the recent and rapid redistribution of species globally. For example, the expansion and contraction of species distributions due to CCC (Parmesan & Yohe, 2003), an increase in artificial transport leading to biological invasions (Vitousek *et al.*, 1997), man-made structures acting as bridges and barriers for dispersal (Adams *et al.*, 2014; Bishop *et al.*, 2017), and habitat loss and fragmentation (Warren *et al.*, 2001; Cushman, 2006; Reino *et al.*, 2013) have all redistributed species.

Ecological systems have already been affected CCC and studies have shown that species vary greatly in their responses (Parmesan & Yohe, 2003; Bellard *et al.*, 2012). The unprecedented velocity of CCC has led to environmental changes at a rate which may outpace the potential adaptation of species and in response species must alter their distributions in line with these shifts (Loarie *et al.*, 2009). A global meta-analysis by Parmesan & Yohe (2003) found that terrestrial species ranges have shifted on average by 6.1km per decade towards the poles and an advancement in spring-time phenology by 2.3 days per decade. Climate-related local extinctions have already occurred in hundreds of species across a range of habitats and climatic zones and, under CCC predicted for the end of the century, these extinctions could increase two-fold to five-fold (Wiens, 2016). Ultimately, the ability for the species to shift their distribution to new locations in line with changing climates depends on dispersal capabilities, habitat availability and abundance which will determine the supply of recruits to new areas (Mair *et al.*, 2014).

The distributions of marine invertebrates tend to conform to their thermal tolerance limits (Sunday *et al.*, 2012); therefore in line with warming waters, species are shifting their distributions to higher latitudes (Helmuth *et al.*, 2006; Mieszkowska *et al.*, 2006; Cheung *et al.*, 2009). Range shifts have already been observed in the marine environment and have occurred much faster than in terrestrial systems, with reported poleward shifts of over to 50 km per decade (Mieszkowska *et al.*, 2005; Sorte *et al.*, 2010; Poloczanska *et al.*, 2013). Meta-analysis by Sorte *et al.* (2010) showed that 75% of range shifts already experienced by marine species were in the poleward direction, in line with recent CCC. Contractions in species trailing range limits (tropical range edge) have been estimated to be up to five times slower than the rate of leading edge expansions (Poloczanska *et al.*, 2013). As the global climate continues to rapidly change, shifts in species ranges are expected to continue and the ability to predict potential shifts under CCC is key for the conservation and management of ecosystems.

1.3 Ecological niche modelling

Some of the earliest examples of estimating species niches in a geographical space involved the interpolation of occurrence records to produce ‘distribution maps’ (Grinnell, 1904, 1917). Since then, ecological niche models (ENMs) have been developed using a variety of mathematical approaches with the aim of describing biogeographic patterns and predicting species distributions in line with multiple environmental parameters. Early ENM approaches included statistical methods such as bioclimatic envelopes and convex hulls (Carpenter *et al.*, 1993). Through the development and accessibility of mathematical techniques, mapping and programming tools, and open access datasets for species occurrence and climatic data, the advancement of ENMs has been greatly facilitated (Guisan & Zimmermann, 2000). Subsequently, this has led to the utilisation of ENMs across a broad range of topics such as biogeography, invasion and conservation biology, habitat and species management, and climate change research. The number of publications using ENMs techniques has been increasing every year (Robinson *et al.*, 2011; Pacifici *et al.*, 2015). Despite widely available environmental and ecological data, relatively fewer studies in the marine environment have been conducted compared to the terrestrial environment (Robinson *et al.*, 2011; Robinson *et al.*, 2017).

Two popular types of ENMs are correlative and mechanistic models, with correlative models being the most popular and widely used throughout the literature. Correlative approaches use empirical statistical models to correlate the geographic distribution of a species with the environmental conditions at their respective locations. These models require presence and/or absence, or abundance records and data on the environment such as temperature, salinity and substrate to infer the species' niche (Figure 1.1) (Buckley *et al.*, 2010; Pacifici *et al.*, 2015). Assuming species' distributions are in equilibrium with the surrounding climate (i.e., they live in all suitable areas and are absent from unsuitable ones, Hutchinson, 1957), the models estimate the probability that a species is present under any given environmental conditions. Typically, biotic interactions are not explicitly incorporated into correlative models, however, occurrence records implicitly reflect factors such as competition and predation, and thus the models predict the realised niche of the species (Pearson & Dawson, 2003; Soberón & Peterson, 2005).

The applicability of correlative models for predicting distributions under CCC has been debated as they often lack information on key variables which influence species distributions (Thuiller, 2004; Evans *et al.*, 2015), such as how CCC will affect physiology, dispersal and potentially lead to species adaptation (Robinson *et al.*, 2011; Gillson *et al.*, 2013; Peterson *et al.*, 2015). A key assumption of correlative ENMs is that the processes which constrain the population range edges are stable over time and space. This is unlikely to hold as CCC conditions are expected to alter the physiological processes and create novel species associations which may change the fundamental and realised niche of a species (Williams & Jackson, 2007; Buckley *et al.*, 2010; Robinson *et al.*, 2011; Kissling *et al.*, 2012). Studies using hindcasting approaches (for example, predicting current distributions from modelling past occurrence and environmental data) have shown low to moderate model accuracy when modelling to non-analog climates (Araújo *et al.*, 2005; Dobrowski *et al.*, 2011; Veloz *et al.*, 2012; Uribe-Rivera *et al.*, 2017). Nonetheless, correlative ENMs are relatively quick and easy to run compared to other modelling techniques and, when treated with caution, contribute important first steps towards predicting distributions under future climates. Advancements are often being made to increase their robustness such as the integration of biotic or physiological constraints (Dormann *et al.*, 2012; Wisz *et al.*, 2013). Equally, complementary laboratory experiments which subject species to predicted non-analog climates, particularly multiple stressors, could be used to evaluate correlative ENM predictions to further understand species performance and adaptation under CCC.

The development of mechanistic ENMs has been driven by the desire to incorporate physiological knowledge into estimates of species distributions. Mechanistic models are described as being more robust than correlative models when extrapolating species distributions to future climates and under environmental change as they link functional traits to the environmental variables (Figure 1.1) (Kearney & Porter, 2009; Elith *et al.*, 2010). These models do not correlate occurrence data with environmental data so do not rely on species distributions being in equilibrium with the surrounding climate. Instead, mechanistic models aim to predict a species' fundamental niche through the physiological processes which structure species biogeographic distributions (Kearney *et al.*, 2008; Evans *et al.*, 2015). Physiological processes are responsible for the flow of mass and energy within an individual when it interacts with the environment (Kearney *et al.*, 2010b). Typically, mechanistic model parameter estimates of various physiological processes are acquired through manipulative laboratory and field experiments to understand the responses to the environment (Kearney & Porter, 2009). However, some parameters cannot be measured and need to be estimated through model fitting or calibration to observed data. Responses can then be scaled up from individual fitness to population-level dynamics and mapped into a geographical space.

Although process-based mechanistic models are recognised as being more robust, correlative ENMs are overall simpler and less time-consuming to run (Kearney & Porter, 2009). Detailed physiological data are also lacking for the majority of species, and consequently correlative models have been more popular and used across a wide range of taxa (Pacifici *et al.*, 2015). Modelling observed and measured real-world data also has an obvious attraction for model development and validation. A larger investment is required to derive parameter estimates for mechanistic models (Kearney & Porter, 2009; Elith *et al.*, 2010; Pacifici *et al.*, 2015), however, for species of economic importance or conservation interest, such as non-indigenous species (NIS) or species at risk of extinction, the investment is worthwhile (Kearney & Porter, 2009).

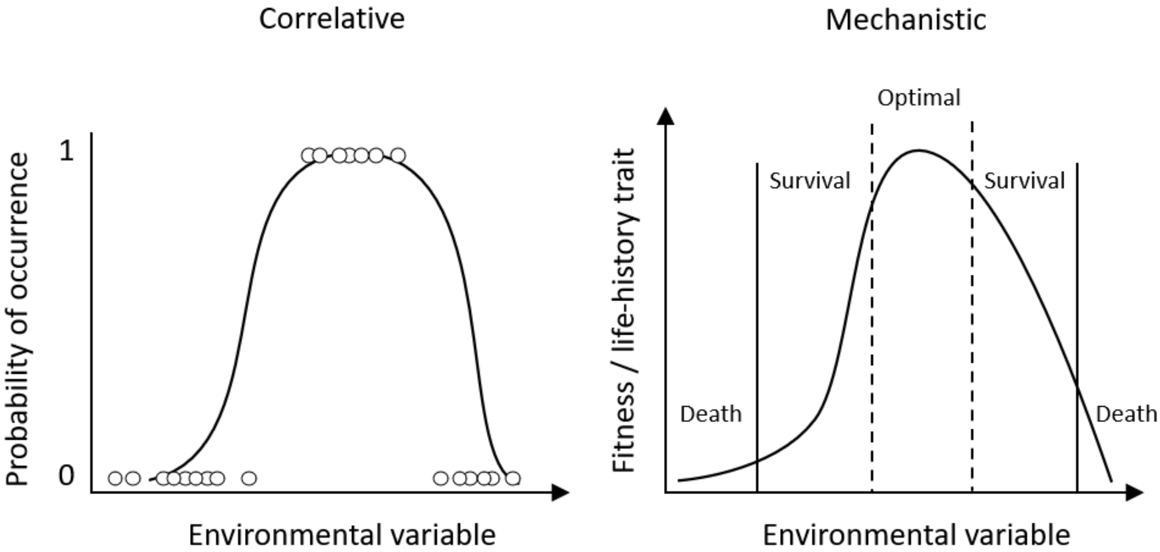


Figure 1.1 Concept of the data used in correlative and mechanistic species distribution models. The correlative model concept shows the likelihood of a species occurring within a range of environmental temperatures. The mechanistic model concept shows a performance curve of fitness (such as survival, growth, and reproduction) as a function of the environmental conditions. Redrawn from Kearney *et al.* (2010b).

The applications of correlative models versus mechanistic models have been widely discussed in the literature (Elith *et al.*, 2010; Kearney *et al.*, 2010b; Peterson *et al.*, 2015), however, the use of both models on the same species is rarely undertaken. There are suggestions that these models complement each other and provide useful predictions of spatial patterns and the viability of populations for use in conservation and management planning (Pacifici *et al.*, 2015; Rougier *et al.*, 2015). Mechanistic ENMs on the sunfish *Alosa alosa* have predicted similar forecasts in distributions to correlative models under future climate scenarios but provide a more in depth understanding of potential distribution changes (Rougier *et al.*, 2015). Kearney *et al.* (2010b) found that both models predicted a contraction in the northern range of the greater glider *Petauroides volans* due to a lack of water under a 3°C increase in air temperature. Buckley *et al.* (2010) showed correlative and mechanistic models performed similarly in predicting current distributions of a butterfly and a reptile species, however, mechanistic models predicted overall larger shifts in response to CCC. Making robust predictions is the ultimate goal when using ENMs to forecast distributions with CCC and thus there is likely greater potential through the use of both physiological and occurrence data.

1.4 Marine non-indigenous species

Non-indigenous species (NIS) are described as species which have been introduced to locations outside of their natural range as a result of human-mediated transport. In the marine environment, species are transported from their native regions to new locations either unintentionally by anthropogenic vectors such as shipping, live food and bait trade, man-made corridors (such as the Suez Canal) and ocean debris, or intentionally for purposes such as aquaculture (Bax *et al.*, 2003; Hulme Philip, 2009; Katsanevakis *et al.*, 2013; Bailey, 2015; Campbell *et al.*, 2017; Therriault *et al.*, 2018). If the species can survive the novel conditions, they can become established and form self-sustaining populations which may further spread from these points of introductions to new locations (Eno *et al.*, 1997; Manchester & Bullock, 2000; Jensen *et al.*, 2004; Hellmann *et al.*, 2008). Over 1000 aquatic NIS have been introduced to the northeast Atlantic and European waters with more than 800 taxa likely to have self-sustaining populations (Gollasch, 2006; Tsiamis *et al.*, 2018). Shipping is the main vector of introduction on the northeast Atlantic coast accounting for 47% of introductions, with aquaculture accounting for 13% (Gollasch, 2006; Savini *et al.*, 2010). NIS can also act as a vector for further NIS introductions, for example, the importation of the farmed bivalves *Magallana gigas* and *Ruditapes philippinarum* were responsible for the introduction of non-target invertebrate and algae species through attachment to packaging material, fouling on shells or parasitizing bivalve tissues fouling (Savini *et al.*, 2010). In addition, NIS can have a positive effect on the spread and abundance of other NIS (Wonham *et al.*, 2005; Heiman *et al.*, 2008). For example, biogenic reefs of the NIS *Ficopomatus enigmaticus* promoted denser aggregations of other NIS than a comparable native biogenic reefing species (Heiman *et al.*, 2008).

NIS have the potential to alter the communities and ecosystems they are introduced to through species displacement by competition, predation or smothering, and hybridization with native species (Huxel, 1999; Sakai *et al.*, 2001; Muhlfeld *et al.*, 2014). The replacement of specialist native species with generalist NIS through extinctions and introductions are expected to lead to more uniform communities and a reduction in biodiversity, known as global homogenisation of biodiversity (McKinney & Lockwood, 1999; Olden *et al.*, 2004). There is a growing consensus that CCC may facilitate the spread of NIS which will further alter the global distribution of species (Dukes & Mooney, 1999; Carlton, 2000; Occhipinti-Ambrogi, 2007; Hellmann et al., 2008; Rahel & Olden, 2008; Occhipinti-Ambrogi & Galil, 2010; Smith et al., 2012). NIS have already experienced range expansions and an increase in abundance with warming over the last 50 years (Rius et al., 2014). Further, range expansions of NIS are expected throughout this century in both marine and terrestrial systems (Occhipinti-Ambrogi, 2007; Rahel & Olden, 2008; Pecl et al., 2017). Investigations into the synergies between NIS and CCC will undoubtably increase scientific understanding of how species, communities and ecosystems may change in the future.

NIS can be classed as invasive if they have negative impacts on the environment, the local economy or recreation (Nichols *et al.*, 1990; Travis, 1993; Grosholz Edwin *et al.*, 2000; Molnar *et al.*, 2008; Alvarez *et al.*, 2011). One such example is the zebra mussel *Dreissena polymorpha* which was introduced to the USA in the 1980s from the Black, Caspian and Azov Seas by ship ballast water. *D. polymorpha* are reported to out-compete the native mussel species for space and food, therefore impacting local biodiversity, and causing a large economic impact through damaging ship's hulls, docks and clogging water pipes (Pimentel *et al.*, 2000; Strayer, 2009). Invasive NIS are recognised by the Convention on Biological Diversity (CBD) as one of the greatest drivers of biodiversity loss and ecosystem service change. The need for monitoring NIS abundance, spread and impact is acknowledged at national and international levels, for example in Europe, the Marine Strategy Framework Directive (MSFD) Descriptor 2 outlines the need for monitoring NIS to achieve Good Environmental Status of European marine waters (European Commission, 2017).

1.4.1 *Magallana gigas* – a non-indigenous case study

An economically important and highly successful NIS is the Pacific oyster, *Magallana gigas* (formerly *Crassostrea gigas*, Thunberg, 1793). *M. gigas* is native to the warm temperate regions of the northwest Pacific at latitudes between 30-40°N (Troost, 2010). It has been introduced into more than 66 countries for use in aquaculture and has subsequently established wild populations in at least 17 countries making it a global NIS (Herbert et al., 2016). Global aquaculture production since the 1950s has increased approximately 4.5 times with major producers including China, Japan and France (FAO, 2019). It was believed that European waters were too cold for *M. gigas* to reproduce, leading to its introduction for aquaculture purposes in the 1960s in the UK and Europe after a decline in the native oyster fisheries, likely from overfishing (Troost, 2010; Humphreys *et al.*, 2014). Shortly after introduction, natural spatfall was observed outside of aquaculture locations (Spencer *et al.*, 1994; Reise, 1998) and self-sustaining wild populations have established on the coastline. *M. gigas* are fast growing, reaching marketable size within two years of seeding, have high survival rates and the ability to occupy a range of habitat types (Troost, 2010). These traits make them both popular in aquaculture activities globally and also a successful NIS.

M. gigas are a coastal species found within the intertidal coastal zone and tidally dominated estuaries within their native and introduced range. They settle on hard substrates, such as bedrock and cobbles, shell fragments and pebbles on sandy/muddy shores, on other oysters, and on artificial structures. *M. gigas* broadcast spawn and the larvae are gregarious (Tamburri *et al.*, 2007), enabling them to settle in large numbers and can lead to highly complex three-dimensional reefing populations which can transform the locations they inhabit. Large eco-engineered reefs exist in its introduced range such as along the east coast of England, north and west coast of France, with some of the densest reefs occurring in the Wadden Sea, Oosterschelde estuary, where densities can reach 500 - 700 individuals per m^2 (Markert *et al.*, 2010; Wrange *et al.*, 2010), and up to 2000 live and dead oysters per m^2 (Markert *et al.*, 2013).

M. gigas are often classed as an invasive species as reefing populations can have negative impacts on native species, such as altering the composition of blue mussel, *Mytilus edulis*, beds (Fey *et al.*, 2010), and displacing sea grass, *Zostera marina*, beds (Wagner *et al.*, 2012). Oyster reef formation has led to the modification of habitats protected by the EU Habitat Directive, for example the deterioration of *Sabellaria alveolata* reefs in the Bay of Mont-Saint-Michel (Dubois *et al.*, 2006; Desroy *et al.*, 2011). The overall success of *M. gigas* in recent years has been attributed to warm summers and mild winters (Diederich *et al.*, 2005; Wrange *et al.*, 2010). Alternatively, oyster reefs have been shown to have positive effects on native species. For example, in the Bay of Brest in France (Lejart & Hily, 2011), and Colne Estuary in the UK (Herbert *et al.*, 2018), oyster reefs displaced infaunal species, but overall macro-invertebrate species biomass and richness increased, particularly intertidal grazers and predators of *M. gigas*. Similarly, moderate densities of *M. gigas* have been shown to create thermal refugia for grazers in British Columbia, Canada (Padilla, 2010). Studies in the UK (Herbert *et al.*, 2018), Europe (Markert *et al.*, 2013) and Argentina (Escapa *et al.*, 2004) found that *M. gigas* reefs have benefitted wading bird species by leading to greater feeding success and intake rates of prey.

Previous experimental studies suggest *M. gigas* can tolerate a wide range of environmental conditions, with growth occurring in temperatures between 10 – 40°C and salinities of 10 – 30 (Mann *et al.*, 1991). Optimum temperatures for *M. gigas* growth, reproduction and other physiological processes occur between 18 – 23°C (Malouf & Breese, 1977; Mann, 1979; Spencer *et al.*, 1994; Bougrier *et al.*, 1995). With climatic warming expected to continue towards the end of the century, warming waters will likely shift the geographical range of *M. gigas* to higher latitudes and potentially increase their abundance and spread in their already introduced range. Increasing SST may also promote spatfall during the summer and an increase in spat survival during the winter, subsequently leading to population increase (Troost, 2010). Warming has already been found to increase *M. gigas* recruitment in the Wadden Sea (Diederich *et al.*, 2005). Hindcast modelling approaches have attributed warming to the northward expansion of *M. gigas* distributions in Europe over the last 50 years (Thomas *et al.*, 2016). As a highly successful NIS and eco-engineering species, it is especially important to understand the effects of future CCC conditions on *M. gigas* fitness and their potential distributions.

1.5 Specific aims

Given the ecological importance of predicting changes in NIS distributions in the future, it is clear that a more comprehensive mechanistic understanding of NIS responses to CCC is needed. There is equally a need to compare the outcomes of popular modelling techniques and how these may influence the conclusions of modelling species distributions. This thesis adopts an integrative approach modelling at individual and population-levels to investigate the effects of CCC on both *M. gigas* biological functioning and distributions.

In Chapter 2, patterns between present day observational records and environmental conditions were used to investigate how NIS may thrive in novel conditions. Native and introduced *M. gigas* niches were examined in multi-dimensional environmental space to assess the potential niche shifts between ranges on a global scale. An assessment of common analytical methods for determining niche changes was undertaken in parallel to determine their ability to detect niche shifts. Correlative ENMs were then used to examine habitat suitability and latitudinal shifts expected by the end of the century in geographic space.

Novel mechanistic approaches were undertaken in Chapters 3 and 4 to investigate how CCC will affect the physiology and life-history traits of *M. gigas*. In Chapter 3, the effect of multiple climate ‘stressors’ on oxygen uptake, clearance and growth were measured in a comprehensive mesocosm experiment to assess the potential tolerance of *M. gigas* to future conditions. The experiment went beyond short-term studies by exposing adult individuals to long-term warming, ocean acidification and reduced salinities.

Cohort-level changes in life-history traits under environmental change were investigated in Chapter 4 using a mechanistic approach by integrating an individual-based model with the bioenergetic dynamic energy budget (DEB) model. The DEB model was parameterised to estimate growth, maturity and reproduction of individual *M. gigas* around the coastline of the northeast Atlantic and regional seas. An innovative approach was used to incorporate inter-individual variability into the model using laboratory-derived data and literature values to estimate key parameters in the model. The model was then used to predict changes in life-history traits in geographic space between present day and forecasted CCC conditions for the end of the century.

Chapter 5 summarises the main conclusions of this thesis and highlights the importance of integrating mechanistic underpinnings when examining how environmental change will affect species distributions. Findings were placed into context with the current literature to discuss the potential trends in how *M. gigas* will be impacted by CCC. With the rarity of correlative and mechanistic ENMs being conducted on the same organism, a comparison of these modelling approaches was made with emphasis on the benefits of combining both techniques. Areas which require further research were identified with an aim to progress scientific understanding of how NIS will be distributed under CCC conditions and how consideration of modelling approaches will make for more robust predictions.

1.6 Publications and author contributions

The following details the Chapters in this thesis, their publication status, and CRediT (Contributor Roles Taxonomy) author statements.

Chapter 2 has been prepared for submission for publication as:

Pack, K.E., Rius, M. & Mieszkowska, N. Rapid niche shifts as possible drivers for the spread of a non-indigenous species under novel environmental conditions.

Author contributions – Kathryn E. Pack: conceptualization, methodology, software, formal analysis, investigation, visualization, writing - original draft, writing – review & editing. Marc Rius: conceptualization, validation, writing – comments & reviewing. Nova Mieszkowska: conceptualization, writing – comments & reviewing.

Chapter 3 has been published in the journal Marine Environmental Research as:

Pack, K.E., Rius, M. & Mieszkowska, N., (2021). Long-term environmental tolerance of the non-indigenous Pacific oyster to expected contemporary climate change conditions. *Marine Environmental Research*, *164*, p.105226.

Author contributions – Kathryn E. Pack: conceptualization, methodology, software, formal analysis, investigation, visualization, writing - original draft, writing – review & editing. Marc

Rius: validation, visualization, writing – comments & reviewing. Nova Mieszkowska: methodology, validation, writing – comments & reviewing.

Chapter 4 has been prepared for submission as:

Pack, K.E., Rius, M. & Mieszkowska, N., Variable responses to contemporary climate change across geographic region: an inter-individual simulation approach using the life-history traits of the Pacific oyster.

Author contributions – Kathryn E. Pack: conceptualization, methodology, software, formal analysis, investigation, visualization, writing - original draft, writing – review & editing. Marc Rius: validation, writing – comments & reviewing. Nova Mieszkowska: validation, writing – comments & reviewing.

Chapter 2 Identifying niche shifts in Pacific oysters highlight their ability to spread in novel environmental conditions

Abstract

Identifying niche shifts is key for forecasting future species distributions. Non-indigenous species (NIS) are one of the greatest threats to biodiversity and understanding how niche shifts affect NIS' spread is fundamental. Here we modelled present day native and introduced niches, as well as the potential geographical extent, of the widely distributed NIS *Magallana gigas.* We investigated niche shifts in both non-analog and analog environmental spaces and predicted geographical spread of *M. gigas* under contemporary climate change (CCC) conditions. Two frameworks were used: (1) the two-dimensional Centroid shift, Overlap, Unfilling and Expansion (COUE) framework and (2) the *n*-dimensional hypervolume framework to quantify the niches. The niches were then tested for equivalency by comparing the observed and randomised overlaps. Ensemble ecological niche models (ENMs) were then used to predict habitat suitability for the present day and two future CO_2 emission scenarios. The *n*-dimensional hypervolume framework indicated that the introduced niche of *M. gigas* has shifted to encompass new environmental conditions compared to the native niche. The COUE framework implied no niche shift in two-dimensional space, but the first two dimensions only accounted for a small proportion of the overall environmental variability. Ensemble ENMs revealed suitable areas in the present day where *M. gigas* has yet to be recorded and predicted both a poleward expansion and a tropical contraction of suitable habitat for *M. gigas* by 2100. We revealed that *M. gigas* has rapidly shifted its niche since its first record as introduced over 50 years ago, suggesting a mechanism that may facilitate present day and future spread. In addition, the results showed that *M. gigas* can tolerate novel environmental conditions. This study also demonstrates the importance of modelling niche dynamics in multi-dimensional space for predicting NIS distributions under CCC conditions.

2.1 Introduction

Non-indigenous species (NIS) are one of the biggest threats to global biodiversity (Bax *et al.*, 2003; Molnar *et al.*, 2008) and understanding their potential distributions in the near future is a priority for biodiversity management (Sinclair *et al.*, 2010; Guisan *et al.*, 2013). Preventing the establishment of NIS is recognised as the most efficient way of reducing their impact on ecosystems (Simberloff *et al.*, 2013) and analyses predicting habitat suitability of NIS are fundamental for preventing NIS introductions and controlling their spread (Therriault & Herborg, 2008; Jiménez-Valverde *et al.*, 2011; Leidenberger *et al.*, 2015). Ecological niche models (ENMs) are popular mathematical models used to increase our understanding of suitable habitats and predicting areas that may be at risk of invasion (Thuiller *et al.*, 2005; Václavík & Meentemeyer, 2012; Mainali *et al.*, 2015). In addition, ENMs can forecast range expansions and contractions under contemporary climate change (CCC) conditions (Elith & Leathwick, 2009; Elith *et al.*, 2010) such as poleward range shifts (Cheung *et al.*, 2009; Saupe *et al.*, 2014; Jones & Cheung, 2015; Jueterbock *et al.*, 2016). In the marine environment, range shifts are an order of magnitude faster than terrestrial ecosystems (Sorte *et al.*, 2010), and thus investigating potential NIS distributions and areas at risk of invasion with CCC is of high importance. By the end of the century, the oceans will experience environmental conditions without modern analog due to CCC (Williams & Jackson, 2007) and this is expected to lead to native species extinctions and more frequent NIS introductions, as well as the creation of novel ecological communities (Pecl *et al.*, 2017). Although an increasing number of studies using ENMs suggest that marine NIS will expand their ranges and/or shift their ranges poleward as a result of ocean warming (de Rivera *et al.*, 2011; Saupe *et al.*, 2014; Goldsmit *et al.*, 2018), less is known about the stability of niche space over time.

The main assumptions of correlative ENMs are that a species' niche is stable in space and time and that the species is in equilibrium with the environment (i.e. they live in all suitable areas and are absent from unsuitable ones) (Hutchinson, 1957; Elith *et al.*, 2010). When modelling NIS, these assumptions are unlikely to be valid due to the nature of species introductions. NIS are artificially transported into a new location where the species does not yet inhabit all suitable areas (Gallien *et al.*, 2012). This raises the question of whether to model with data from only their native range in ENMs (where the species is likely to be in equilibrium) or the entire range (Guisan & Thuiller, 2005; Early & Sax, 2014). Studies using only the native range have poorly predicted habitat suitability in introduced ranges (Beaumont *et al.*, 2009; Verbruggen *et al.*, 2013), due to growing evidence of so-called 'niche shifts' (Figure 2.1) (Broennimann *et al.*, 2007; Reiss *et al.*, 2014; Parravicini *et al.*, 2015). Niche shifts describe the divergence in the physical and environmental requirements of a species over time and geographical space due to ecological and evolutionary changes (Broennimann *et al.*, 2007). CCC has the potential to alter species' niches and identifying if NIS can undergo rapid niche shifts indicates how the species may respond to novel climates (Guisan *et al.*, 2014; Moran & Alexander, 2014). Coupling these investigations with ENM studies improves our forecasting accuracy and increases our understanding of the potential spread of NIS under CCC (Tingley *et al.*, 2014; Parravicini *et al.*, 2015). For example, ENMs that account for niche changes (by combining data from both native and introduced ranges) have led to models with higher predictive power across both ranges and under future CCC scenarios (Broennimann & Guisan, 2008; Beaumont *et al.*, 2009; Pili *et al.*, 2020). Quantifying niche changes, such as the degree of overlap or expansion, has recently become a rapidly expanding field of research with the development of several frameworks (Broennimann *et al.*, 2012; Blonder *et al.*, 2014). However, studies directly comparing different frameworks are rare (Pili *et al.*, 2020) and further work is required to understand how these may affect the overall evaluation of niche shifts.

Quantifying niche dynamics between different NIS geographic ranges requires a distinction between analog and non-analog environments (Figure 2.1) (Guisan *et al.*, 2014). If the introduced niche shifts into non-analog climates (i.e., where conditions are not experienced in the native range), it cannot be assumed that the niche has shifted as it could simply be a factor of these environmental conditions being unavailable in the native range (Mandle *et al.*, 2011; Guisan *et al.*, 2014). In analog climates (i.e., where environmental conditions are available in both native and introduced ranges) niche changes demonstrate 'true niche shifts' as the introduced individuals inhabit common environments that the native do not (Figure 2.1). Nonetheless, colonisation of non-analog climates from the introduced range still provides crucial information on the potential tolerance of NIS to novel climates and has important implications for future management strategies (Early & Sax, 2014). The majority of studies modelling niche shifts do not distinguish between non-analog and analog climates and therefore may just be identifying environmental conditions that are unavailable in one range (Guisan *et al.*, 2014).

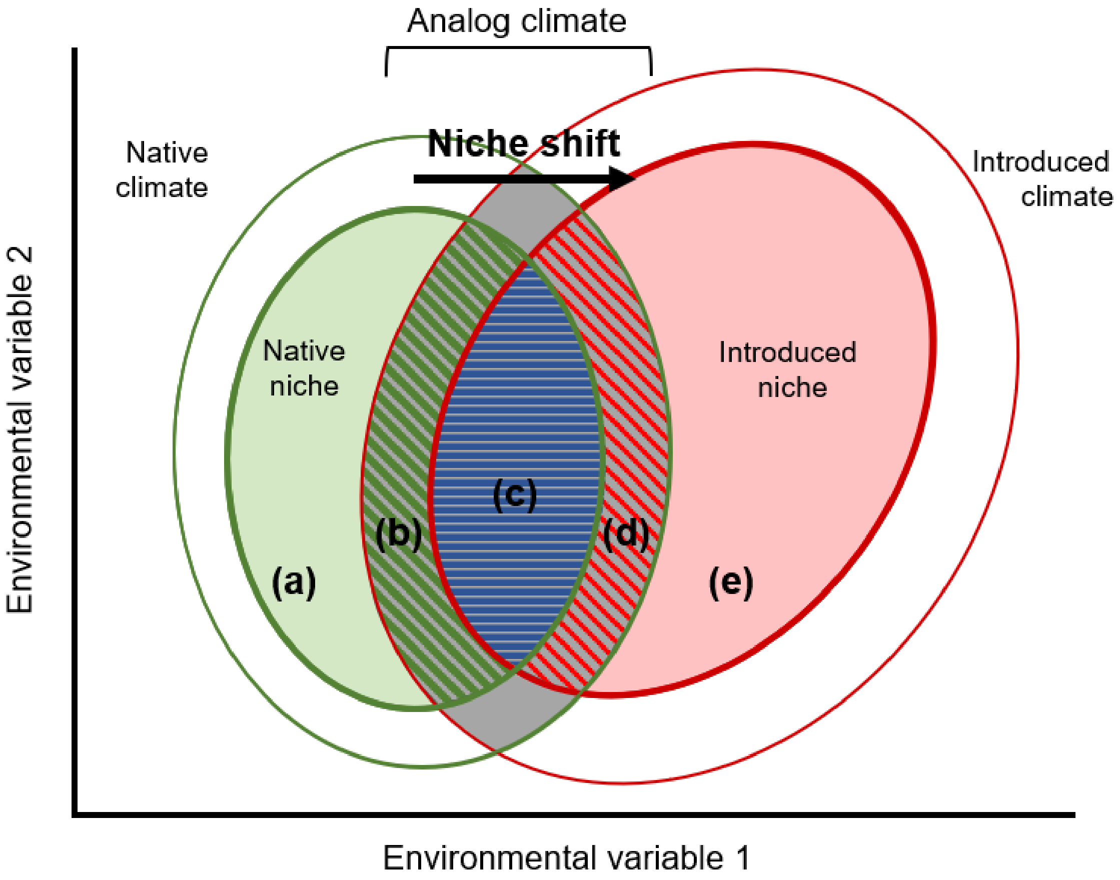


Figure 2.1 A two-dimensional representation of a niche shift from the native (green) to introduced (red) climate spaces. The thin, outer solid lines show all the environmental conditions available in the native and introduced ranges. The grey area shows the environmental conditions that exist in both ranges, known as the analog climate. The green and red thick lines depict the native and introduced niches, respectively. Conditions inside the native niche that are non-analog to the introduced range. (b) ‘Niche unfilling’ showing analog conditions filled by the native niche but not filled by the introduced niche. (c) ‘Niche overlap’ showing analog conditions that both the native and introduced niches occupy. (d) ‘Niche expansion’ showing conditions in the introduced niche not occupied by the native niche. (e) Conditions inside the introduced niche that are non-analog to the native range. The quantification of b, c, and d imply the level of niche shift (or niche conservatism) between the native and introduced niches. Note that the introduced niche is larger than the native niche, which would be expected considering the extensive introduced range of *Magallana gigas*. Figure redrawn from Guisan *et al.* (2014).

Here, we first assessed the potential for a highly successful NIS the Pacific oyster, *Magallana gigas*, to shift its niche in non-analog and analog climates using different frameworks for quantifying niche shifts. *M. gigas* has wild populations in more than 17 countries mainly due to the species' artificial introductions for aquaculture purposes (Herbert *et al.*, 2016). Field observations show that warming over the last few decades has already facilitated the spread of *M. gigas* along the coastlines of Europe and the US (Diederich *et al.*, 2005; Wrange *et al.*, 2010; Valdez & Ruesink, 2017). Laboratory investigations have also shown that *M. gigas* can tolerate a wide set of environmental CCC conditions (Pack *et al.*, 2021). Studying whether *M. gigas* has undergone rapid niche shifts during its invasion may further highlight its ability to thrive under novel CCC conditions. In this study we used ENMs with data from both native and introduced ranges to forecast if, under continued warming scenarios predicted by the end of the century, *M. gigas* distributions will continue to extend poleward as environmental conditions become more habitable. We hypothesised that (1) quantifying the degree of niche overlap in non-analog and analog environmental space would show the introduced niche of *M. gigas* has expanded compared to the native niche, (2) two commonly used niche dynamic frameworks would have similar results in terms of overlap and expansion of *M. gigas* niches, and (3) ensemble ENMs would forecast a poleward range shift of suitable habitat for *M. gigas* by the end of the century.

2.2 Methods

2.2.1 Environmental layers

Present-day environmental layers for the surface ocean were obtained from Bio-ORACLE (version 2.0) at 5 arcminute (9.2 km) resolution (Tyberghein *et al.*, 2012; Assis *et al.*, 2018). This database contains global variables collected from satellite sensors and interpolated *in situ* measurements averaged across 2000-2014 (Assis *et al.*, 2018). For modelling in both environmental and geographical space, we used five environmental variables that are known to be biologically relevant to sessile filter-feeders and were not highly correlated when tested for collinearity (Pearson's correlation coefficient of $r > 0.75$). These included temperature, salinity, pH, chlorophyll concentration and calcite concentration (Table 6.1).

To estimate future climatic conditions, a bias correction method using predicted environmental conditions from the Hadley Centre Global Environment Model – Earth System (HadGEM-ES) general circulation model from phase five of the Coupled Model Intercomparison Project (CMIP5) (downloaded from https://esgf- node.llnl.gov/projects/ cmip5) was applied to the Bio-ORACLE present-day layers. Simulated monthly values for each variable were extracted for 2000-2014 and 2090-2100 and the mean for each period calculated per 1° x 1° grid cell for two scenarios based on the Intergovernmental Panel on Climate Change (IPCC) ‘Representative Concentration Pathways’: RCP4.5 (stabilisation scenario) and RCP8.5 (‘business as usual’ scenario). The change factor (delta) between the simulated present day and future variables for each scenario were calculated for each grid cell and the delta applied to the Bio-ORACLE observations to estimate future conditions (Navarro-Racines *et al.*, 2020). Calcite was removed from future projections as a measure of end of the century as calcite concentration was not available from the HadGEM-ES model.

2.2.2 Species records

Global presence-only occurrence records for *M. gigas* were downloaded from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/species/7820753) and contrasted with literature data. The data were cleaned to obtain a high-quality dataset containing georeferenced records or collected museum records. Dead and washed-up individuals as well as records which were on land or unverified in the literature were excluded. In total there were 1864 unique presence records before spatially aggregating points to one per 1° x 1° environmental grid cell, leaving 663 records.

2.2.3 Comparison of niches in environmental space

Species records were split into two data sets containing native (N = 54) and non-indigenous (N = 609) records and environmental data for each of their ranges extracted. The densities of introduced and native occurrences with each environmental variable were compared in a univariate space. Then, two popular modelling methods were used to quantify the niches in environmental space; the widely used Centroid shift, Overlap, Unfilling and Expansion (COUE) framework (Broennimann *et al.*, 2012) and the *n*-dimensional hypervolume framework (Blonder *et al.*, 2014) which measure the degree of overlap and environment equivalency between niches.

2.2.3.1 The COUE framework

Using the COUE framework the niches were compared in two-dimensional space using Schoener’s *D* metric of niche overlap (Broennimann *et al.*, 2012). Principal components (PC) analysis was used on the extracted environmental data from the native and introduced ranges. The first two PCs accounted for 57% of the variability. The environmental space was divided into 100 grid cells and the density of occurrences within the environmental space was estimated using a kernel density estimator (Broennimann *et al.*, 2012; Parravicini *et al.*, 2015). Schoener's *D* metric quantified the degree of overlap of the two niches, calculated using

$$\mathrm{D} = 1 - \frac{1}{2}\left(\sum_{ij}\left|z_{1\,ij} - z_{2\,ij}\right|\right)$$

where z_{1ij} is the space the native range occupies, z_{2ij} is the space the non-indigenous range occupies. The z terms are based on the relative occurrence for the species in the grid cell relative to the frequency of that environmental condition, thus, ensuring an unbiased comparison of occurrence densities between different ranges where environments are not equally available. Shoener's *D* metric ranges between 0 (no overlap) to +1 (complete overlap) (Warren *et al.*, 2008; Broennimann *et al.*, 2012).

A test of niche equivalency was performed to assess whether the observed overlap (*D*) was significantly different to a null distribution of 1000 generated *D* metrics from randomly reallocating the occurrences of both niches into two datasets (Warren *et al.*, 2008; Broennimann *et al.*, 2012). The null hypothesis that the niches are identical was rejected if the observed *D* was below the 5th percentile of the null distribution. A test for niche similarity was performed to assess if the observed *D* was significantly different to a null distribution of 1000 generated *D* metrics when accounting for geographic availability of environmental conditions (by randomly distributing one niche over its background whilst the other is unchanged). The null hypothesis that the niches are dissimilar was rejected if the observed *D* was greater than the 95th percentile of the null distribution (Warren *et al.*, 2008; Broennimann *et al.*, 2012). If the observed *D* is less than the null distribution, it indicates niche divergence and if the observed *D* is greater than the null distribution then the niches are more similar than random (Warren *et al.*, 2008; Broennimann *et al.*, 2012). A significant difference from the niche similarity test would indicate differences in the environmental niche space the two species occupy and that these differences are not due to the environmental conditions that are geographically available.

Niche stability, the proportion of environments within the introduced niche shared with the native niche, niche expansion, the proportion of environments of the introduced niche that do not intersect with the native niche, and niche unfilling, the proportion of environments not currently filled by the invasive niche (Guisan *et al.*, 2014) were reported. Niche metrics described above were calculated in R version 4.0.3 (R Core Team, 2019) with the e*cospat* package version 3.1 (Di Cola *et al.*, 2017).

2.2.3.2 The *n*-Dimensional Hypervolume Framework

As noted above, the first two PC in the COUE framework accounted for only 57% of the total variability in the five environmental variables, therefore important information on the differences between the niches may not have been satisfactorily captured in these first two components. This may be expected since the PC method does not make use of any information on groupings in the data such as the two different populations.

The *n*-dimensional hypervolume framework was used to assess differences in the niches within a multidimensional environmental space (Hutchinson, 1957; Blonder *et al.*, 2014). This framework is based on Hutchinson's proposed *n*-dimensional hypervolume which quantifies the fundamental niche of a species and is used widely in ecology (Hutchinson, 1957). The hypervolume for a species is defined as the space the species occupies within independent axes based off the environmental variables. The introduced and native niches were quantified in five dimensions, accounting for 100% of the variability in the environmental data. The five PCs of the original five environmental variables were used to allow a comparison with the COUE framework. Multidimensional hypervolumes for the native and introduced niches were generated using the Gaussian kernel density estimation method (Blonder *et al.*, 2014). Hypervolume niche metrics and analyses were conducted using the *hypervolume* R package (Blonder *et al.*, 2014).

To assess the differences between the niches, Jaccard's index and Sørensen-Dice index were calculated by:

Sørensen-Dice $S(A,B) = \frac{2|A \cap B|}{(|A| + |B|)}$

Jaccard $J(A,B) = \frac{|A \cap B|}{(A \cup B)} = \frac{|A \cap B|}{(|A| + |B|) - (A \cap B)}$

where A and B are the two hypervolumes, ∩ is the intersection between the two hypervolumes and ∪ is the union of the two hypervolumes (Blonder *et al.*, 2014). Both indices are variations on the concept of the proportion of the total volume occupied by both populations in the intersection region. Both indices range between 0 and 1, with 1 indicating equivalency and 0 indicating no intersection. Similar to the COUE equivalency test, the Sørensen-Dice and Jaccard indices were compared to a null distribution from 1000 iterations to assess significance. Jaccard and Sørensen-Dice metrics were also calculated for the first two PCs (similar to the COUE framework) to allow for a more direct comparison between the two frameworks.

2.2.3.3 Analog environment

To better understand if changes in the introduced niche were as a result of a 'true niche shift', the two niches were modelled as above but in analog environments, which were extracted using the *ecospat* package in R (R Core Team, 2019). Based off Mesgaran *et al.* (2014), the package uses Mahalanobis distance to detect covariate correlations between the univariate range of covariates. The presence records and associated climates within the analog environment were then modelled in environmental space.

2.2.3.4 Partial least squares

The first two PCs may not contain information pertinent to the differences between native and introduced niches, especially when the first two components only explain a relatively low percentage of the total variation. This implies that visualisations based on the first two PCs may be uninformative. Partial Least Squares (PLS), used as a discriminant analysis technique, may better illustrate population differences as it maximises the covariance between the environmental data from the two niches. As the PLS approach can be influenced by sample sizes, the datasets were balanced by clustering the introduced records using a k-means approach into 54 clusters (i.e., number of records in the native range) and the centroids of each cluster formed into a new dataset of 54 records. This clustering approach ensured that the new dataset best covered the space of the introduced niche. The new factors and scores from the PLS were extracted (equivalent to PCA).

2.2.4 Habitat suitability modelling

To predict the current and future habitat suitability of *M. gigas* around the globe, ENMs were calibrated using occurrence records from both the native and introduced ranges, as a broad geographical extent allows for a closer approximation of the fundamental niche (Phillips *et al.*, 2006; Broennimann *et al.*, 2007; Broennimann & Guisan, 2008).

Four widely used presence-only models, BIOCLIM, Mahalanobis distance, Maxent and Boosted Regression Trees (BRT), were used to model the realised niche of *M. gigas*. The bioclimatic envelope model BIOCLIM creates a rectilinear 'envelope' in the environmental space, defined by the maximum and minimum records of the species on each environmental variable (Tsoar *et al.*, 2007). The model determines the range of conditions suitable for a species by treating the environmental data at the species' presence points as distributions of percentiles. Then environmental data within each grid cell of the entire study area is compared to the distribution percentiles of the occurrence to calculate relative suitability within one grid cell. Values nearer the median (50th percentile) are considered most suitable for the species (Tsoar *et al.*, 2007; Duan *et al.*, 2014).

Mahalanobis Distance (Mahal) allows for modelling in a multidimensional climatic space using an elliptical envelope as opposed to a rectilinear approach (Farber & Kadmon, 2003; Tsoar *et al.*, 2007). The model computes the distances from each point (presence data matched to the 5 environmental variables) to the mean value of the niche (centroid), weighted by the covariances of variables. The Mahalanobis distances are calculated by

$$MD^2 = (x - m)^T \, C^{-1} \, (x - m)$$

whereby MD is the distance, x is the vector of points, m is the vector of mean values of each variable, C is the covariance matrix of the environmental variables and T denotes a matrix transpose. To obtain a measure (probability) for the habitat suitability, a univariate kernel density was first constructed based on the *MD*s of the presence points comprising the model. The *MD*s for the grid cells in the global environment were then calculated with reference to the mean and covariance of the model. Finally, to obtain a habitat suitability, the environmental *MD*s were compared to the kernel density of the model *MD*s and the corresponding tail areas for each point calculated to provide the probability. This approach effectively quantifies how 'far away' the global points are from the model.

Maxent uses a machine learning algorithm to estimate habitat suitability by finding the probability distribution of maximum entropy. This is based on the principal that species will spread as far as possible without ecological constraints with a probability distribution closest to uniform (Phillips *et al.*, 2006). Two probability densities are used to calculate the potential distribution of the species, one for the environmental variables at the presence locations and one of the environmental variables at a set of background points (where presence at these locations is unknown). The ratio between these densities gives the relative habitat suitability for the presence of a species for each point in the study area. The distribution which maximises the similarity between presence and background points is chosen (Phillips *et al.*, 2006; Elith *et al.*, 2011; Merow *et al.*, 2013).

BRT is a machine learning ensemble method which builds regression (decision) trees and combines them to produce a final prediction. Tree-based models partition the environmental (predictor) space to identify regions with homogeneous responses based on the relationships between presence-absence data and environmental (predictor) variables (Elith *et al.*, 2008). The boosting method increases accuracy of the model by weighting input data in subsequent trees depending on how it performed in the previous tree (Elith *et al.*, 2008) then combining the models. Where absence data are unavailable, pseudo-absence records can be used.

An ensemble model of the four models was used to estimate habitat suitability of *M. gigas* globally. Each individual model was run using a bootstrap with replacement method, replicated 100 times and the median model determined. Habitat suitability in the ensemble model was calculated as the mean probability per grid cell weighted by their performance (area under the curve, see below). Habitat suitability was modelled for the present day using all five present day environmental variables and for two end-of-the-century scenarios based on RCP4.5 and RCP8.5 projections (Table 6.1). The end-of-the-century models were trained on environmental variables and occurrence records in the present day then projected into conditions for each scenario.

2.2.4.1 Model validation and variable importance

To evaluate model performance, the area under the receiver operating characteristic (ROC) curve (AUC) and true skill statistic (TSS) were calculated based on 20 model runs with a randomly sampled training and test data set of 75% and 25% of the presence records, respectively.

The importance of each of the five variables in the present-day model was examined using a leave-one-out technique. BIOCLIM, Mahalanobis distance, Maxent and BRT were run and evaluated based on models with only four of the five environmental variables and the mean AUC and TSS for each leave-one-out model was calculated based on 20 randomly sampled training and test datasets. The changes in the AUC and TSS between the models were then compared.

2.2.4.2 Latitudinal shift in habitat suitability

The average poleward shift of suitable habitat for *M. gigas* was predicted between the present-day ensemble model and the two end of the century ensemble models. Firstly, both ensemble models were split geographically into northern and southern hemispheres to account for the differences in the direction of movement above and below the equator. Then, the latitudinal centroids (C), weighted by habitat suitability, were calculated using

$$C = \frac{\sum_{i=1}^{N} Lat_i \times Hs_i}{\sum_{i=1}^{N} Hs_i}$$

where Lat_i is the latitude at the centre of the spatial cell (i), Hs_i is the habitat suitability in the cell, and N is the total number of cells (Cheung *et al.*, 2009). The difference between the latitudinal centroid was then calculated and converted to kilometres using:

$$Latitudinal\ shift\ (km) = \left(Lat_p - Lat_f\right)\frac{\pi}{180} \times 6378.2$$

where Lat_p and Lat_f are the latitudinal centroids for present day and future, respectively (Cheung *et al.*, 2009; Jones & Cheung, 2015) and 6378.2 is the Earth’s diameter in kilometres. Habitat suitability was averaged per 1° latitude for the present day and end of the century models and the difference calculated.

2.3 Results

2.3.1 Niche overlap

2.3.1.1 COUE and hypervolume niche shifts

The univariate density curves showed that the biggest difference between the climatic niches occurred for temperature where the optimum temperature in the native niche was 19.6°C and the optimum in the introduced was 12.1°C (Figure 2.2a). The introduced niche occupied a similar but broader set of conditions than the native niche for salinity, pH and calcite (Figure 2.2b, c, e).

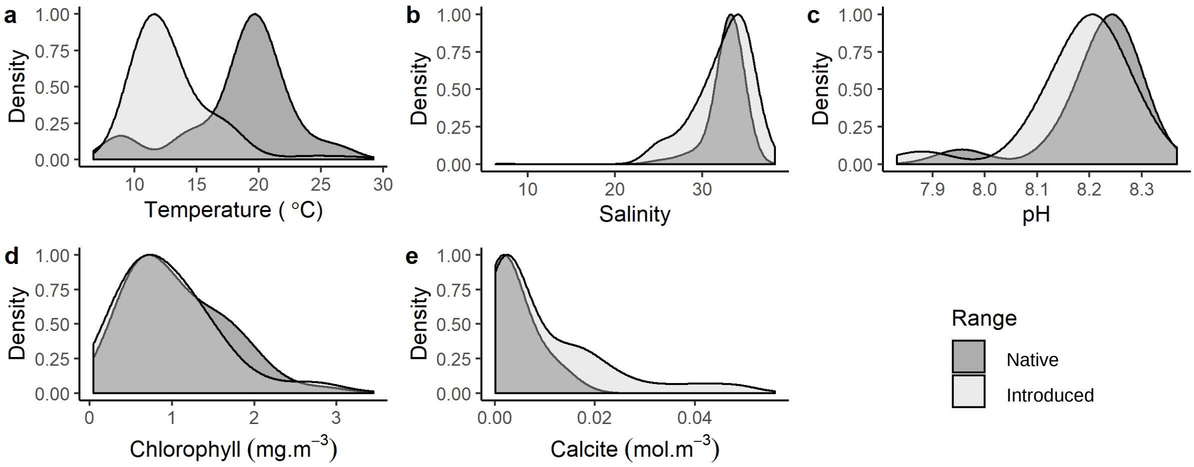


Figure 2.2 The scaled kernel density of native and introduced range occurrences of *Magallana gigas* for the environmental variables used in the ensemble models. The five environmental variables include temperature (a), salinity (b), pH (c) chlorophyll (d), and calcite (e).

The COUE framework suggested that the introduced niche covered a broader set of environmental conditions than the native niche (Figure 2.3a). Schoener's *D* metric indicated that niche overlap was moderately low (*D* = 0.12) and the climatic niche of introduced *M. gigas* has expanded by approximately 30% compared to the native (Figure 2.3a) with niche stability at 70% and unfilling niche at 0%. The null hypothesis of niche equivalency was accepted (p = 0.21, Figure 2.3b) implying the niches were equivalent. The environments occupied by the introduced niche were more similar to the native niche than expected by chance (p = 0.032) (Figure 2.3c). These results were expected as the native niche was completely overlapped by the introduced niche in Figure 2.3a. The environments occupied by the native niche were not more similar than expected by chance to the introduced niche (p = 0.10) (Figure 2.3d), reflecting the expansion in the introduced niche.

Jaccard and Sørensen-Dice indices were moderately high in two-dimensional space at 0.34 and 0.51, respectively (Table 2.1), reflecting the overlap observed in Figure 3a. Only 14% of the native niche was unique and 64% of the introduced niche was unique. These results imply that *M. gigas* in the introduced range have colonised nearly all the available climate conditions occupied by the native niche and has expanded into novel climates.

Table 2.1 The metrics for determining the proportion of the native and introduced niches that are unique, and Jaccard and Sørensen-Dice indices for the union between the native and introduced niches in environmental space. The metrics were quantified in two-dimensional and five-dimensional principal components space for the total environment (combined non-analog and analog environments) and the analog space.

	Total environment		Analog environment	
	2 dimensions	5 dimensions	2 dimensions	5 dimensions
Fraction of unique niche outside of the overlap (native / introduced) (%)	14% / 64%	66% / 83%	50% / 75%	86% / 87%
Jaccard index	0.34	0.13	0.20	0.07
Sørensen-Dice index	0.51	0.23	0.33	0.13

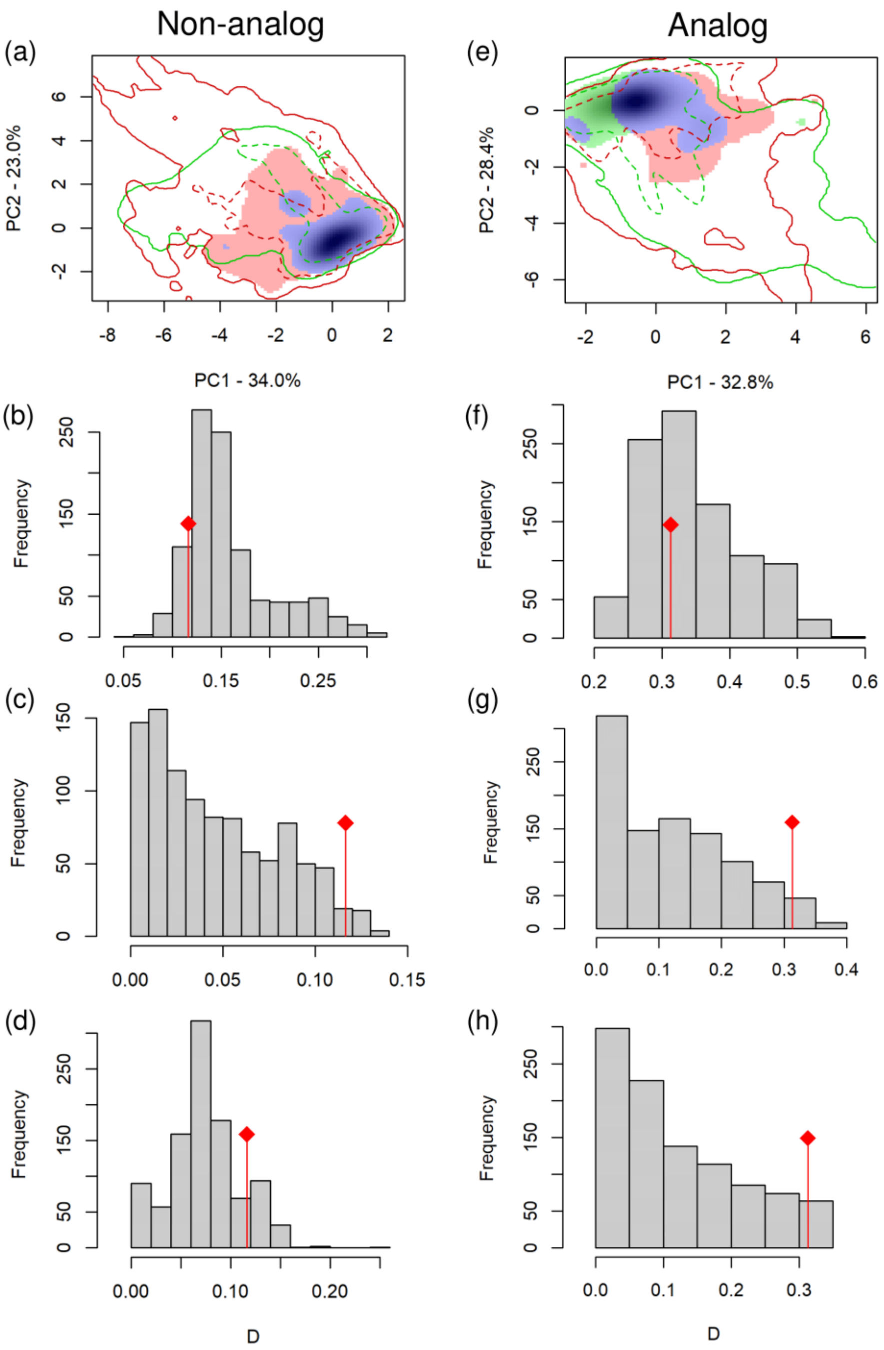


Figure 2.3 Principal components niche comparisons in two-dimensional space using the COUE framework in non-analog (a-d) and analog spaces (e-h) of *Magallana gigas*. The niches of *M. gigas* in the native and introduced ranges and the overlap in environmental space (a, e). The solid and dashed lines represent 100% and 75% of the available environmental space in the native (green) and introduced (red) ranges and shading indicates the density of occurrences. Blue indicates overlapping of the niches, green indicates unfilling in the native niche and red indicates expansion in the introduced range. Histograms showing the null distribution of *D* from 1000 iterations compared to the observed

Schoener's *D* metric (red diamond) for niche equivalency (b, f), and similarity for the introduced to native niche (c, g) and native to introduced niche (d, h).

Similar to the COUE framework, the five-dimensional hypervolume showed the introduced niche covers a broader range of environmental conditions than the native niche (Figure 2.4a). The first plot of the hypervolume (PC1 vs PC2, Figure 2.4) is synonymous to the COUE plot (Figure 2.3a). There was low overlap at the 95% percentile probability boundary of the hypervolumes with 0.23 and 0.13 from the Sørensen-Dice and Jaccard indices, respectively (Table 2.1). Contrary to the two-dimensional metrics, 66% of the native hypervolume was unique and 83% of the introduced hypervolume was unique (Table 2.1). The null-hypothesis of niche equivalency was rejected (Sørensen-Dice: p=0.003, Jaccard: p=0.003, Figure 2.4b, c), thus the niches were not more equivalent to each other than expected by chance in a five-dimensional space.

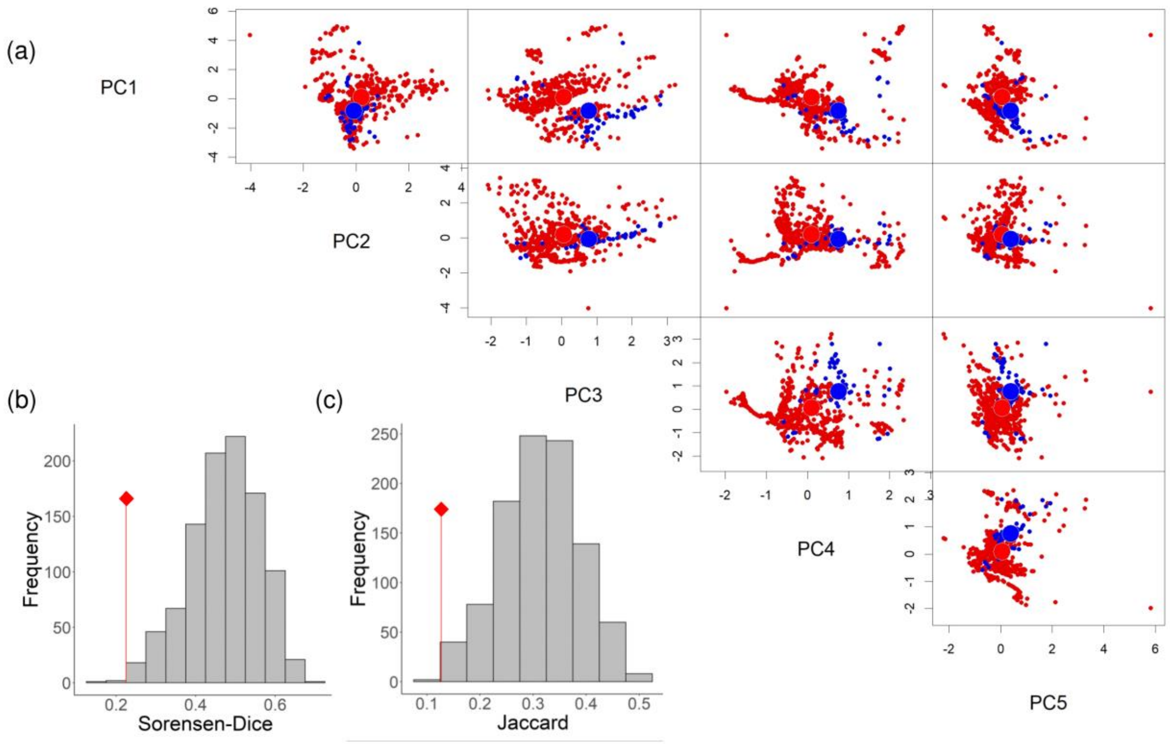


Figure 2.4 (a) Five-dimensional hypervolume in pairwise, two-dimensional space comparing the niches of the native (blue) and introduced (red) ranges of *Magallana gigas* in non-analog space. The filled circles indicate the centroid of the hypervolume and the small, filled dots represent true species presence records. The native points overlay introduced points. The observed values from the Sørensen-Dice (b) and Jaccard indices (c) (red diamond) are compared to a histogram of the null distribution of simulated values using a randomisation method with 1000 iterations.

2.3.1.2 Niche shifts in analog environments

Isolating the analog environment showed that approximately 61.7% of the introduced occurrences (376 of the total 609) exist in areas with environments analogous to the native range, with the remaining 38.3% living in environments deemed non-analog. From the COUE framework, the Schoener index implied moderate overlap, $D = 0.31$, with an expansion in the introduced niche of 17.8%, niche stability of 82.2% and niche unfilling of 24.1% (Figure 2.3e). The null hypothesis of niche equivalency was accepted ($p = 0.39$, Figure 3f) implying the niches are the equivalent. The environments were also more similar than expected by chance for both niches (Figure 2.3g, h). The two-dimensional Jaccard and Sørensen-Dice indices for the analog space were 0.20 and 0.34, respectively with 50% of the native niche and 75% of the introduced niche being unique (Table 2.1).

In analog space, a clear separation in the native and introduced hypervolumes can be observed between the niches between PC2 and PC3 (Figure 2.5a). The Sørensen-Dice and Jaccard indices for the five-dimensional hypervolume indicated very low intersection at 0.07 and 0.13, respectively, and a high proportion of the native and introduced niches were unique, 86% and 87%, respectively (Table 2.1). The niches were considered not equivalent as the observed Sørensen-Dice Jaccard indices were less than 95% of simulated values in the null distribution (Sørensen-Dice: $p<0.001$, Jaccard: $p<0.001$, Figure 2.5b, c).

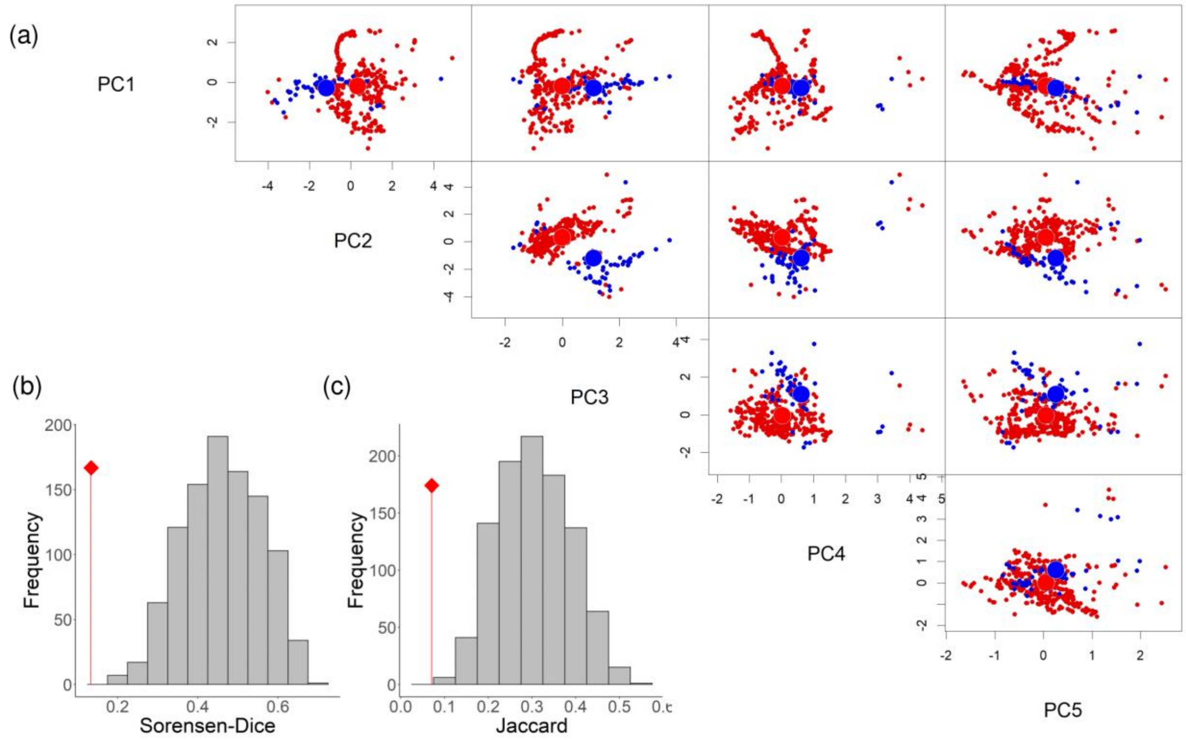


Figure 2.5 (a) Five-dimensional hypervolume in pairwise, two-dimensional space comparing the niches of the native (blue) and introduced (red) ranges of *Magallana gigas* in an analog environmental space. The large, filled circles indicate the centroid of the hypervolume and the small, filled dots represent true species presence records. The observed values from the Sørensen-Dice (b) and Jaccard (c) indices in the analog environmental space (red diamond) are compared to a histogram of the null distribution of simulated values using a randomisation method with 1000 iterations.

2.3.1.3 Partial least squares

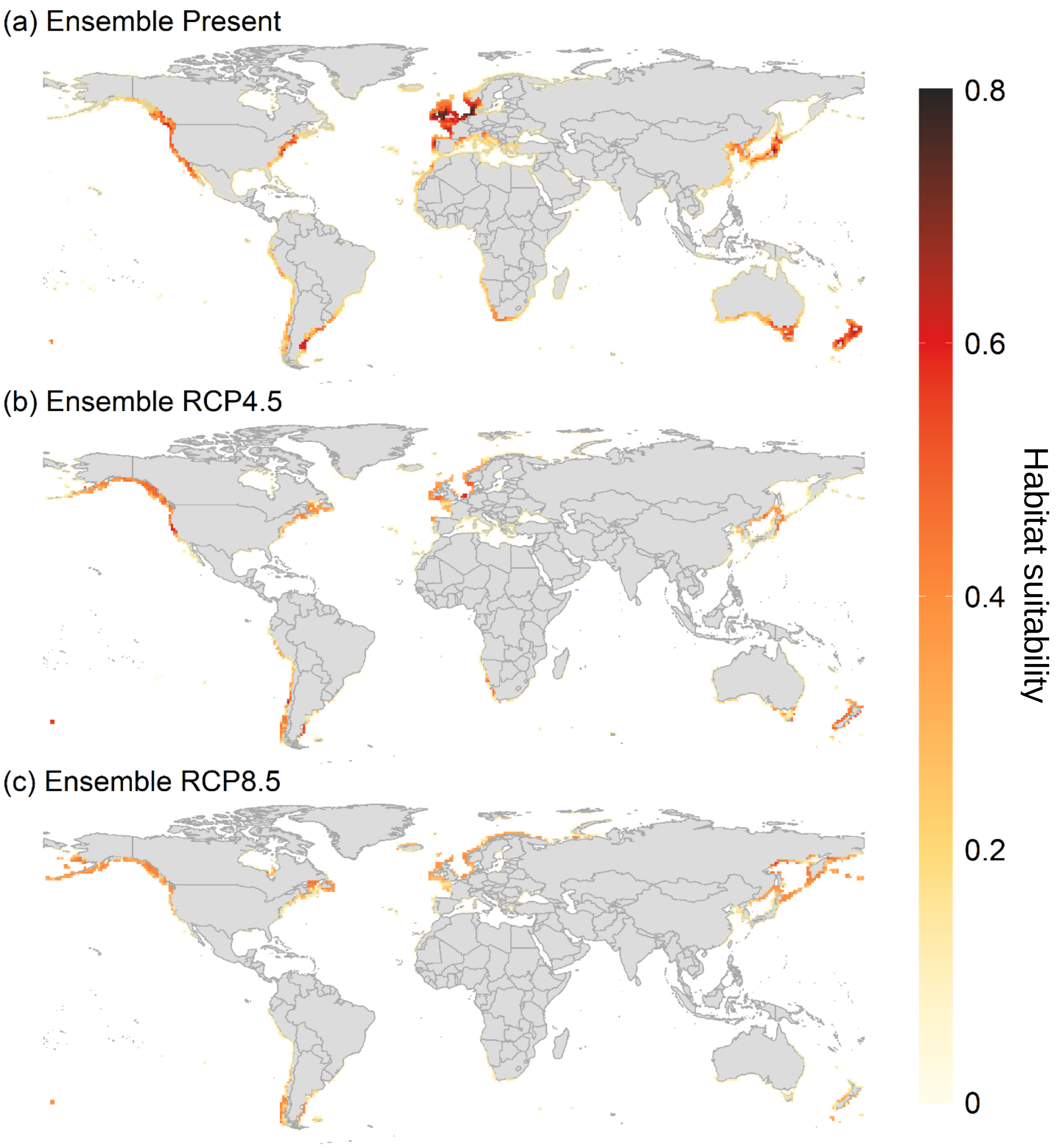
Partial least squares were consistent with the hypervolume statistics showing a clearer separation between the native and introduced niches within the first two PLS factor (Figure 6.1). The first PLS is predominately based on temperature in contrast with calcite, hence temperature is largely responsible for the separation between the native and introduced niches (Table 6.2). The pairwise PC plots misleadingly suggest a high level of overlap with the COUE framework implying a complete overlap of the native by the introduced niches (Figure 2.3). This was reflected in the eigenvectors which show that none of the variables have a strong influence on the axes (Table 6.2), thus not representing the difference between the native and introduced niches.

2.3.2 Ecological niche modelling

Moderate to high habitat suitability in temperate regions of the northwest and northeast Pacific, north Atlantic and Australasia were predicted for the present day, with the northern European coast and UK predicted to have the most suitable habitat for *M. gigas*, highlighting areas where dense populations can currently exist (Figure 2.6a). The model predicted areas of moderate habitat suitability in areas where few presence records have been recorded, such as the coasts of South America and South Africa and east coast of the US. The final ensemble model had high predictive ability with an AUC of 0.92 and the TSS of 0.74. Standard deviations implied a low level of variation of habitat suitability (Figure 6.2).

Overall, habitat suitability decreased for both scenarios predicted for the end of the century compared to the present-day ensemble model (Figure 2.6b, c). Habitat suitability for *M. gigas* was predicted to increase at higher latitudes such as the west coast of Canada and Alaska, northwest Europe and northeast Asia by the end of the century in both scenarios, (Figure 2.6b, c). A decline in habitat suitability was predicted in some regions, such as along the coasts of Australasia, southern Africa, and south America, particularly under the worst-case scenario (RCP8.5) (Figure 2.6c).

Under both RCP scenarios, the two envelope models, BIOCLIM and Mahalanobis distance, predicted low to no suitable habitat by the end of the century (Figure 6.3). Maxent and BRT models were therefore responsible for the predicted habitat suitability in the ensemble models. All four models had good accuracy (Figure 2.7). The leave-one-out method for variable importance showed consistent results across all four models. The removal of temperature had the greatest effect on the AUC and TSS. Temperature was therefore the most important predictor of habitat suitability for *M. gigas*. The other four variables had minimal impact on the model accuracy when omitted (Figure 2.7).



(a) Ensemble Present

(b) Ensemble RCP4.5

(c) Ensemble RCP8.5

Figure 2.6 Ensemble maps for habitat suitability for *Magallana gigas* along the world's coastline for the present day (a) and the end of the century based on RCP4.5 and RCP8.5 scenarios (b, c), respectively.The ensemble predictions are based on the median BIOCLIM, Mahalanobis distance, Maxent and BRT predictions.

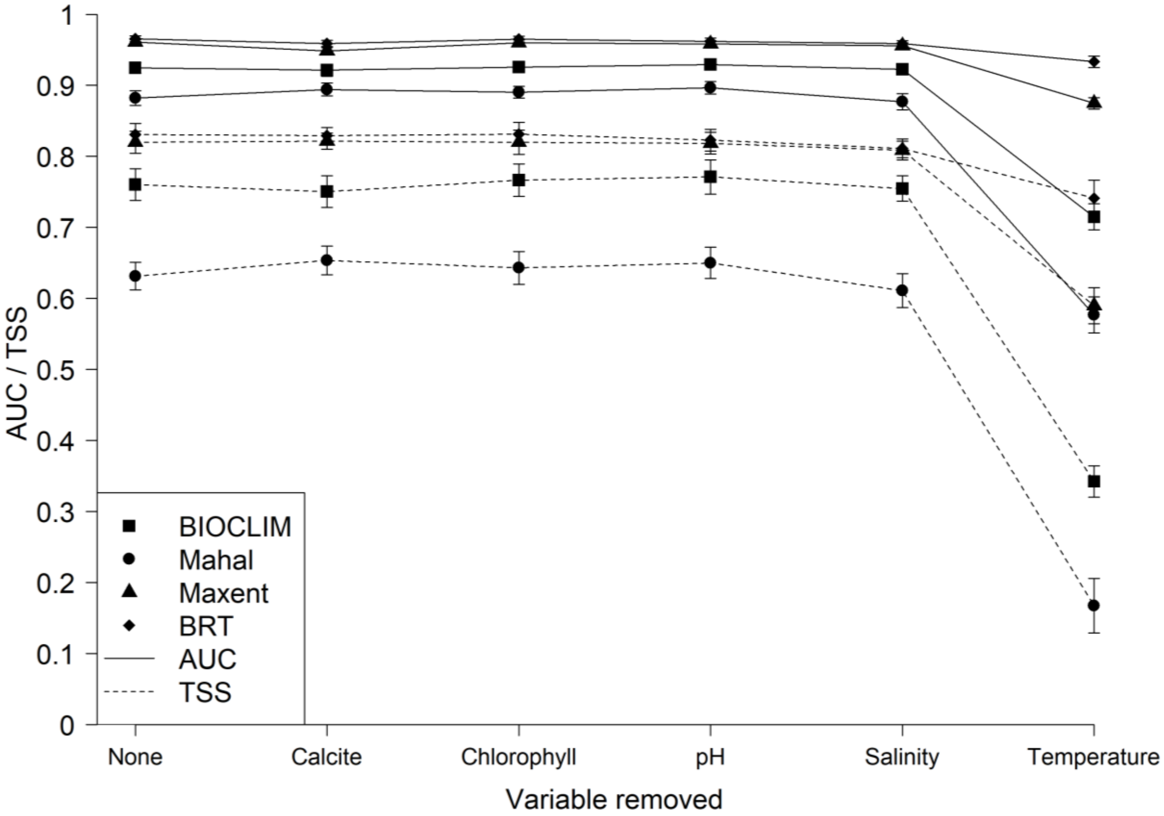


Figure 2.7 The mean (± standard deviation) AUC and TSS resulting from the removal of each environmental variable from the present-day ecological niche models. The model validation statistics were calculated for BIOCLIM, Mahalanobis distance, Maxent and BRT using a 75% train and 25% test data set and averaged over 20 replicates.

Both the northern and southern hemisphere latitudinal centroids of habitat suitability shifted polewards by the end of the century in both IPCC scenarios (Table 2.2). As expected, the predicted shift in the latitudinal centroids were more extreme for RCP8.5 (924.4 km and 785.4 km) than for RCP4.5 (501.7 km and 203.5 km). The latitudinal differences between the present day and future scenarios showed that habitat suitability decreased in lower temperate latitudes but increased in the higher latitudes by approximately 10-25% (Figure 2.8).

Table 2.2 The predicted latitudinal shift in *Magallana gigas* under RCP4.5 and RCP8.5 climate change scenarios. The latitudinal centroids for both the present day and end of the century ensemble models were determined for the northern and southern hemispheres. The predicted future latitudinal shifts were then calculated as the difference between the present and future centroids and expressed in kilometres.

	Present day centroid (decimal degrees)		Future centroid (decimal degrees)		Difference (decimal degrees)		Distance (km)	
Hemisphere	N	S	N	S	N	S	N	S
RCP4.5	45.5	34.6	50.0	36.6	4.5	2.0	501.7	203.5
RCP8.5			53.8	41.7	8.3	7.1	924.4	785.4

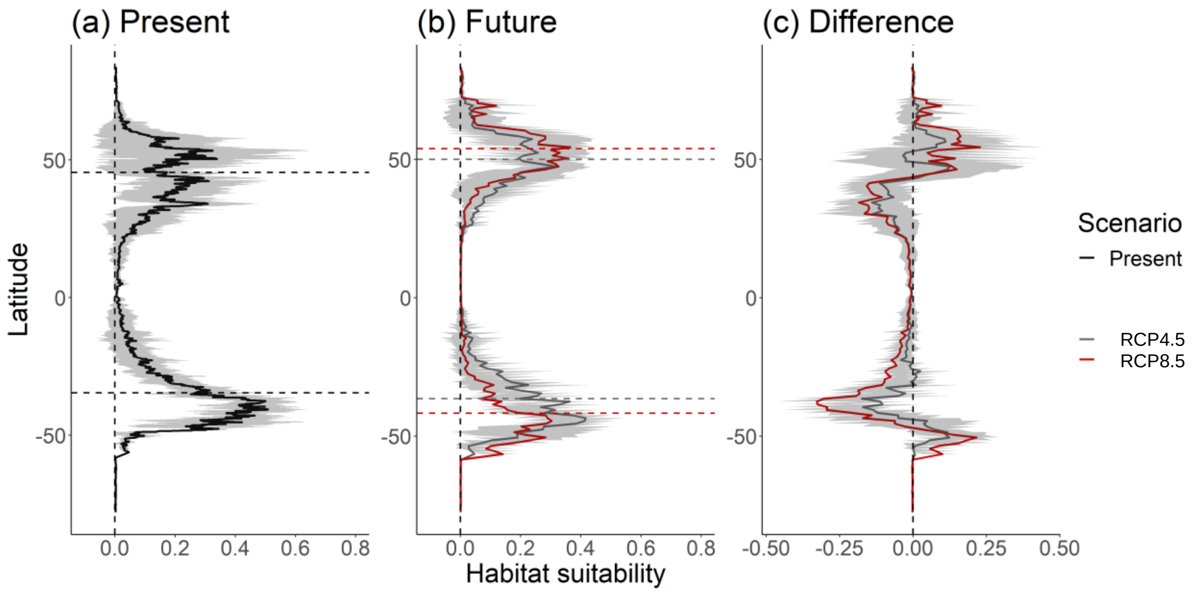


Figure 2.8 Latitudinal mean habitat suitability per 1° latitude for (a) present day and (b) two scenarios for the end of the century and (c) difference between the two. The dotted lines indicate the latitudinal centroids for the different models. The shaded area represents standard deviation.

2.4 Discussion

In environmental space, introduced *M. gigas* have shifted their niche relative to the native niche in both analog and non-analog environments, implying that *M. gigas* can thrive in novel environments. The ability to shift niches could ultimately facilitate its spread under CCC conditions. We found inconsistent results from examining niche shifts using two popular frameworks. The five-dimensional hypervolume framework implied niche shifts in the introduced niche, however, the two-dimensional COUE framework implied niche conservatism. The first two PCs used in the COUE framework explained a low amount of the variability in the environmental data and therefore were unlikely to contain the information relevant to the differences between the native and introduced niches. This study highlights the need for careful interpretation of the results when comparing niches in two-dimensional space and suggests the use of higher dimensions to give a better understanding of the differences between the two niches. Areas of suitable climates for the NIS *M. gigas* were generated for both the present day and end of the century, with the species range predicted to increase towards the poles and contract towards the tropics under two forecasted CCC scenarios by 2100. This agrees with several ENM studies which show that towards the end of the century, NIS are predicted to undergo a poleward range shift (de Rivera *et al.*, 2011; Lowen & DiBacco, 2017; Goldsmit *et al.*, 2018) due to ocean warming.

The results from this study support previous findings showing that NIS across a range of habitats and taxa are undergoing rapid niche shifts in their introduced ranges (Li *et al.*, 2014; Tingley *et al.*, 2014; Parravicini *et al.*, 2015; Torres *et al.*, 2018; Pili *et al.*, 2020; Zhang *et al.*, 2020). Parravicini *et al.* (2015) demonstrated that 33% of the invasive tropical fishes studied in the Mediterranean Sea show expansions in their introduced niches and concluded that ENMs which do not account for niche shifts may underestimate their potential spread. In freshwater systems, up to 90% of the 22 invertebrate species exhibited significant changes in their introduced niche compared to their native niche (Torres *et al.*, 2018). Identifying niche shifts gives an indication of the potential for a species to adapt and spread into novel climates both currently and in the future, which may ultimately increase NIS success with CCC.

Our modelling in analog climates indicated a ‘true’ shift has occurred in the introduced niche of *M.* gigas over a relatively short time since introduction for aquaculture. Several factors may contribute to an observed shift in the realised niche in the introduced range (Pearman *et al.*, 2008; Alexander & Edwards, 2010): expansion in the introduced niche or unfilling in the native niche may be a result of rapid evolution (Alexander, 2013; Moran & Alexander, 2014; Sotka *et al.*, 2018), a change in biological interactions (e.g. competition and predation), or changes in dispersal capabilities (Rödder & Lötters, 2009; Alexander & Edwards, 2010; Atwater *et al.*, 2018). Rapid evolutionary changes such as adaptation during early life-history stages to novel climates (Whitney & Gabler, 2008; Hoffmann & Sgrò, 2011), hybridisation with native species (Muhlfeld *et al.*, 2014) and broadening environmental tolerances (Davidson *et al.*, 2011; Tepolt & Somero, 2014) are common observations in studies on NIS. *M. gigas* has been shown to be genetically diverse in both native and introduced populations (Boom *et al.*, 1994; English *et al.*, 2000) and exhibit high phenotypic plasticity in terms of growth and survival across a wide range of environmental conditions (Hamdoun *et al.*, 2003; Taris *et al.*, 2006; Li *et al.*, 2018). For example, growth in adult oysters occurs in temperatures between 10-40°C and salinities of 10-30, and can spawn across a wide range of conditions (Troost, 2010). This broad environmental tolerance suggests the niche shift in analog climates is likely due to increased availability of suitable habitats due to, for example, reduced competition or predation within in the introduced range. This is further supported by the high proportion of *M. gigas* existing in non-analog climates. Future studies should couple their investigations with genetic analyses or experiments investigating species physiological tolerances between individuals from native and introduced ranges, and biotic interactions to determine the underlying cause behind these niche shifts in NIS and gain insight into how species niches change over time.

Habitat suitability models can be useful for guiding NIS monitoring programmes that can aid conservation and management efforts (Crall *et al.*, 2013). The present-day models suggest there are climatically suitable areas of the globe where *M. gigas* have not yet been recorded, for example in South America and South Africa. Similarly, modelling in environmental space highlighted areas of unfilling in the native niche. These results are likely a factor of either *M. gigas* not having been introduced, not yet to spread to these locations from their points of introduction, or survey effort in these areas being low. Occurrence records for marine invasive species tend to be opportunistic or incidental (Phillips *et al.*, 2009; Guillera-Arroita *et al.*, 2015), therefore lending themselves to spatial bias, a lack of true absence records and thus, may not fully represent a species' niche (Elith *et al.*, 2006). The present habitat suitability maps for *M. gigas* can, however, be used to highlight areas at potential risk to invasion and guide targeted surveys, particularly in under-represented areas, which would ultimately increase occurrence records and make for more robust model predictions (Ruiz & Hewitt, 2002; Feeley & Silman, 2011).

The present and end-of-the-century ENMs predicted suitable habitats vulnerable to future invasion. However, it relies on whether the species could be introduced or successfully spread to these areas. Factors such as natural (propagules/larvae) or artificial (shipping and aquaculture) dispersal and biological interactions are rarely incorporated into ENMs (Wisz *et al.*, 2013) but are an important influence on invasion success and are often the cause for NIS absence from areas of its fundamental niche (Hastings *et al.*, 2005; Araújo & Guisan, 2006; Briscoe *et al.*, 2019). There have been advances in hybridizing ENMs that incorporate dispersal models which have shown to increase accuracy in predicting NIS distributions (Václavík & Meentemeyer, 2009; Wisz *et al.*, 2013). However, whilst incorporating biological interactions has made recent progress (Araújo & Luoto, 2007; Araújo *et al.*, 2014), challenges remain in determining which interactions are important for structuring communities and having sufficient data on geographical scales. Predictions of *M. gigas* distributions would highly benefit from inclusion of these biotic factors to determine their realised niche on regional and local scales and with CCC.

The COUE and hypervolume frameworks used for examining native and introduced niches showed contrasting results. The hypervolume for both the total and analog environmental space supported the likelihood that introduced *M. gigas* have encountered a niche shift. These results were inconsistent with the COUE framework which found the niches to be equivalent and similar, implying niche conservatism. The five-dimensional hypervolumes showed that there were large unique fractions of both niches occurring outside their overlap (Figures 4, 5). It is likely, however, that the COUE framework is limited by comparing niches in only two dimensions. Other studies comparing both of these popular frameworks are rare but have similarly shown differences in the results of niche shifts (Pili *et al.*, 2020). Conversely, Tingley *et al.* (2014) found both methods provided similar results, however, the first two PCs in their study accounted for 88.9% of the variability in the data. It is likely therefore that modelling in higher dimensions would be unlikely to change their conclusions. It is common for this percentage to be low in studies investigating niche shifts, including in the present study where correlations between the environmental variables are low. The first two PCs do not necessarily contain information relevant to the differences between species, as PC analysis only attempts to explain variability in the environmental data. The use of the *n*-dimensional hypervolume framework allows up to 100% of the variability in the environmental data to be accounted for, therefore providing a more complete understanding of the differences between the native and introduced niches.

Sørensen-Dice and Jaccard indices predicted low niche overlap in *M. gigas* niches, however, the two-dimensional PC plots (Figure 2.3) did not represent this difference. The pairwise PC plots misleadingly suggested a high level of overlap. This provided evidence that the PCs did not in themselves contain the relevant information to enable a visualisation of the niche differences, thus niche overlap analyses using only the first two PCs should be interpreted with caution. For visualising the data, the PLS approach found new factors (analogous to PCs) specifically to explain species differences using the first two PLS factors and provides an informative 2D projection. Two PCs allows for a simpler interpretation of high-dimensional data, however, in cases where the first two PCs account for a low amount of the variability in the dataset, higher-dimensional techniques or PLS should be explored.

2.5 Conclusion

This study has revealed rapid niche shifts in a highly successful marine NIS in its introduced range. This niche divergence and broad environmental tolerances expressed by *M. gigas* highlights its ability to establish in novel climates and may facilitate its spread under CCC. From comparing the popular COUE and *n*-dimensional hypervolume frameworks, we highlighted that modelling in higher dimensions should be considered for analysing niche overlap, especially when low dimensions do not describe a high amount of the variability in environmental variables. In addition, we predicted a poleward expansion and tropical contraction of suitable habitat by the year 2100 under two RCP scenarios. Ultimately, although exploring niche shifts of highly successful NIS advances understanding on NIS spread, the underlying causes of niche shifts require further investigation before they can be truly integrated into ecological niche models.

Chapter 3 Long-term environmental tolerance of the non-indigenous Pacific oyster to expected contemporary climate change conditions

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Abstract

The current global redistribution of biota is often attributed to two main drivers: contemporary climate change (CCC) and non-indigenous species (NIS). Despite evidence of synergetic effects between these drivers, studies assessing the long-term effects of CCC conditions on NIS fitness remain rare. We examined the interactive effects of warming, ocean acidification and reduced salinity on the globally distributed marine NIS *Magallana gigas* (Pacific oyster) over a ten-month period. Individuals were exposed to a range of environmental conditions reflecting current and predicted conditions for the end of the century in the northeast Atlantic Ocean. Growth, clearance and oxygen consumption rates were measured monthly to assess individual fitness. Our results showed that lower salinity had a significant, permanent effect on *M. gigas*, reducing and increasing clearance and oxygen consumption rates, respectively. Neither predicted increases in seawater temperature and reduced pH had a long-term effect on the species physiology. Although reduced salinity has the potential to negatively affect *M. gigas*, our results showed that temperature and pH conditions predicted for the end of the century will not affect adult physiology and survival. These results suggest that *M. gigas* will remain a globally successful NIS and predicted CCC conditions will continue to facilitate the competitive dominance of this NIS in the near future.

3.1 Introduction

Non-indigenous species (NIS) and contemporary climate change (CCC) are two of the most significant threats to global biodiversity. From their main points of introduction (e.g. agricultural exploitations, harbours and aquaculture sites), NIS can spread to surrounding areas and establish new populations, becoming invasive (Eno *et al.*, 1997; Manchester & Bullock, 2000; Richardson *et al.*, 2000; Jensen *et al.*, 2004; Hellmann *et al.*, 2008). In addition, NIS can negatively impact native biodiversity and alter the structure and functioning of ecosystems (Nichols *et al.*, 1990; Carlton & Geller, 1993; Travis, 1993; Grosholz Edwin *et al.*, 2000). Knowledge of the potential impacts of CCC on marine NIS has advanced rapidly in recent years through the use of laboratory and field experiments (for example Lemasson *et al*., 2018; Miranda *et al*., 2019; Nguyen *et al.*, 2020), habitat suitability modelling (for example Sarà *et al*., 2018; D'Amen & Azzurro, 2019; Zhang *et al*., 2020) and mechanistic modelling (Thomas *et al*., 2016). Mounting evidence suggests that CCC is likely to facilitate NIS spread and alter the current global distribution of species (Dukes & Mooney, 1999; Carlton, 2000; Occhipinti-Ambrogi, 2007; Hellmann *et al.*, 2008; Rahel & Olden, 2008; Occhipinti-Ambrogi & Galil, 2010; Smith *et al.*, 2012).

Anthropogenic activities have led to both an increase in global temperatures and ocean acidification over the last 150 years (Caldeira & Wickett, 2003, 2005; Gattuso *et al.*, 2015; IPCC, 2019). It is expected that by the end of the century, global surface temperatures and ocean pH will rise by 2 - 4°C and decrease by 0.3 - 0.4 units, respectively, relative to 1986 – 2005 (Caldeira & Wickett, 2003; Sabine *et al.*, 2004; Caldeira & Wickett, 2005; IPCC, 2019). In response to these environmental changes, species distributions are shifting to higher latitudes and altitudes, or deeper depths in the oceans (Parmesan & Yohe, 2003; Parmesan *et al.*, 2005; Helmuth *et al.*, 2006; Hickling *et al.*, 2006; Mieszkowska *et al.*, 2006; Cheung *et al.*, 2009; Chen *et al.*, 2011; Pecl *et al.*, 2017). Range expansions and increases in abundance have already been reported on NIS that have experienced a 50-year period of warming (Rius *et al.*, 2014). Consequently, range expansions of NIS are expected throughout this century in both marine and terrestrial ecosystems (Occhipinti-Ambrogi, 2007; Rahel & Olden, 2008; Pecl *et al.*, 2017). A meta-analysis of NIS performance under CCC conditions showed that NIS displayed more positive responses to increased ocean acidification and warming than native species (Sorte *et al.*, 2013), probably due to successful NIS being able to survive across a wider range of these parameters. Overall, the potential positive effects of CCC on NIS may ultimately facilitate NIS dominance in the near future.

The environmental factors linked to CCC rarely act in isolation and interactions between multiple environmental stressors are known to exacerbate the effects of CCC on species performance (Przeslawski *et al.*, 2005; Staudt *et al.*, 2013; Delorme & Sewell, 2014; Przeslawski *et al.*, 2015). It is therefore crucial to study the combined effects of multiple abiotic stressors on species physiology to fully understand how CCC will affect the success of NIS. However, assessments of the effects of multiple stressors, particularly those using more than two stressors, are uncommon with the majority of CCC experiments focusing on short-term exposures (Kroeker *et al.*, 2013). Although these experiments provide key insights into how CCC affects the physiology of both native and NIS, short-term experiments may not account for the acclimation of the species to experimental conditions and only provide limited evidence of chronic stress responses (Hollister *et al.*, 2005; Leuzinger *et al.*, 2011; Dupont *et al.*, 2013; Smith & Dukes, 2013; Stewart *et al.*, 2013; Suckling *et al.*, 2015). Data from long and short-term experiments have revealed contrasting results (Form & Riebesell, 2011; Dupont *et al.*, 2013; Munday *et al.*, 2013; Suckling *et al.*, 2015), with species showing acclimation and resilience only in long-term and/or trans-generational exposure to abiotic stressors (Donelson *et al.*, 2011; Munday, 2014; Palumbi *et al.*, 2014; Suckling *et al.*, 2015; Ross *et al.*, 2016). Long-term studies are therefore crucial for accurate predictions of the effects of CCC on species fitness. Another advantage of long-term experiments is that they can encompass seasonal changes in environmental conditions, which are often overlooked in short-term experiments. By including maximum and minimum temperatures, an assessment can be made of the effects of stressors across phenological cycles.

In this study we assessed how changes in key environmental conditions, as predicted under CCC at the end of the 21st century, interact and affect the long-term performance of the highly successful marine NIS the Pacific oyster, *Magallana gigas* (Thunberg, 1793). From its native range in northeast Asia, *M. gigas* has been introduced into over 65 countries for use in aquaculture worth approximately $1.2 – $1.4 billion per year (Figure 7.1a). *M. gigas* has already established wild populations in more than 17 countries (Figure 7.1b) , making it a globally successful NIS (Herbert *et al.*, 2016). *M. gigas* is classified as an invasive species due to its ability to spread and form extensive reefs, modifying the habitats and threatening indigenous biodiversity (Richardson *et al.*, 2000; Lejart & Hily, 2005; Smaal *et al.*, 2008; Troost, 2010; Holm *et al.*, 2016).

There are a wealth of studies investigating environmental change on *M. gigas* fitness, however, contrasting results have shown both neutral/positive (Havenhand & Schlegel, 2009; Falkenberg *et al.*, 2019) and negative (Kurihara *et al.*, 2007; Lannig *et al.*, 2010;

Barros *et al.*, 2013; Lemasson *et al.*, 2018) effects of warming and ocean acidification on adult and larval stages. Whilst the majority of these experiments have shown the short-term sensitivity of *M. gigas* to CCC, *M. gigas* may acclimate and express resilience to these conditions in the long-term. Further investigation is therefore needed to assess the effects of prolonged, seasonal exposure of adult *M. gigas* to predicted CCC conditions and how the long-term interactive effects between altered abiotic factors will contribute to their continued success.

Here, *M. gigas* were exposed to varying levels of three abiotic stressors, temperature, pH and salinity, over a ten-month period. We hypothesised that: (1) long-term exposure to expected CCC conditions and reduced salinity would negatively affect *M. gigas* fitness, and (2) the manipulated environmental conditions will have synergistic interactions, ultimately affecting the performance of *M. gigas*.

3.2 Methods

3.2.1 Mesocosm set up and conditions

We created a mesocosm system with 12 independent experimental treatments (Figure 3.1). Each treatment consisted of a closed system with a header and footer tank circulating approximately 200 litres of natural, untreated, filtered seawater from Plymouth Sound through six, nine litre experimental tanks. The 12-level (2 temperature x 3 pH treatments x 2 salinity) factorial experiment included different temperature (ambient and +4 °C), pH (ambient at 8.1, 7.7 and 7.5), and salinities (34 and 20) levels (Figure 3.1). Temperature and pH were chosen to reflect ambient and forecasted projections from both IPCC and UKCP09 reports (Jenkins *et al.*, 2009; Lowe *et al.*, 2009; Hughes *et al.*, 2017; IPCC, 2019). Reduced salinity is a key range limiting factor for marine species, often having a negative impact on species physiology and survival (Cognetti & Maltagliati, 2000; Paavola *et al.*, 2005; Braby & Somero, 2006; Pourmozaffar *et al.*, 2020), and thus salinity was manipulated to reflect the tolerance range of *M. gigas* with conditions experienced in northwest Europe as intertidal coastal and estuarine organisms. Salinities above 20 are regarded as important for the establishment of Pacific oysters and adult oysters having been observed in salinities ranging from 20 (Scandinavian coast (Wrange *et al.*, 2010)) to more than 35. *M. gigas* are also common in estuaries where salinity fluctuates on a semi-diurnal basis. Each of the 12 treatments was run for 10 months between June 2018 to March 2019.

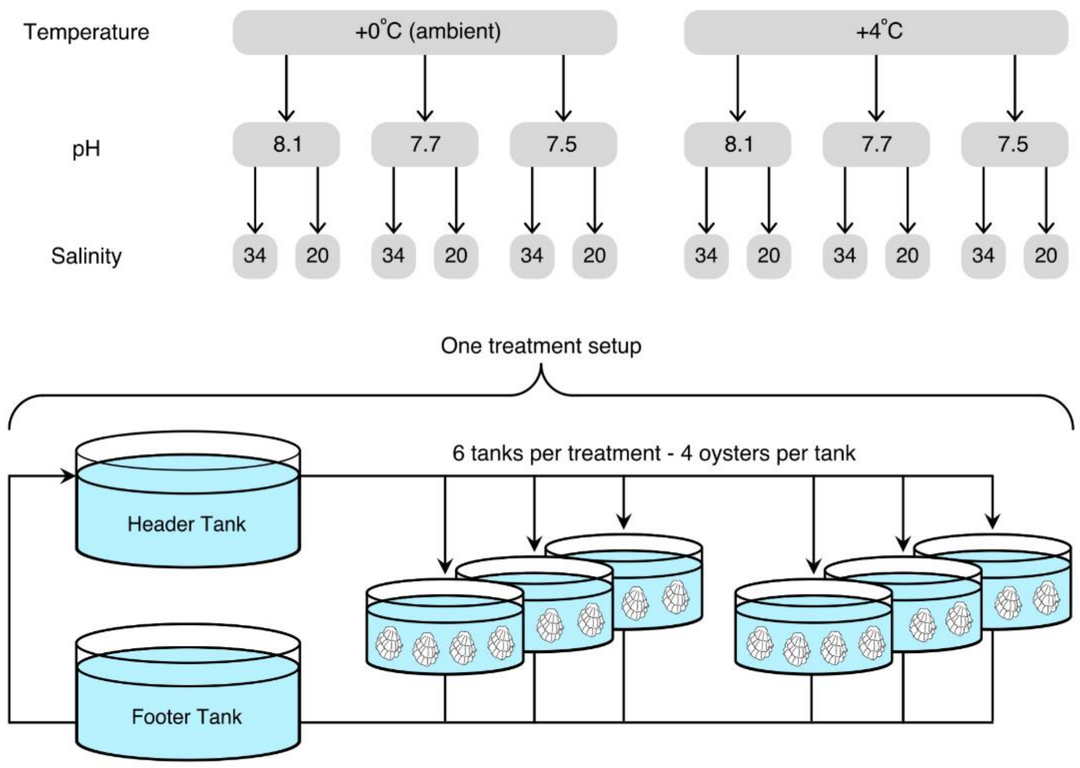

Figure 3.1 Experimental design used for the 12-level factorial experiment and the layout of each closed treatment system. Treatment refers to each of the 12 independent combinations of the environmental parameters. The six, nine litre tanks per treatment acted as the units of replication.

The pH was regulated using Aqua Medic pH computers, which administered CO_2 when the pH deviated by 0.02 above the treatment value. To reflect seasonality in natural systems, daylength and temperature were adjusted at the start of every month, with seawater temperature reflecting the average sea surface temperature at L4 station in the Western English Channel off the coast of Plymouth (www.westernchannelobservatory.org.uk) (Figure 3.2). Air temperature was used to control ambient seawater temperature and was adjusted to 2°C below the monthly average at L4 to achieve the desired seawater temperatures. Seawater temperature in the +4°C treatments were achieved by placing heaters in the reservoir tanks. Seawater temperatures varied by ±0.5°C across the two temperature levels. A 10% water change with filtered seawater occurred twice a week and at the same time freshwater was added to reduce salinity to 20 in half of the treatments.

Total alkalinity for each treatment was measured every other week using an Alkalinity Titrator (Model AS-ALK2, Apollo SciTech, Bogart). The water chemistry recorded for each treatment is shown in Table 7.1.

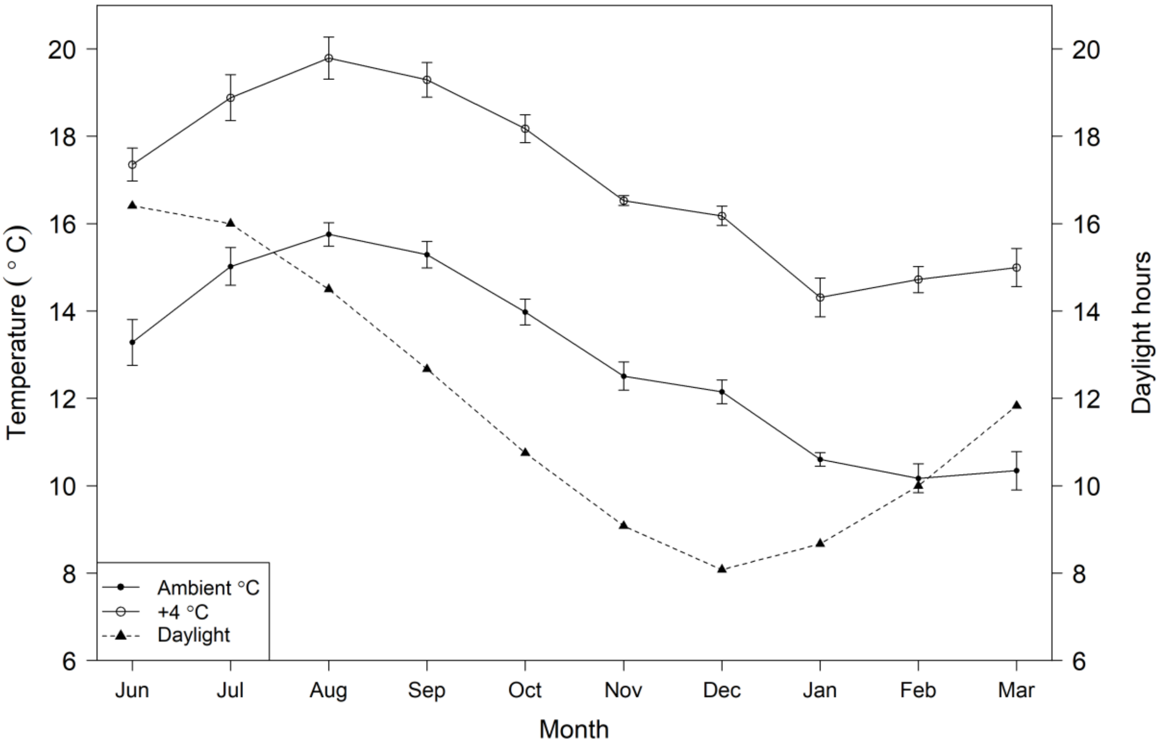

Figure 3.2 Monthly mean seawater temperature (ambient and +4ºC) and daylight hours in the mesocosm system between June 2018 and March 2019.

Adult *M. gigas* individuals (60 - 113 mm maximum length) were collected at the end of March 2018 from the low intertidal zone of the River Yealm estuary (50.3098°N, 4.0537°W), which is 15 km away from the laboratories of the Marine Biological Association of the United Kingdom (50.3641°N, 4.1391°W) where the experiments were conducted. The collected individuals were placed in insulated containers that were transported to the laboratory within one hour. Once cleaned of epibionts, a total of 288 oysters were randomly allocated to tanks, with 24 *M. gigas* per treatment across six replicate tanks, i.e. four oysters per tank (based off Utting & Spencer, 1991) (Figure 3.1). *M. gigas* were initially acclimated to their temperature and salinity treatments for four weeks prior to introducing CO_2 to the systems, then acclimated for a further four weeks before measuring physiological parameters. Oysters were fed with a diet of *Isochrysis galbana* and *Tetraselmis sp.* (Instant Algae® by Reed Mariculture) five days a week at an amount equivalent to 2% of the mean oyster dry weight (dry weights based on destructively sampling a representative sample of oysters from the Yealm Estuary) (Helm & Bourne, 2004). The concentration of food in the tanks at each feed was in the order of x10^8 cells per litre. Tanks were checked prior to feeding and dead oysters removed; only 11 oysters died over the duration of the experiment.

3.2.2 Growth

Initially, all 288 oysters were weighed to the nearest 0.01g prior to treatment exposure to obtain a baseline weight. Weight of the oysters was then assessed at the start of each month (with the exception of January and February). Every oyster was removed from their tank, carefully dried to remove excess water from the shell and total live wet weight (shell and wet tissue) of each individual oyster was measured. Weight change was then determined as the difference in the monthly weight compared to baseline weight.

3.2.3 Physiological measurements

Physiological measurements were taken during the fourth week of each month, after *M. gigas* were exposed to the monthly environmental conditions for three weeks. Daily feeding was stopped two days prior to measuring physiological parameters to obtain values at a routine metabolic rate. Oysters were returned to their respective tanks after physiological measurements were taken.

3.2.3.1 Clearance rate

The clearance rates for *M. gigas* (i.e. the volume of water cleared of algal cells per hour) were measured to assess their efficiency to remove seston within each treatment. Clearance rates were measured on six individual oysters from each treatment (one haphazardly selected from the replicate tanks). Oysters were placed in an enclosed chamber with 1 litre of filtered seawater with temperature, pH and salinity levels matching their respective treatments. Once the oyster was visibly feeding (valves open) a concentration of 2×10^8 cells per litre (below pseudofaeces production threshold) of *Isochrysis* sp. was added to the water and the oyster left to feed for 30 minutes. Strong, continuous aeration was used to keep the water constantly mixed and prevent the settlement of algae cells. Water samples at the beginning and end of each 30-minute period were collected and the cell concentration of each sample analyzed using a Beckman Coulter Counter Z Series. Clearance rate (*CR*) was calculated from the exponential decrease in cells using the following equation described in Coughlan (1969):

$$CR = V \times \ln(C0) - \ln(C1)/t$$

where *V* is the volume of water in the enclosed chamber, *C1* and *C2* are the concentration of cells before and after 30 minutes, respectively, and *t* is the time in hours. Clearance rates were then standardised to 1 g total wet weight of the oyster. Total wet weight was used to standardize the rates due to oyster size and condition having an effect on physiological parameters. As a control, tanks were run without oysters to assess potential algal settlement during clearance rate measurements.

Due to unforeseen circumstances, the clearance rates in August from all four treatments with a pH of 8.1 were removed from the analysis due to an equipment failure leading to measurements being unreliable.

3.2.3.2 Oxygen consumption

Oxygen removal from the water by *M. gigas*, a proxy for metabolic demand (Treberg *et al.*, 2016), was measured monthly (last week of every month) using a fibre-optic oxygen logger (Piccolo2; PyroScience). Oxygen consumption rates were obtained from four oysters per treatment (one randomly selected from four tanks per treatment). Individuals were isolated in a closed chamber with 1 litre of seawater with temperature, pH and salinity levels matching their respective treatments. Oysters were left to acclimatize to the chamber for at least 15 minutes before measuring oxygen concentration. Once the oysters began to uptake oxygen (valves opened), after the acclimatizing period, oxygen concentration was recorded every second for a minimum of 30 minutes. If the oyster closed its values during the recording, the timer was restarted when valves were opened to ensure 30 minutes of continuous oxygen decline in the water. Seawater was continuously stirred during each trial with a magnetic stirrer to ensure oxygen was equally mixed throughout the water. If the individual remained shut for more than 60 minutes, and therefore was not taking up oxygen, the individual was replaced with another from within the same tank. Oxygen in the water did not fall below 70% saturation during any of the trials and therefore did not limit oxygen consumption (Ren *et al.*, 2000). Oxygen removal in control tanks, without oysters, was measured for each treatment each month to determine the potential rate of decline from bacterial respiration.

Oxygen consumption was estimated as the rate of oxygen decrease per second in the chamber. Linear regression was used to obtain the average rate of oxygen consumption.

The rate was taken after the first ten minutes of the oyster consuming oxygen to allow time for the oyster to reach a steady state of respiration. The rate of change was then scaled up to obtain a rate of uptake per hour and standardised to 1 g total wet weight of the oyster by dividing the rate by the total wet weight (including shell) of the oyster.

3.2.4 Data analysis

Weight change from baseline, clearance rates and oxygen consumption rates were analysed separately using linear, mixed effect, repeated measures analysis of variance (RM-ANOVA) models with an autocorrelated error structure (Quinn & Keough, 2002). The models included a term for month and the 12 treatments (see details in Figure 3.1) were fitted as a 2x2x3 factorial with main effects, 2-factor interactions, and the 3-factor interaction (Quinn & Keough, 2002). Month-by-treatment interactions were also fitted. For weight change, individual oyster was used in the model as the repeated measure, and for clearance and oxygen consumption rates, tank was used as the repeated measure.

Assumptions of parametric tests were checked by analysing normality, which was assessed by plotting theoretical quantiles with versus standardised residuals (Q-Q plots) and using Shapiro-Wilk test; and homogeneity of variances, which was tested by plotting residuals versus fitted values and Levene test. All assumptions were met, except for clearance rate where there was evidence of non-normality. A non-parametric ANOVA (randomization test) was performed and the results were consistent with the parametric test, therefore given the conclusions are the same, we have reported the values from the parametric model. All models were fitted in R (R Core Team, 2019).

3.3 Results

3.3.1 Growth

Oysters lost an average of approximately 0.5g in weight in the first month after establishment in the mesocosm. Weight increased at the start of the experiment before decreasing for all treatments to a minimum in September (Figure 3.3a). There were statistically significant interactions between month and the three treatment factors however, no clear or consistent treatment-related trends were observed (Figure 3.3b, c, d).

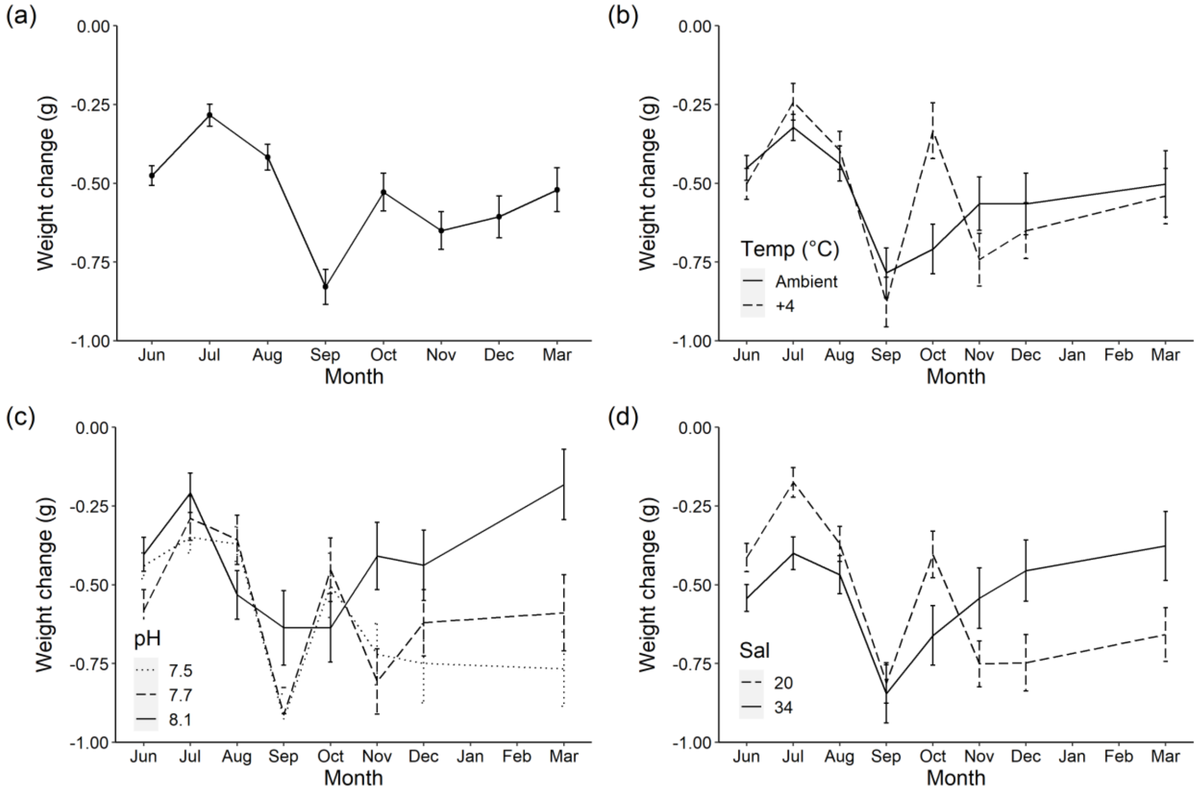

Figure 3.3 Mean weight change (g ± standard error) from their baseline weight at collection between June 2018 and March 2019 (a) across all treatments, (b) averaged for treatments at ambient or +4 °C to investigate temperature effect (c) averaged for treatments at a pH of 8.1, 7.7 or 7.5 to investigate pH effects and (d) averaged for treatments at a salinity of 20 or 34 to investigate salinity effect.

3.3.2 Clearance rate

Overall, mean clearance rates were highest at the beginning of the experiment in June and July 2018 at a maximum of 0.024 (±0.001) l hr^{-1}, standardised to 1g total weight. Clearance rate then decreased by more than half in August at 0.011 (±0.001) l hr^{-1} and reached a minimum in January 2019 at 0.005 (±0.0004) l hr^{-1}. Clearance rate was also relatively stable between November 2018 and March 2019 (Figure 3.4a).

The estimate of the autocorrelation parameter for both clearance rate models was 0.04 indicating almost complete independence of the measurements over time. There was no significant three-factor or two-factor interaction between any of the factors nor was there a significant long-term effect of temperature or pH (Figure 3.4b, c). There was a statistically significant difference between the two salinity levels, with a larger volume of water cleared in a salinity of 34 compared a salinity of 20 (Table 3.1, Figure 4d). There was no significant interaction between month and salinity, therefore the difference between the salinity levels was constant over time. Oysters in a salinity of 20 cleared an estimated 0.0016 (±0.0004) l hr^{-1} less per month, approximately 20% less than those in a salinity of 34.

Overall, mean clearance rate across all treatments did not change with actual temperature of the water (Weighted linear regression: $R^2 = 0.38$, $F_{1,8} = 4.78$, $p = 0.06$). Further, the salinity effect (difference between the two salinity levels per month) did not correlate actual temperature (Weighted linear regression: $R^2 = 0.39$, $F_{1,8} = 5.02$, $p = 0.06$).

Table 3.1 Repeated measures ANOVA output stating the degrees of freedom, F-statistic and p-values for each individual factor and their interactions. Significant effects are denoted with an asterisk.

	Clearance rate			Oxygen consumption rate		
	df	*F* (*df*, 94)	*P*	*df*	*F* (*df*, 101)	*P*
Month	9	112.1	<0.0001*	9	21.8	<0.0001*
Temperature	1	0.04	0.83	1	11.29	0.001*
pH	2	0.11	0.90	2	1.44	0.24
Salinity	1	10.1	<0.002*	1	7.37	0.009*
Temp X pH	2	0.95	0.39	2	0.71	0.50
Temp X Salinity	1	0.72	0.40	1	0.06	0.81
pH X Salinity	2	0.85	0.43	2	1.17	0.32
Temp X pH X Salinity	2	1.68	0.19	2	0.35	0.71
Month X Temp	9	0.21	0.99	9	2.05	0.03*
Month X pH	18	0.72	0.78	18	0.89	0.59
Month X Salinity	9	1.63	0.11	9	0.77	0.65

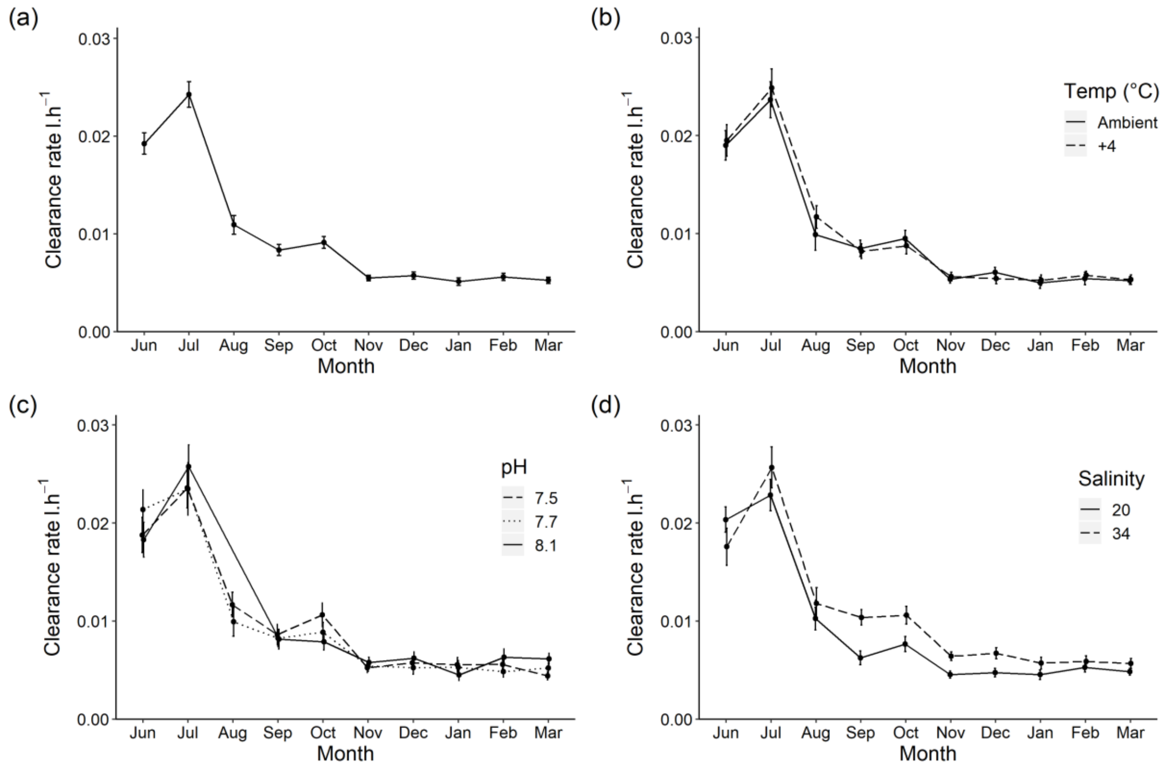

Figure 3.4 Mean clearance rates (l hr^{-1} ± standard error) between June 2018 and March 2019 (a) across all treatments, (b) averaged for treatments at ambient or +4 °C to investigate temperature effect, (c) averaged for treatments at a pH of 8.1, 7.7 or 7.5 to investigate pH effects and (d) averaged for treatments at a salinity of 20 or 34 to investigate salinity effect. All rates are standardised to 0.01g total weight.

3.3.3 Oxygen consumption

Mean oxygen consumption rate across all treatments was highest between June and September 2018 before decreasing between September 2018 at 0.0077 (±0.0024) mg hr^{-1}, standardised to 1g total weight, to March 2019 at 0.0038 (±0.0019) mg hr^{-1} (Figure 3.5a). This decrease coincided with a decrease of 6°C between the warmest and coldest months of the experiment. Consumption was high at the beginning of the experiment although temperatures in June and July 2018 are similar to those in October and November 2018 where rates were lower.

The estimate of the autocorrelation parameter for oxygen consumption rate models was 0.04 indicating almost complete independence of the measurements over time. There was no significant interaction between any of the three experimental factors. There was a significant effect of temperature (Table 3.1, Figure 3.5b). This was observed as those at +4°C had either equal to or higher oxygen consumption rates than the ambient treatments.

There was a significant interaction between month and temperature, therefore the difference in oxygen consumption rates between the temperature levels was not constant over time. There was, however, a large difference between factors during the first couple of months and minimal difference in oxygen consumption rates between August and January (Figure 3.5b).

Oxygen consumption rate had no long-term trend with pH (Figure 3.5c) and overall, the effect of pH was not statistically significant. There was a statistically significant effect of salinity (Table 3.1, Figure 3.5d). There was no significant interaction between month and salinity, therefore the observed differences between the two salinity levels was constant over time. On average, a salinity of 20 led to an estimated 0.00056 (±0.0002) mg hr^{-1} more oxygen being consumed, approximately 10%, compared to those kept at a salinity of 34. Oxygen consumption increased significantly with increasing actual temperature (Figure 7.2) (Weighted linear regression: $R^2 = 0.89$, $F_{1, 8} = 66.42$, $p < 0.001$) at 0.0004 mg hr^{-1} every 1°C increase. The salinity effect was not significantly affected by actual temperature.

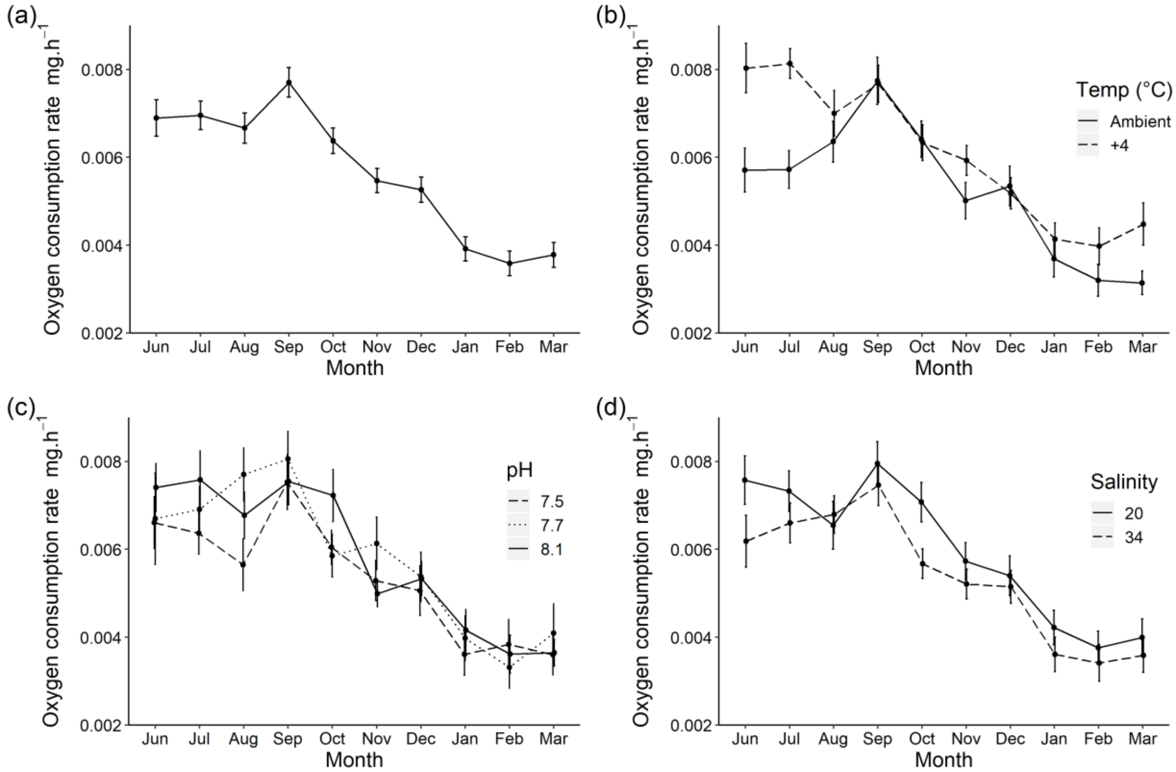

Figure 3.5 Mean oxygen consumption rates (mg hr^{-1} ± standard error) between June 2018 and March 2019 (a) averaged across all treatments (b) averaged across treatments at ambient or +4 °C to investigate temperature effect, (c) averaged across treatments at a pH of 8.1, 7.7 or 7.5 and (d) averaged across treatments at a salinity of 20 or 34. All rates are standardised to 0.01 g total weight.

3.4 Discussion

Our long-term mesocosm experiment showed that reduced salinity conditions had a statistically significant, persistent impact on the physiology of *M. gigas*. In turn, water temperature and pH had little to no impact on clearance and oxygen consumption rates of *M. gigas*. This suggests that key environmental conditions as predicted by the end of the century will not negatively affect adult physiology and survival of this highly successful NIS. Our study highlights the importance of conducting long-term, seasonal experiments to fully understand the tolerance of NIS to abiotic stressors.

Broad environmental tolerance and phenotypic plasticity to environmental change are common traits of NIS compared to native species in marine and terrestrial environments (Daehler, 2003; Funk, 2008; Davidson *et al.*, 2011; Tepolt & Somero, 2014). The ability of a species to alter its physiology and morphology to novel environmental conditions, such as CCC, may give them a competitive advantage over other species and, in the case of NIS, enable them to spread to a wide range of habitats (Stachowicz *et al.*, 2002; Davidson *et al.*, 2011). Our results support growing evidence that successful NIS have high environmental tolerance and will tolerate predicted future environmental conditions.

Salinity had a constant effect on *M. gigas* physiology over the duration of the experiment. It may therefore be physiologically necessary for *M. gigas* individuals to increase oxygen consumption rates and decrease clearance rates to ensure survival in areas of freshening. Other physiological studies have shown that *M. gigas* have faster growth and gonadal development at a salinity of 30 and reduced growth and larval mortality at lower salinities (Shumway & Koehn, 1982; Muranaka & Lannan, 1984; Brown & Hartwick, 1988; His *et al.*, 1989). Environmental stressors such as low salinity result in changes in water chemistry (Dickinson *et al.*, 2012; Casas *et al.*, 2018b) and osmotic pressure (Maoxiao *et al.*, 2019), which in turn increases energy expenditure (increase metabolic rate) or reduced energy storage capacity leading to reduced fitness, survival and growth (Lannig *et al.*, 2006; Dickinson *et al.*, 2012; Maoxiao *et al.*, 2019). Our results showed that a salinity of 20 led to an increase in energy demand of *M. gigas*, as shown by an increased oxygen uptake (Hawkins & Hilbish, 1992; Lannig *et al.*, 2006; Sokolova *et al.*, 2012), therefore may have had a negative impact on performance. This negative effect of salinity has also been observed in European flat oysters (*Ostrea edulis*) and eastern oysters (*Crassostrea virginica*) (Hutchinson & Hawkins, 1992; Dickinson *et al.*, 2012).

Decreased clearance rates with salinity have already been reported as a stress response in other bivalves (Wang *et al.*, 2011). Our results are consistent with the results found in Gray & Langdon (2018) with *M. gigas* which showed a decrease in clearance rates under reduced salinity conditions. Sarà *et al.* (2008) described how clearance rate decreased with lower salinities in the non-indigenous bivalve *Brachidontes pharaonis* but salinity followed the normal-shaped tolerance curve (decline in rates towards the extremes) and concluded this species can tolerate a wide range of salinities. Although lower salinities may be less favourable, *M. gigas* may be able to tolerate and survive these conditions better over the long-term compared to indigenous species. Whilst lower salinities may reduce the fitness of *M. gigas*, areas with low salinity such as estuaries have fewer competing species and predators, therefore settlement will likely occur in these locations if conditions are tolerable to larval stages (Gunter, 1955).

It has been proposed that organisms inhabiting coastal areas and exposed to a range of temperatures and carbonate chemistry are more likely tolerant of future warming and ocean acidification (Range *et al.*, 2012). *M. gigas* individuals used in our experiment were collected from a low-intertidal, estuarine environment that is classed as highly stressful for marine organisms as temperature, salinities and pH fluctuate on a daily basis (Lannig *et al.*, 2006; Range *et al.*, 2012). Local adaptation to this type of environment may explain why our manipulation of temperature and pH showed little to no long-term effect on *M. gigas* physiology. Although ocean acidification has been shown in many cases to suppress the growth and important physiological processes such as feeding and respiration (Range *et al.*, 2012; Barros *et al.*, 2013; Gazeau *et al.*, 2013; Ivanina *et al.*, 2013; Bressan *et al.*, 2014; Zhao *et al.*, 2017), some species show neutral or positive effects to near-future pH levels (Ries *et al.*, 2009; Matoo *et al.*, 2013; Gazeau *et al.*, 2014). Zhang *et al.* (2012) found that *M. gigas* have an extensive set of genes that leads to unique adaptation to the stressful conditions of intertidal and estuarine environments. Further, both adult and early life-history stages of *M. gigas* have shown to have a high degree of plasticity in their physiology, such as thermal stress (Hamdoun *et al.*, 2003), resource allocation and feeding (Honkoop *et al.*, 2003; Ernande *et al.*, 2004; Dutertre *et al.*, 2007), reproductive timing (Fabioux *et al.*, 2005), growth (Bayne, 2002; Taris *et al.*, 2006), and circadian rhythms (Mat *et al.*, 2012).

No clear temperature effect was observed in clearance rates whereby the overall rates were relatively similar between the highest and lowest temperatures. A similar trend has been recorded in *Crassostrea virginica* with no difference in clearance rate between individuals in the winter (17 °C) and summer (27 °C) (Casas *et al.*, 2018b). Seasonality can have an important influence on physiological energetics. Studies have shown that clearance rates in bivalves are not always temperature dependent as seasonal cycles in life history traits (reproduction and growth) can lead to variation in filtration rates in bivalves, typically with reduced feeding in the winter months and an increase in spring and summer (Hornbach *et al.*, 1984; Viergutz *et al.*, 2012; Rahman *et al.*, 2020). For example, Viergutz *et al.* (2012) showed that at peaks in clearance rate of the invasive bivalve *Corbicula fluminea* likely corresponded to spawning patterns increasing food (energy) demand. In our study, *M. gigas* clearance rates were not directly influence by seawater temperature, however, high rates were measured in the spring/early summer (at the start of the experiment). These rates were followed with a decrease in oyster weight in all treatments. *M. gigas* typically spawn between July and October in Europe which leads to a substantial decrease in wet meat weight (up to 50%) (Enríquez-Díaz *et al.*, 2009; Bernard *et al.*, 2016; Reise *et al.*, 2017; Ubertini *et al.*, 2017; Balić *et al.*, 2020). It is therefore likely that an increase in energy demand (and therefore clearance rate) occurred prior to spawning in August and September.

Whilst a seasonal pattern in clearance rate is likely to have been observed, acclimation to new environmental conditions at the start of the experiment may have also led to increased clearance rates through an increased stress response. Acclimation can be characterised by an initial stress response (for example, increased metabolic rate) followed by a stabilization of the organism's response (Suckling *et al.*, 2015). The acclimation of species to new environmental conditions can take several months (Dupont *et al.*, 2013; Suckling *et al.*, 2015; Pintor *et al.*, 2016) and, as clearance rates were high at the very start of the experiment, the effects of species acclimation on *M. gigas* cannot be fully ruled out.

A seasonal effect on oxygen consumption was observed across all treatments in line with changes in SST. Similar trends in oxygen consumption rates have been reported *in situ* for *M. gigas* where the highest and lowest oxygen consumption rates occurred in the summer and winter, respectively (Mao *et al.*, 2006; Casas *et al.*, 2018b). Increasing oxygen consumption with actual temperature agrees with several studies on marine bivalves (Bougrier *et al.*, 1995; Ren *et al.*, 2000; Sarà *et al.*, 2008; Casas *et al.*, 2018b), reflecting an increase in physiological and biochemical reactions with warming. Seasonality in metabolic demand may also reflect life history cycles, which are often linked to seawater temperature (Clarke, 1993; Casas *et al.*, 2018a). Oxygen consumption rates also showed a significant effect of temperature with month, however, the effect of +4°C was variable. Rates were similar to that of the ambient temperature treatment with the exception of June and July and, to a lesser extent, February and March where +4°C is associated with higher oxygen consumption rate (Figure 4b). The effects of end of the century temperatures on *M. gigas* may therefore be dependent on time of the year.

Although the adult oysters used in this study exhibited no negative effect with ocean acidification, studies on early life-history stages have shown vastly different results. Ocean acidification has been shown to have a negative effect on the development and calcification of early life stage *M. gigas* under pH values predicted for 2100 and 2300 (Kurihara *et al.*, 2007; Parker *et al.*, 2010) and varying effects on fertilization due to intraspecific differences between populations (Havenhand & Schlegel, 2009; Parker *et al.*, 2010; Barros *et al.*, 2013). Studies over multiple generations are rare but give an important insight on the potential carry-over effects between different life stages. These studies would increase understanding regarding trans-generational acclimation which has been shown in a variety of species to reduce the effects of CCC (Donelson *et al.*, 2011; Munday, 2014; Parker *et al.*, 2015; Ross *et al.*, 2016). For a more complete understanding of the long-term effects of CCC on individual species, it is crucial for future work to incorporate individuals from multiple populations and multiple generations into their experimental designs to investigate both intraspecific differences and the potential acclimation of a species through trans-generational carry-over effects to environmental change.

3.5 Conclusion

This long-term multiple stressor study on *M. gigas* demonstrated that a globally distributed NIS is tolerant to key CCC stressors, as predicted for the end of the century. Our results imply that NIS with broad environmental tolerances like *M. gigas* may thrive under expected CCC conditions, potentially leading to an increase in NIS populations and further impacting native biodiversity (Dubois *et al.*, 2006; Kelly *et al.*, 2008; Lejart & Hily, 2011; Anglès d'Auriac *et al.*, 2017). Although previous studies have shown negative synergistic effects of CCC factors on organism fitness, we found no interactive effects between any of the three stressors over the long-term. However, further long-term, trans-generational studies are required to investigate the presence of possible synergistic effects across multiple life-history stages (Rius *et al*., 2010). Our results also demonstrated how seasonality may influence physiological rates and the importance of allowing the studied organism to reach a physiologically stable state (Suckling *et al.*, 2015), which is key for interpreting laboratory experiments of differing temporal lengths. Ultimately, the long-term effects of CCC on NIS are still relatively unknown and continued research in this area will advance our understanding on the physiological resilience of NIS to environmental change.

Chapter 4 Variable responses to contemporary climate change across geographic regions: an inter-individual simulation approach using the life-history traits of the Pacific oyster

Abstract

Predicting the effects of contemporary climate change (CCC) on species' physiological performance is crucial for making robust predictions of species distributions. The Dynamic Energy Budget (DEB) is a powerful bioenergetic model for predicting the impacts of environmental changes on individual fitness. However, variability in individual physiological rates are rarely incorporated into DEB models and as a consequence DEB studies fail to consider the magnitude of species responses to CCC. Here, DEB modelling was used considering inter-individual variability and region-specific environmental variation to predict the effect of CCC on the life history traits of the non-indigenous Pacific oyster (*Magallana gigas*). Inter-individual variability was incorporated by simulating a unique set of seven parameters per oyster based on values measured in a laboratory or reported in the literature. Regional variation considered conditions along northeast Atlantic, Mediterranean and North Sea coastlines. We found that patterns in growth, maturity and reproduction varied in response to local changes in chlorophyll concentrations, and to a lesser extent temperature under CCC conditions. Future warming increased the number of spawning events and fecundity at high latitudes potentially facilitating a poleward range expansion. Higher chlorophyll concentrations increased oyster length, number of spawning events and number of oysters reaching maturity particularly in areas of the Mediterranean Sea. Incorporating inter-individual variability highlighted that average changes in life-history traits predicted for the end of the century may not lead to observable changes in the wild. It was clear that small changes in parameter means may result in markedly different estimates of life-history traits under CCC, and studies which use fixed values (i.e. not considering inter-individual variability) may underestimate model uncertainty. This study showed that simulation approaches incorporating inter-individual variability make robust predictions of species responses on large spatial scales and provide estimates of the potential establishment and spread of non-indigenous species under CCC.

4.1 Introduction

Physiological tolerances are fundamental in determining the geographical distribution of species (Kearney & Porter, 2009). Contemporary climate change (CCC) is expected to have a significant impact on species distributions (Parmesan & Yohe, 2003; Thomas *et al.*, 2004; Chen *et al.*, 2011) and thus predicting the physiological performance of species under novel conditions is crucial (Helmuth *et al.*, 2004). Robust ecological niche models (ENMs, including species distribution models) have been developed to better understand the relationship between species and the environment (Elith & Leathwick, 2009) and have become important in policy-level management and climate change research (Rodríguez *et al.*, 2007; Guisan *et al.*, 2013). The majority of ENMs, however, correlate occurrence data to environmental variables (i.e. correlative ENMs) and do not account for the mechanisms underpinning species responses to different environments. Hence, they may come under scrutiny when extrapolating to future non-analog climates (Fitzpatrick & Hargrove, 2009; Bell & Schlaepfer, 2016). Mechanistic ENMs move beyond identifying spatial patterns from correlations by determining the physiological constraints on species functioning that are key for structuring species biogeographic patterns (Kearney *et al.*, 2010b; Kearney & Porter, 2020). As a result, they may be more robust when modelling CCC conditions (Elith *et al.*, 2010). Whilst mechanistic ENMs are slowly increasing in popularity, it is still relatively unknown how both multiple environmental changes and model specification impact predicted distributions when considering individual-level mechanisms (Brook *et al.*, 2008; Johnston *et al.*, 2019).

Climatic conditions drive the exchange of energy and mass within organisms (Kearney & Porter, 2009; Tomlinson *et al.*, 2014). For example, varying environmental conditions such as food availability and temperature can alter energy expenditure and individual fitness which ultimately has bottom-up population-level effects (Grant & Porter, 1992; Helmuth *et al.*, 2006). Bioenergetic models focus on the acquisition and allocation of energy, and thus lend themselves to predicting distributions by estimating patterns in growth and reproduction in response to environmental stimuli (Martin *et al.*, 2012). One example of these models is the Dynamic Energy Budget (DEB) model, which describes how energy is assimilated, stored and utilised for metabolic processes throughout all life-history stages. DEB models thus consider the development, growth, structural maintenance and reproductive output of an individual, and can predict mortality and sub-lethal responses (Pouvreau *et al.*, 2006; Kearney *et al.*, 2010a; Kooijman, 2010). DEB theory was first used in the 1980s (Kooijman, 1986) and has since become a very popular tool for estimating underlying physiological trends. This is partly because the fundamental equations in the DEB model are applicable across different taxa and life-history stages (Sousa *et al.*, 2010).

DEB models are often used to study a species' underlying responses to environmental change (Sarà *et al.*, 2011; Thomas *et al.*, 2011; Sarà *et al.*, 2013b; Montalto *et al.*, 2014; Maar *et al.*, 2015; Mangano *et al*., 2020). By integrating the DEB theory with spatial environmental data, species functioning can be estimated in geographic space and can be used to predict distributions and range shifts (Kearney *et al.*, 2010b; Kearney *et al.*, 2012; Mangano *et al.,* 2019; Tan *et al*., 2021; Giacoletti *et al.*, 2021). In a terrestrial example, Kearney (2012) predicted seasonal and geographical variation in growth, maturation time and reproductive outputs of the North American lizard, *Sceloporus undulatus* and found that maturation time was mostly explained by climate, whilst reproduction was mostly explained by body size. In the marine environment, Sarà *et al.* (2013b) showed through DEB modelling that the subtidal areas of the Mediterranean Sea provide a suitable habitat for the non-indigenous species (NIS) *Brachiodontes pharaonic.* DEB modelling has also been used to model historic climate-driven shifts of *Magallana gigas* by investigating its reproductive niche with changes in food availability and sea surface temperature (Thomas *et al.*, 2016). The application of DEB theory for spatial modelling is, however, relatively limited in the literature (but see examples such as Thomas *et al.* (2011); Sarà *et al.* (2018); Thomas & Bacher (2018)). With the recognised importance of having robust models for predicting species distributions, DEB modelling could be applied on larger spatial scales to assess environmental changes on species physiology in both terrestrial and marine realms.

The DEB literature is extensive with examples of modelling across a wide range of taxa (Molnár *et al.*, 2011; Martin *et al.*, 2013; Arnall *et al.*, 2019; De Cubber *et al.*, 2020), however, parameters used for estimating the assimilation and utilisation of energy are typically fixed averaged values representing a whole population. Although fixed values allow for simplicity in DEB parameterisation and modelling, intraspecific variability within populations is not being represented (Boersch-Supan & Johnson, 2019; Koch & De Schamphelaere, 2020). Additionally, experimental variability in the determination of DEB parameter values is rarely captured. Inter-individual variation can have important ecological and evolutionary implications and play a key role in facilitating niche evolution (Bolnick *et al.*, 2011; Violle *et al.*, 2012; Des Roches *et al.*, 2018). Moreover, it is vital that CCC-induced changes in biological outputs are considered relative to the variability within the simulated cohort so that the magnitude of any changes can be put into context. Individual-based models (IBM) that explicitly model heterogeneity by assigning individual organisms their own unique set of DEB parameters can be used to simulate the physiological variability of biological functions, but have only been incorporated into a handful of DEB models to date (for example (Duarte *et al.*, 2010; Martin *et al.*, 2012; Martin *et al.*, 2013; Koch & De Schamphelaere, 2020; Arnould-Pétré *et al.*, 2021). This bottom-up approach can be used to estimate population-level effects as differences in vital physiological rates will reflect the contribution the individual makes towards maintaining the population (Martin *et al.*, 2013; Pethybridge *et al*., 2013; Johnston *et al.*, 2019).

Incorporating inter-individual variability into DEB modelling was demonstrated by Koch & De Schamphelaere (2020) on the copepod *Nitocra spinipes*. Two influential DEB parameters were simulated from a log-normal distribution, namely maximum surface area specific assimilation rate and the maturity thresholds, which then allowed them to reproduce the variability observed in experimentally derived physiological data. Martin *et al.* (2013) varied the DEB parameter maximum specific ingestion rate for the water flea *Daphnia magna* from a log-normal distribution and found their model successfully predicted population growth rates. Duarte *et al.* (2010) calibrated a DEB-IBM to simulate mussel growth over time by randomly assigning 20 varying parameter values to each individual from ranges in the literature. The model reasonably predicted observed growth of harvested mussels. Introducing inter-individual variability makes for a more biologically realistic model and furthers the application of DEB-based modelling (Bolnick *et al.*, 2011; Boersch-Supan & Johnson, 2019).

Bivalves are a model organism for applying DEB theory as they conform to the assumption that organisms are isomorphic (i.e. their shape stays the same as they grow) and, subsequently, DEB models have been parameterised for a range of native and non-indigenous marine and freshwater bivalves (Saraiva *et al.*, 2011; Lavaud *et al*., 2017; Sarà *et al.*, 2018; Haberle *et al.*, 2020). Several studies have used the DEB to examine life-history traits of the Pacific oyster *Magallana gigas*, however, these studies use fixed parameter values for their models, most of which originate from three key papers (Pouvreau *et al.*, 2006; van der Veer *et al.*, 2006; Bernard *et al.*, 2011). Previous publications on *M. gigas* (Thomas *et al.*, 2016; Thomas & Bacher, 2018; Palmer *et al.*, 2021) have explored the variation in growth and reproduction through varying external drivers, i.e. temperature and food, but have kept DEB model parameters fixed. For example, Thomas & Bacher (2018) investigated spatial patterns of population responses by modelling individual cohorts of *M. gigas* over 15 years with regional environmental parameters. Some authors have also performed sensitivity analysis of DEB model outputs by changing parameter values in systematic ways (Bacher & Gangnery, 2006; Duarte *et al.*, 2012).

This present study is the first to comprehensively combine both inter-individual variability into parameter estimates and large-scale spatial patterns in environmental variables to predict the effects of CCC on NIS life-history traits. A DEB-IBM approach was developed to forecast changes in growth, maturity and reproduction of the non-indigenous Pacific oyster, *M. gigas*, around the northeast Atlantic, Mediterranean Sea and North Sea under two end-of-the-century CCC scenarios. Here, we used new experimental data from the field and mesocosm (Pack *et al.*, 2021), together with literature data to derive seven key DEB parameter means and standard deviations. These were then used to simulate unique parameter sets for individual oysters. In this way, it was possible to evaluate the changes caused by CCC relative to the variability within the simulated cohort and so put the magnitude of any changes into context. It is hypothesised that (1) the interaction of multiple environmental variables would alter present day spatial patterns in growth and reproduction with CCC in the study area, (2) *M. gigas* reproductive output would increase at higher latitudes in line with warming at the end of the century, (3) modelling with inter-individual variability would reflect real-world observations of life-history traits in populations, and (4) predictions from the DEB model are sensitive to small changes in parameters.

4.2 Methods

4.2.1 Dynamic energy budget model description

The standard DEB model equations are derived from Kooijman (2010) (Table 4.1, Figure 4.1). Food and body temperature are assumed to be central to the DEB theory as primary drivers of an organism's metabolism (Kooijman, 2010; Sarà *et al.*, 2013a). Assuming the structural volume V of the organism is proportional to the surface area, the energy available for physiological processes is determined by the energy assimilation rate P_A. The parameter P_A is calculated using the volume together with the maximum surface-area-specific assimilation rate P_{Am} (a function of ingestion rate), food density, immersion time (the time available for feeding in intertidal bivalves) and temperature at each time interval, for example each day (Table 4.1, Eq. 1). Food density is incorporated through a Hollings type II functional response. The scaled functional response, f, which varies between 0 and 1 (Table 4.1 Eq. 2), is a quantification of the amount of food available and the organism's capacity to ingest it.

The model assumes the energy assimilated from the ingestion of food is stored in a reserve E. From this reserve, a fixed fraction κ is used for somatic maintenance and structural growth. The remaining energy fraction $(1-\kappa)$ is used for maturation maintenance, reproduction and production of gametes in adults (Figure 4.1). Energy allocation to the gonad has been incorporated into the DEB model based on equations and parameters from Bernard *et al.* (2011). Somatic maintenance is given priority over maturation and reproduction and, if energy utilisation is insufficient to cover maintenance costs, the organism fails to grow (van der Meer, 2006).

All physiological rates are dependent on body temperature. In the DEB model, the effect of temperature follows the Arrhenius relationship where physiological rates increase in an exponential relationship with temperature (Kearney *et al.*, 2010a). This enables the model to incorporate changes in metabolic rates in line with species tolerances (Table 4.1, Eq. 3) where, outside of upper and lower (T_H, T_L, respectively) boundaries, physiological rates drop rapidly.

To determine the state of the organism at a given time point, a set of differential equations are solved using the organism's DEB parameter set, its state at the previous time point and the current temperature and food concentration. The solution to each equation determines the energy in the reserves, E, the structural volume, V, energy level available for maturity and reproduction, E_R, and the energy content of the gametes, E_{Go}, respectively (Table 4.1, Eqs. 15-18) (Nisbet *et al.*, 2000). To fit the DEB model, R code was modified from Kearney & Porter (2020) (NicheMapR).

Table 4.1 Dynamic energy budget model equations used to model growth and reproduction of *Magallana gigas.*

	Description	**Equation**
(1)	Assimilation rate	$P_A = \{P_{Am}\} . f \, . \, V^{2/3} . T_{im}$
(2)	Functional response	$f = \dfrac{X}{X + X_K}$
(3)	Temperature effect	$C_T = exp\left\{\dfrac{T_A}{T_1} - \dfrac{T_A}{T}\right\} . \left(1 + exp\left\{\dfrac{T_{AL}}{T_1} - \dfrac{T_{AL}}{T_L}\right\} + exp\left\{\dfrac{T_{AH}}{T_H} - \dfrac{T_{AH}}{T_1}\right\}\right) . \left(1 + exp\left\{\dfrac{T_{AL}}{T} - \dfrac{T_{AL}}{T_L}\right\} + exp\left\{\dfrac{T_{AH}}{T_H} - \dfrac{T_{AH}}{T}\right\}\right)$
(4)	Reserve mobilization rate	$P_{C1} = \dfrac{E/V}{[E_G] + \kappa \, . \, E/V} \, . \, \dfrac{[E_G] \, . \, \{P_{Am}\} \, . \, V^{2/3}}{[E_m]} + [P_M] . V$
(5)	Structural growth rate	$P_G = \kappa \cdot \dot{p}_{C1} - \dot{p}_M$
(6)	Maturity maintenance rate	$P_J = \min(V, V_p) \, . [P_M] \, . \, \dfrac{1 - \kappa}{\kappa}$
(7)	Maturation and reproduction rate	$P_R = (1 - \kappa) \, . \, P_{C1} - P_J$
(8)	Gamete mobilization rate	$P_{C2} = \dfrac{\{P_{Am}\}}{[E_M] . V^{1/3}} + \dfrac{(1 - \kappa) . E \; \{P_{Am}\} \, . \, V^{2/3}}{[E_G] \, . \, V + \kappa . E}$
(9)	Emergency maintenance rate	$P_{M2} = \min \, (P_M \, . \, V - \kappa \, . \, P_{C1} \, , \; P_{C2})$
(10)	Gonad allocation rate	$P_{Go} = (P_{C2} - P_{M2})$
(11)	Lysis of structure rate	$P_{L1} = max \, (P_{M1} - (\kappa \, . \, P_{C1} + P_{M2} + P_{L2}), 0)$
(12)	Gamete resorption rate	$P_{L2} = max \left(\dfrac{P_{M1} - (\kappa \, . \, P_{C1} + P_{M2})}{Y_{Go}}, 0\right)$
(13)	Dry meat weight	$DMW = V . d_v + \dfrac{E_{Go} \, . \, d_{Go}}{[E_{Ggo}]}$
(15)	Reserves	$\dfrac{dE}{dt} = (P_A - P_{c1}) . C_T$
(16)	Structural volume	$\dfrac{dV}{dt} = \left(\dfrac{P_G - P_{L1}}{[E_G]}\right) . C_T$
(17)	Development/reproduction	$\dfrac{dE_R}{dt} = (P_R - P_{c2}) . C_T$
(18)	Gametes	$\dfrac{dE_{GO}}{dt} = (P_{GO} - P_{L2}) . C_T$

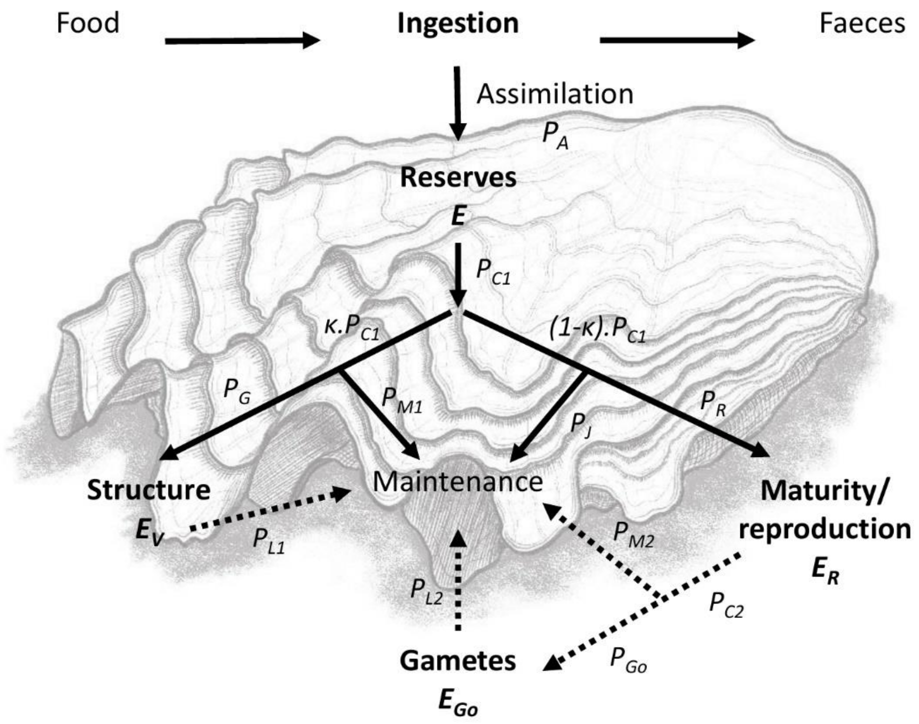

Figure 4.1 Dynamic Energy Budget theory diagram demonstrating the flow of energy in an oyster from ingesting food to growth and reproduction. Based on Bernard *et al.* (2011).

4.2.2 DEB parameters

4.2.2.1 Laboratory derived parameters

A key feature of this study is to introduce real-world variability into the DEB model. This allows changes in oyster physiology and life-history traits with CCC to be put into context and is preferred over fixed values when simulating a cohort of individuals. With regards to *M. gigas* inter-individual variability, three experimental variables were firstly determined from oysters from the River Yealm estuary in south Devon, UK (50.3098°N, 4.0537°W), namely the ingestion rate, the volume to length relationship and the dry mass to structure ratio. From these quantities it was then possible to estimate specific DEB parameters and their distributions for the purposes of the simulations.

4.2.2.2 Maximum surface-area-specific assimilation rate ($\boldsymbol{P_{Am}}$)

Maximum surface-area-specific assimilation rates P_{Am} were firstly derived from the maximum surface-area-specific ingestion rates J_{Xm}. These in turn were calculated for each acclimated Yealm oyster in the control treatment group from the mesocosm experiment in Chapter 3 using the formula from Sarà *et al.* (2013b):

$$Jxm = \frac{CR\ .\ POM\ .\ 18.81}{C_T\ .\ (f\ .\ V^{2/3})}$$

then converted into P_{Am} using

$$P_{Am} = Jxm\ .ae$$

where CR is the clearance rate of water (L/day), POM is the concentration of particulate organic matter (mg/L of *Isochrysis galbana*), C_T is the Arrhenius temperature effect (Table 4.1, Eq. 3), f is the functional response (Table 4.1, Eq. 2) and ae is the assimilation efficiency. The value of 18.81 (mg/J) was used to convert the ingestion rate of cells into energy (joules) based on the calorific content of algae fed to the oysters, *Isochrysis galbana* (Reed Mariculture Inc, 2019) and the conversion of calories into joules assuming 1 calorie = 4.18 joules (Lucas & Beninger, 1985).

The calculated P_{Am} values for oysters in the Yealm estuary reasonably followed a log-normal distribution (Figure 4.2). The mean and standard deviation were estimated and values were randomly sampled from the corresponding log-normal distribution for each individual oyster, similar to Koch & De Schamphelaere (2020). These simulated values could then be used to calculate *M. gigas* assimilation rate P_A in the DEB model (Table 4.1, Eq. 1). The functional response f used to calculate P_A depends on the food density X and the half saturation coefficient X_k (the food concentration at half the maximum ingestion rate). X_k changes with food quality and quantity and was estimated to reflect its linear relationship with food concentration reported in Alunno-Bruscia *et al.* (2011) for each location in the study area.

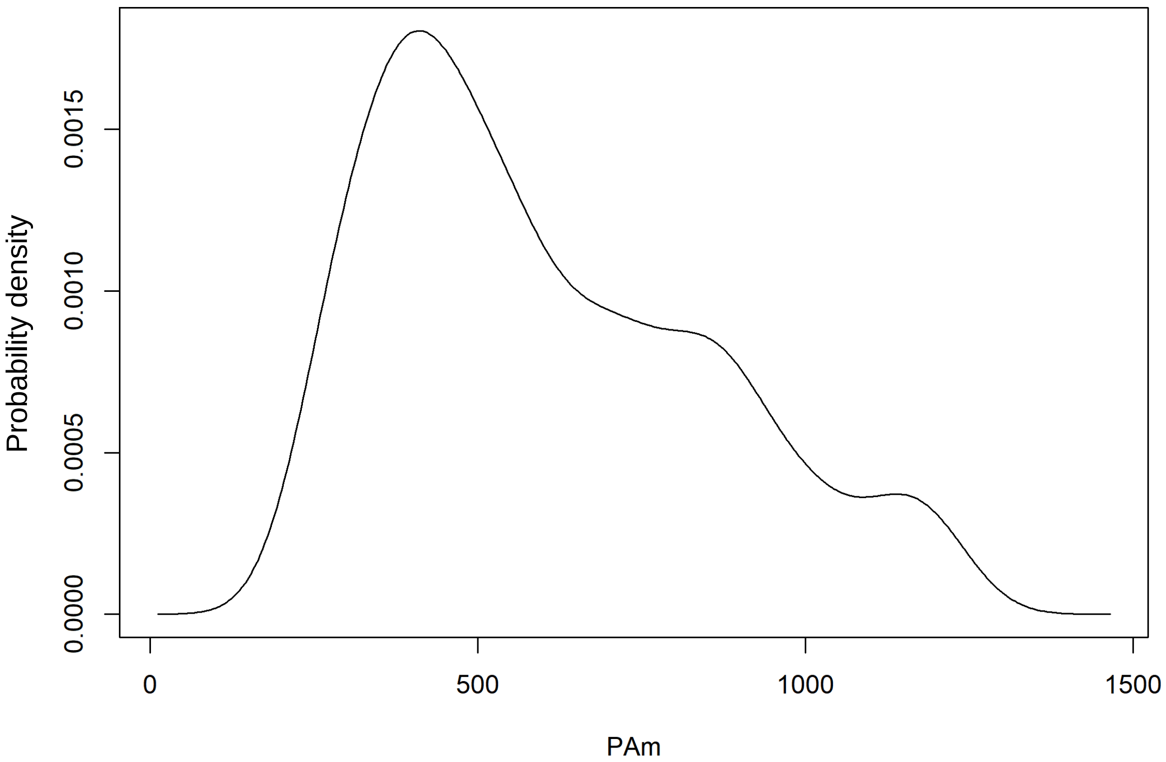

Figure 4.2 The probability density of maximum surface-area-specific assimilation rate (P_{Am}) values calculated from clearance rates of *Magallana gigas* from the Yealm estuary.

4.2.2.3 Volume to length relationship

The standard DEB model assumes that the organism is isomorphic during its life cycle and thus does not change shape during growth (Kooijman, 2010). In the DEB model, structural volume is estimated and converted to total shell length L using the shape parameter δ_M where

$$L = \frac{1}{\delta_M} . V^{\frac{1}{3}}$$

The shape parameter, δ_M, is typically a fixed parameter in the DEB literature, with the majority of studies using a value of 0.175 from van der Veer *et al.* (2006), based on a sample of 30 oysters from the Dutch Wadden Sea. In the present study a specific expression for the relationship between structural volume and length was derived for oysters in the Yealm estuary which is a variation on the above expression. Assuming the density of the wet meat weight (WMW) for benthic invertebrates is equal to 1 g cm^{-3} (Rosland *et al.*, 2009; Sarà *et* *al.*, 2013b), the WMW of oysters can be assumed equivalent to the structural volume V. In November 2019, 100 oysters were collected from the Yealm to coincide with the quiescent period/early gametogenesis stages of *M. gigas* (when gonad weight and therefore WMW is at its lowest point of its seasonal cycle). The lengths and WMWs were then measured. The relationship between length and WMW (i.e. V) from above was rearranged and expressed as the allometric function (Peters, 1983; Ren & Ross, 2001)

$$L = a.WMW^{b}$$

where L is the shell length of the oyster (cm) and WMW is the wet meat weight of the oyster (g). A linear regression between the log of length against log of wet meat weight was used to estimate a and b for oysters in the Yealm (Figure 4.3), with values of 2.75 and 0.42, respectively. The allometric function was then used to determine the length of *M. gigas* at each time point in the DEB model. The allometric function yielded a different numerical expression between length and volume compared to the standard DEB model expression. The parameter b (0.42) can be compared to the value of 1/3 and the value of a (2.75) can be compared to $1/\delta$ [1/ 0.175 = 5.71 in van der Veer *et al.* (2006)]. The Yealm-specific allometric model was more geographically relevant to the present study and so was preferred in the subsequent simulations.

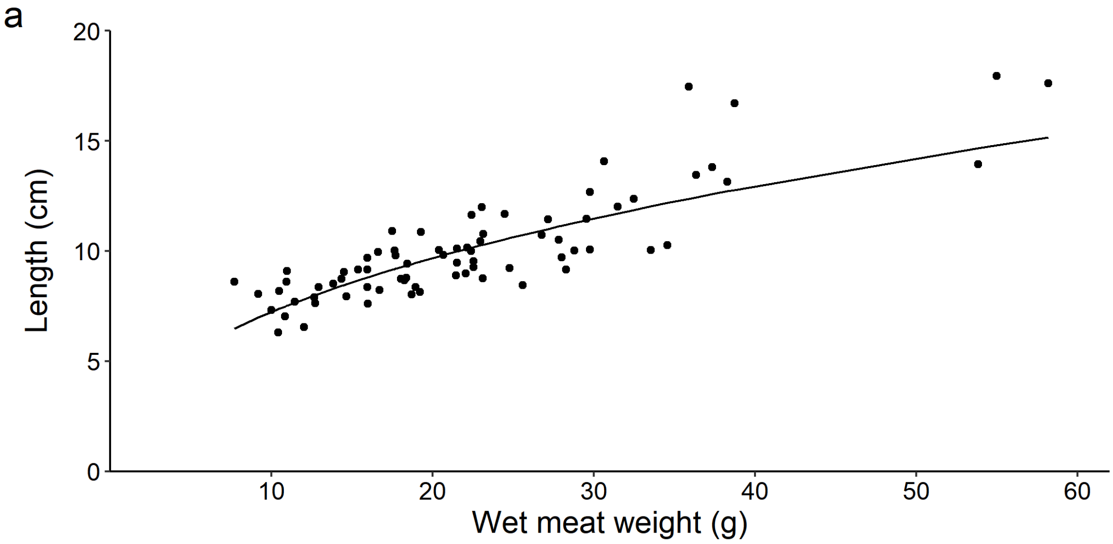

Figure 4.3 Length versus wet meat weight of *Magallana gigas* from the Yealm estuary (n=100) and the line showing the allometric model $L = 2.75\ .\ WMW^{0.42}$.

4.2.2.4 Dry mass ration of structure

The dry mass ratio of structure d_v is used in the DEB model to convert structural volume V, and equivalent WMW, to dry meat weight (DMW) (Table 4.1, Eq. 13). The meat of the 100 Yealm oysters were weighed after being dried for 3 days at 60°C. Similar to P_{Am}, individual variability was introduced for values for d_v by sampling from a log-normal distribution based on the corresponding mean and standard deviation.

4.2.2.5 Literature derived parameters

A literature search on *M. gigas* DEB applications revealed that the parameter values used are generally obtained from six studies, with the majority coming from three key papers (Table 4.2). Five of the reserve and structure parameters ($V_p, P_M, E_m, E_G, \kappa$) (Table 4.2) have been derived in two or more *M. gigas* studies. For each of these parameters, the mean and one standard deviation of the literature values were calculated. This approach is simplistic but given the lack of data in the literature this allows a further degree of variability to be built into the DEB simulations. Then, for each individual oyster simulated, the values were randomly sampled from the corresponding log-normal distributions (to assure non-negativity). For the remaining parameters, values are derived in only a single study in the literature therefore that value in the DEB model remained static.

Table 4.2 Parameter values used in the *Magallana gigas* DEB model and their sources. The sources of the parameters are labelled as (1) mean ± standard deviation of the raw data for parameters derived from field and laboratory data, (2) mean ± standard deviation of the literature derived data, and (3) static literature values from single literature values. Citations for literature derived parameters are provided (see bottom of table).

Description	**Parameter**	**Units**	**Value**	**Source**
Biological parameters				
Volume at maturity (cm^3)	V_p	cm^3	1.27 ± 0.25	(2) 1, 2, 3
Half saturation coefficient	X_k	µg chl-a L^{-1}	-	(2) 5
Immersion time	T_{im}	-	0.8	(3) 4
Reserve parameters				
Maximum surface-area-specific assimilation rate	P_{Am}	J cm^{-2} d^{-1}	632 ± 188	(1)
Volume-specific maintenance cost	P_M	J cm^{-3} d^{-1}	28.8 ± 13.4	(2) 2, 3, 4
Energy content of 1g of reserve	μe	J g^{-1}	19600	(3) 6
Maximum storage density	E_m	J cm^{-3}	4131 ± 1803	(2) 2, 3, 4
Assimilation efficiency	ae	-	0.75	(3)
Structure parameters				
Shape coefficient	δ_M	-	-	(1)
Dry mass ratio of structure	d_v	-	0.18 ± 0.02	(1)
Volume-specific cost of growth	E_G	J cm^{-3}	2900 ± 1000	(2) 2, 3, 4
Fraction of reserves allocated to maintenance and somatic growth	κ	-	0.55 ± 0.10	(2) 2, 3
Reproduction parameters				
Energy per egg	E_0	J	0.001	(3) 2
Egg diameter	L_0	cm	0.05	(3) 2
Dry mass ratio of gonad	d_{go}	-	0.31	(3) 6
Volume-specific cost of gonad	E_{Ggo}	J cm^{-3}	7500	(3) 4
Yield of gonad tissue for maintenance	Y_{Go}	-	0.25	(3) 6
Gonado-somatic index threshold for spawning	G_{SI}	%	35	(3) 1
Spawning temperature threshold	-	°C	18	(3) 1
Temperature effect				

Arrhenius temperature	T_A	K	5800	(3) [2]
Reference temperature	T_1	K	293	(3) [2]
Lower boundary tolerance range	T_L	K	281	(3) [2]
Upper boundary tolerance range	T_H	K	305	(3) [2]
Arrhenius temp. for lower boundary	T_{AL}	K	75000	(3) [2]
Arrhenius temp. for upper boundary	T_{AH}	K	30000	(3) [2]

[1] Pouvreau *et al.* (2006), [2] van der Veer *et al.* (2006), [3] Ren & Schiel (2008), [4] Bernard *et al.* (2011), [5] Alunno-Bruscia *et al*. (2011), [6] Deslous-Paoli & Héral (1988)

4.2.3 Environmental forcing and contemporary climate change scenarios

To investigate the effect of CCC on *M. gigas* life-history traits, temperature and food concentration in the DEB model were varied in line with present day values and end of the century projected values for two end-of-the-century CCC scenarios. End-of-the-century scenarios are based on two of the Representative Concentration Pathways (RCPs) in standard use by the Intergovernmental Panel on Climate Change (IPCC), RCP4.5 (stabilisation scenario) and RCP8.5 (‘business as usual’ scenario). Daily sea surface temperature (SST) data at 1° x 1° geospatial resolution were obtained from the Hadley Centre Global Environment Model – Earth System (HadGEM-ES) from phase five of the Coupled Model Intercomparison Project (CMIP5) (Met Office Hadley Centre, 2020) for the present day between 2010-2020, and projected CCC scenarios between 2090-2100 for the northeast Atlantic, Mediterranean Sea and North Sea coastlines.

Seasonal chlorophyll concentration (µg/L) was used as a proxy for food concentration in the DEB model. Three-monthly mean (seasonal) chlorophyll concentrations at 4km resolution were obtained from MODIS (NASA Goddard Space Flight Center, 2020) between 2010-2020 for the European coastline. The chlorophyll concentrations were aggregated using the mean concentration to obtain a 1° x 1° resolution. To estimate end-of-the-century chlorophyll concentrations, projected chlorophyll concentrations for RCP4.5 and RCP8.5 were extracted for 2090-2100 from the HadGEM-ES model and the three-monthly means calculated. A bias correction method was applied by calculating the percentage change between the present day observed MODIS and present day projected HADGEM-ES concentrations for each time point and 1° x 1° grid cell. This change factor was then used to scale the 2090-2100 HadGEM-ES projections.

4.2.4 DEB-IBM simulations

4.2.4.1 DEB outputs

Inter-individual variability was incorporated using a total of seven parameters ($V_p, P_{Am}, P_M, E_m, d_v, E_G, \kappa$) which were randomly sampled from their corresponding distributions, derived as above, and combined with the static parameters to create a unique set of parameters for each individual oyster. The DEB model differential equations were solved daily to determine the daily change in life-history traits of *M. gigas*. Length was determined using the allometric function as stated above. Time taken to reach maturity was determined as the number of days it took for the individual to reach volume at maturity, V_p. Spawning events were triggered by simultaneously exceeding two thresholds, a temperature threshold at 18°C and a gameto-somatic index (G_{SI}) threshold of 35% (Table 2), where G_{SI} is defined as the ratio between the gonadic mass and total DMW. The number of spawning events reported equates to the total number of times spawning was triggered during the 10-year simulation. To determine total fecundity, the energy in the gamete reserve was converted to the number of eggs per event using the amount of energy per egg, E_0, and the cumulative number of eggs over the 10-year simulation was calculated. The energy in the reproductive and gamete reserves was reduced to zero once spawning had occurred.

4.2.4.2 Model testing and validation

A fundamental test of validity was whether the model reproduced the length distribution of the 100 *M. gigas* collected from the Yealm estuary. Firstly, 1000 oysters were simulated under present day environmental conditions from the grid cell overlapping the estuary (50.5°N, 4.5°W). Secondly, kernel density distributions of the simulated and observed lengths were overlaid to assess the similarity. It is important to note that the oysters from the Yealm estuary were of varying ages, whereas lengths from simulated oysters were taken after ten years. This, however, still provided a reasonable validation of the relationship between observed and simulated outputs.

The DEB model was also validated by comparing shell length over time using independent field data from the literature on *M. gigas* length versus age. Cardoso *et al.* (2007) compared shell length to age (to the nearest year) of *M. gigas* through the analysis of the seasonal incorporation of manganese in the shells from three locations along the European coast.

These sites included Texel (Wadden Sea estuary, The Netherlands 51.5°N, 4.0°E) and Yerseke (Oosterschelde estuary, The Netherlands 53.1°N, 4.7°E) between 2002 – 2003 , and La Rochelle (France, 46.1°N, 1.2°W) between 2003 – 2004. Pogoda *et al.* (2011) measured the growth in average shell length of *M. gigas* over four months at different locations within the German Bight (North Sea 54.3°N, 7.8°W) in 2004. Using the DEB model, daily length of 1000 individuals was simulated using environmental data extracted from the corresponding 1° x 1° grid cells matching the years in which the literature studies were undertaken. The simulated length values were plotted over time to assess the fit of the model against the observed data at each location.

4.2.4.3 Contemporary climate change predictions

The DEB-IBM model was run on each grid cell around the coastline to simulate a cohort of 1000 oysters under present day and both RCP4.5 and RCP8.5 environmental conditions. For each individual oyster, the DEB model was run daily for a 10-year period starting in August, in line with seasonal spawning of in *M. gigas* in Europe (Antonio & Camacho, 2019). Final length, time to maturity, and total fecundity (cumulative number of eggs) for each individual oyster were output from the DEB simulations. For each grid cell the median of each DEB output was calculated for the present day and future by firstly filtering out individuals which did not reach sexual maturity, i.e. volume did not reach the maturity threshold V_p. The percentage change in medians between the present day and the two future scenarios was then calculated.

The median number of spawning events per grid cell for each scenario and the proportion (%) of individuals in each grid cell failing to reach maturity after ten years was calculated for the present day and future scenarios.

For plotting purposes, a threshold was placed on the percentage increases for time to maturity at the 90th percentile to allow for spatial patterns to be more clearly observed. Percentage change in log total fecundity was used due to the magnitudes and ranges of the numbers generated.

4.2.4.4 Parameter importance and sensitivity analysis

A Random Forest model was used to estimate the importance of the seven DEB parameters ($V_p, P_{Am}, P_M, E_m, d_v, E_G, \kappa$) in determining the life history traits: mean final length, time to maturation and total fecundity in *M. gigas*. For each trait, the percentage increase in the mean squared error (MSE) of the predictions was calculated between the original dataset of 1000 simulated oysters and the same dataset where the values one of the DEB parameters were randomly permuted across oysters. This was repeated for each DEB parameter and across all grid cells with the results averaged to produce a summary of the effect of each DEB parameter. Calculations were performed using the *R* package *randomForest* (Liaw & Wiener, 2002).

Sensitivity analysis was then performed to assess how the DEB outputs (mean final length, time to maturation and total fecundity) differ in response to perturbations in DEB parameters. For climates in the Yealm estuary grid cell, the mean of each of the seven simulated parameters was perturbed univariately by ±10% and the DEB model run for 1000 oysters for the present and worst-case scenario RCP 8.5. The sensitivity of the present day and future models was determined as the percentage change between the sensitivity models and the final models.

4.3 Results

4.3.1 Model validation

DEB simulations parameterised with *M. gigas* physiological data from the Yealm estuary and forced with present day temperature and chlorophyll conditions reproduced the length distribution of *M. gigas* from the Yealm estuary (Figure 4.4).

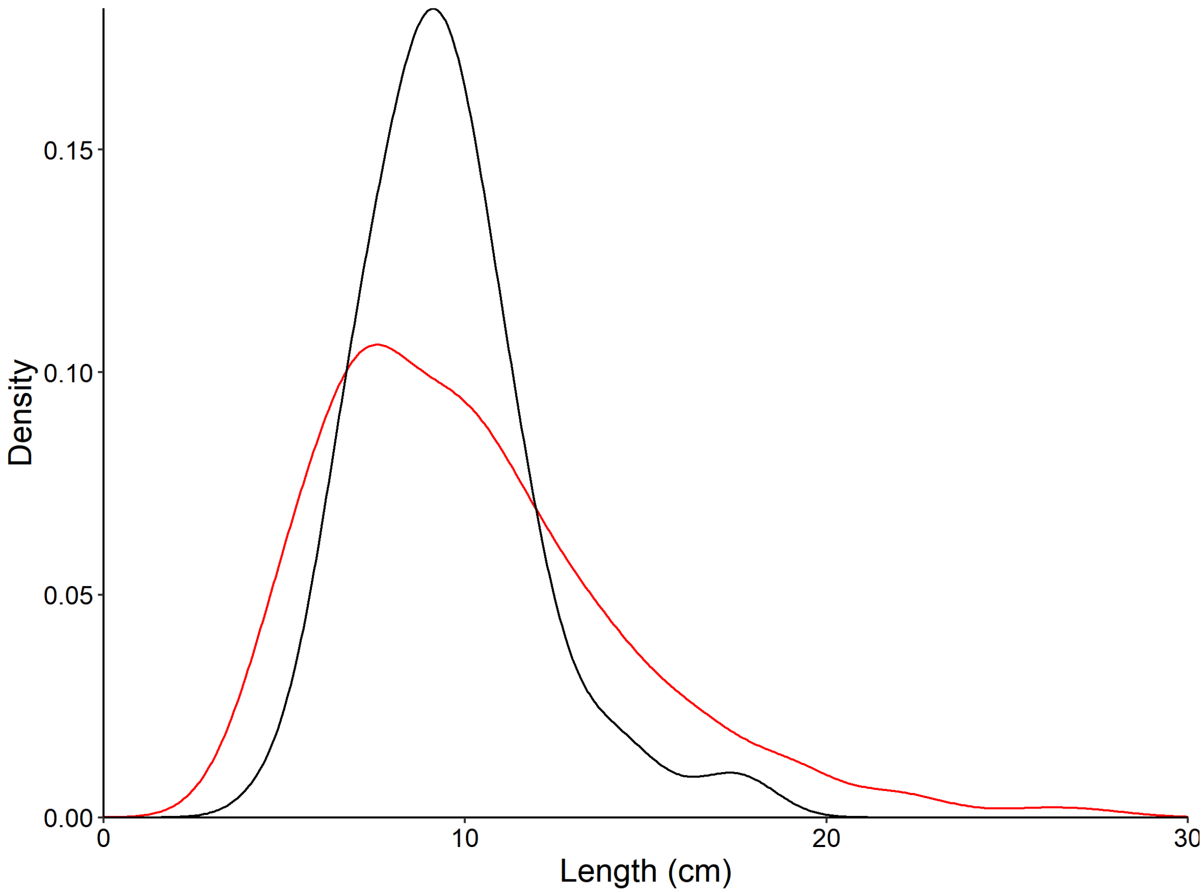

Figure 4.4 A comparison of observed length (black) and simulated length (red) of *Magallana gigas* for the Yealm estuary.

The simulated growth of *M. gigas* over time showed agreement with the independent literature field observations (Figure 4.5). The model had a tendency to over-predict growth at La Rochelle and to slightly over-predict lengths during the first two years at Texel and Yerseke (Figure 4.5a, b). The model produced a good fit with the early years of growth of *M. gigas* at the German Bight (Figure 4.5d), albeit with very little observed data. The inter-individual variability in the simulated cohort (as represented by the 2.5% and 97.5% percentiles) adequately covered the range in lengths in the observed datasets.

Given the many sources of variation contributing to the DEB simulated data (e.g. the DEB model itself, parameter estimation, fluctuating environmental data), plus the sources of variation in the observed data (e.g. access, sampling, local environmental conditions), the level of agreement between the model and the available observed data was high and supported the validity of the model.

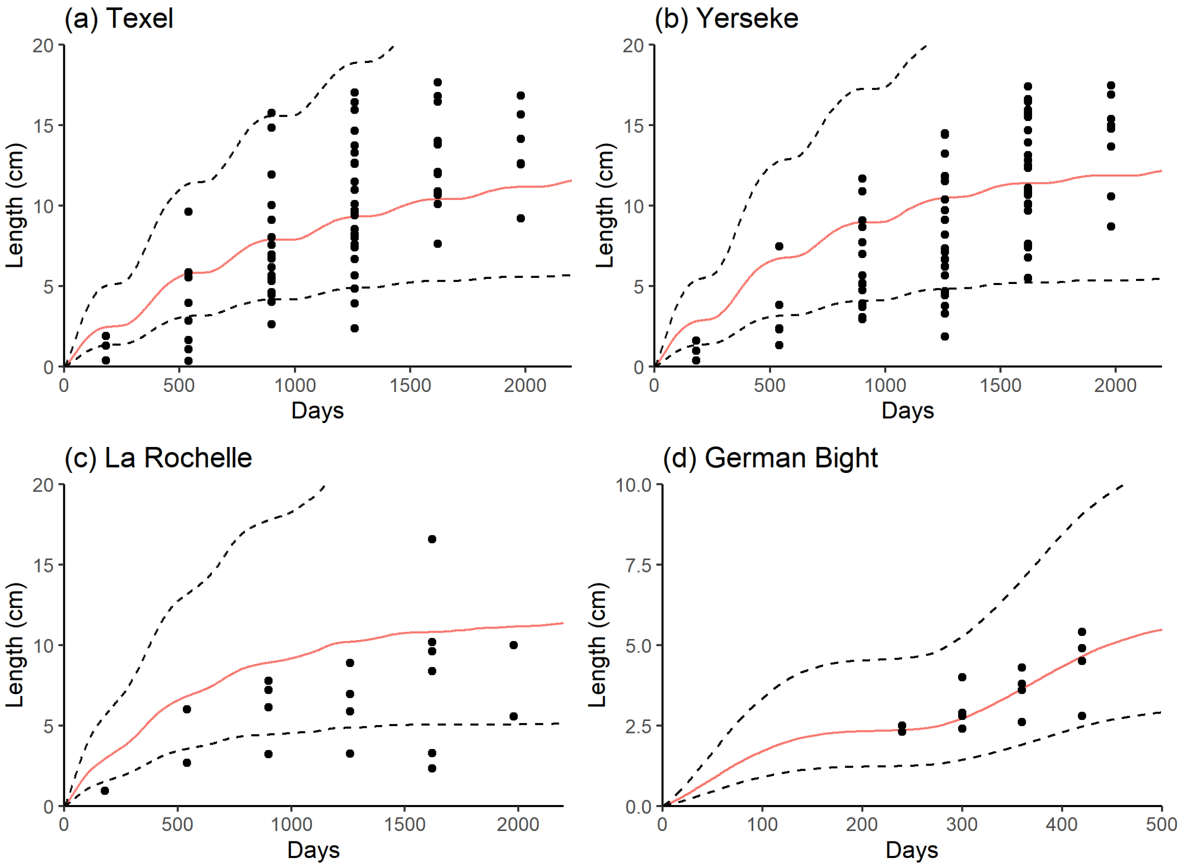

Figure 4.5 Validation of the DEB model comparing length versus age of *Magallana gigas* from the median simulated length (red line) and observed data (black dots). Observed data are from (a) Texel, (b) Yerseke, (c) La Rochelle from Cardoso *et al.* (2007), and (d) The German Bight from Pogoda *et al.* (2011). Observed data represent individual oyster (a-c) and mean oyster length (d). Dotted lines show the 2.5% and 97.5% percentiles of the simulated individuals.

4.3.2 Contemporary climate change effect

Over the study area, SST is predicted to increase by an average of 1.5°C and 3.2°C between the present day and RCP4.5 and RCP8.5, respectively (Figure 4.6a). Warming was more extreme at every location under RCP8.5 with SST predicted to increase by up to 4°C in the Mediterranean Sea and southern North Sea and between 1.5 – 3°C at higher latitudes such as the north coast of Scotland and Norway (Figure 4.6b, c).

Chlorophyll concentrations exhibited a seasonal pattern with maximum values coinciding with spring months where temperatures were cooler. Mean chlorophyll concentrations were similar across present day and future scenarios (2.43, 2.86 and 2.35 µg/L for the present, RCP4.5 and 8.5 respectively), however, future scenarios had more inter-annual variability compared to the present day (Figure 4.6d). Compared to the present day, chlorophyll concentrations are predicted to increase along Mediterranean Sea coastline, northwest France and southwest UK coastlines in both future scenarios and decrease along coastlines in the North Sea (Figure 4.6e, f).

4.3.2.1 Overall impact of environmental changes on life-history traits

In the present day, *M. gigas* were predicted to be larger in lower SST regions with longest oysters coinciding with the highest chlorophyll concentrations (Figure 4.7). Under the two future scenarios, the largest *M. gigas* were predicted to occur across the range of temperatures in the study area where chlorophyll concentrations were higher, suggesting chlorophyll was a key factor limiting length.

M. gigas matured more slowly under high SST and low chlorophyll present day conditions (Figure 4.7). Predictions under the RCP4.5 scenarios showed a similar result to the present day, however, warmer conditions under RCP8.5 led to longer maturation times throughout the temperature range of the study area where chlorophyll concentrations were limiting. Across both present day and future scenarios, the proportion of *M. gigas* not reaching maturation was highest in the high STT and low chlorophyll concentration regions (Figure 4.7).

Present day predictions for total fecundity showed little trend with SST and chlorophyll concentrations with no eggs being produced over the 10-years in the coldest and warmest temperature regions (Figure 7). At the end of the century a larger number of eggs were predicted with higher chlorophyll concentrations, particularly at cooler temperatures. The largest number of spawning events coincided with the largest numbers of eggs where chlorophyll concentrations were highest (Figure 4.7).

Overall, these results suggest that chlorophyll concentration was the main limiting factor in determining growth and maturity over the 10-year simulations in both the present day and future scenarios. Reproduction was limited by the temperature threshold for spawning in cold regions but was likely limited by chlorophyll concentrations when temperatures exceeded this threshold.

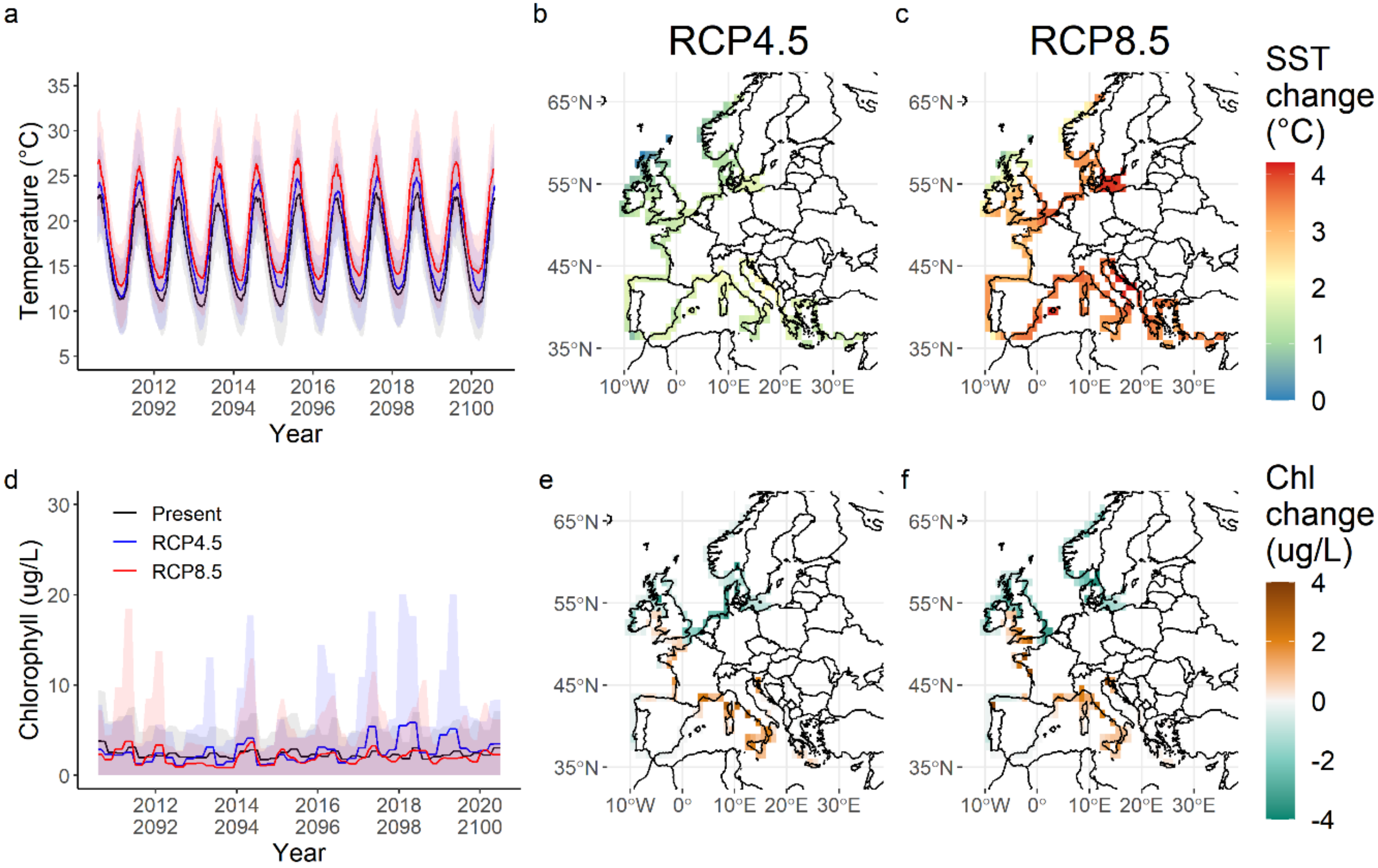

Figure 4.6 Time series and maps of the environmental forcing variables. Time series of mean daily SST (a) and mean seasonal chlorophyll concentrations (d) averaged across the study area for the present day (2010-2020) and end of the century RCP4.5 and RCP8.5 (2090-2100). The change in mean temperature (b, c) and mean chlorophyll concentrations (e, f) between the present day and future scenarios for each grid cell.

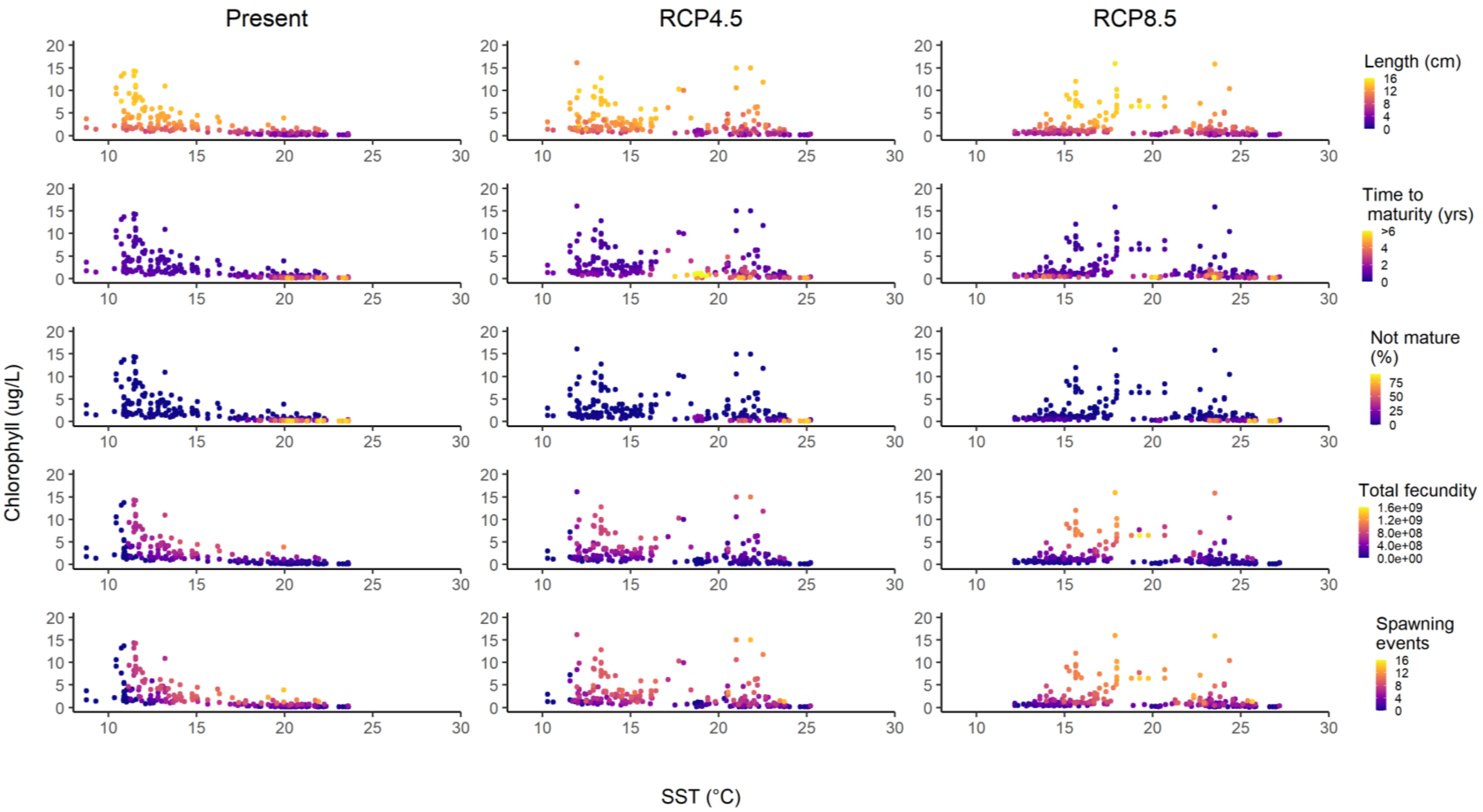

Figure 4.7 The relationships between chlorophyll concentration and SST and their effect on each of the DEB outputs for *Magallana gigas* under the present day, RCP4.5 and RCP8.5 scenarios. Each point corresponds to the mean chlorophyll concentration and SST for each grid cell in the study area and is the median DEB output of 1000 oysters at the end of a 10-year simulation. The median DEB outputs (aside from the proportion not reaching maturity) are based on individuals that reached the maturity threshold V_p.

4.3.3 Spatial variation in life-history traits

In both future scenarios, northern latitudes and the coast of Spain will see smaller oysters relative to the present day with a decrease of up to 50% in length (Figure 4.8). These regions are expected to experience an increase in SST but no increase in chlorophyll concentrations (Figure 4.6). In the southwest of the UK and northwest coast of France *M. gigas* are expected to increase in length by between 10-25%. The largest increases are expected in the northern Mediterranean Sea with oysters expected to more than double in length. It is important to note that at present in the Mediterranean Sea sizes of simulated oysters were estimated to be relatively small compared to other regions (Figure 4.8a). These increases in size tended to coincide with areas where chlorophyll concentrations are predicted to increase by the end of the century (Figure 4.6). Generally, percentage changes were more pronounced under the RCP8.5 scenario.

M. gigas matured at an earlier age in the northern Mediterranean Sea in both future scenarios, decreasing from around 2 years at present to around 1 year. Longer maturation times were predicted along much of the coast of Spain, the UK and Ireland and Norway, increasing from less than one year at present to around 1-2 (Figure 4.9a, b). The Mediterranean Sea had the highest proportions of *M. gigas* not reaching maturity in the present day with up to 80% of simulated oysters not reaching maturity over the 10-year period (Figure 4.9d). The proportion of oysters not reaching maturity decreased in both future scenarios in the north and east of the Mediterranean, with individuals also maturing faster toward the end of the century (Figures 4.9e, f). These areas coincide with end-of-the-century percentage increases in length, suggesting more favourable conditions for growth.

Areas that predict an increase in total fecundity at the end of the century coincided with locations where the number of spawning events increased (Figure 4.10). Log total fecundity showed the largest percentage increases in areas where oysters were predicted to decrease in size, such as along the coast of Norway, Sweden and Denmark (Figure 4.10b, c). These are areas where the spawning threshold of 18°C was frequently exceeded during the summer months under the future scenarios leading to between 1-5 spawning events over the 10-year period. In the northern Mediterranean Sea an increase in fecundity and spawning events are predicted for the end of the century (Figure 4.10). Under RCP8.5, several regions are predicted to experience multiple spawning events per year, for example approximately 13-15 spawning events occurred over the 10-year simulation along the southwest coast of the UK and northwest coast of France.

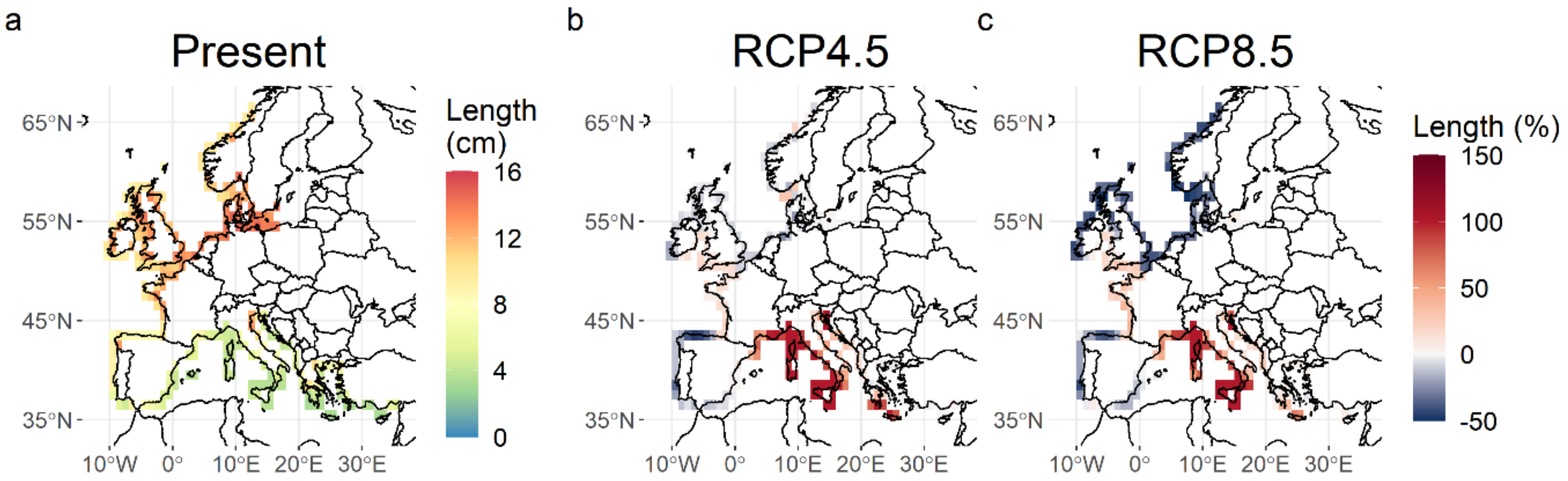

Figure 4.8 Present day length (a) and the percentage change in the mean final length of *Magallana gigas* between the present day and RCP4.5 (b), and RCP8.5 (c). Results are based on the median final length and mean DMW at the end of a 10-year DEB simulation.

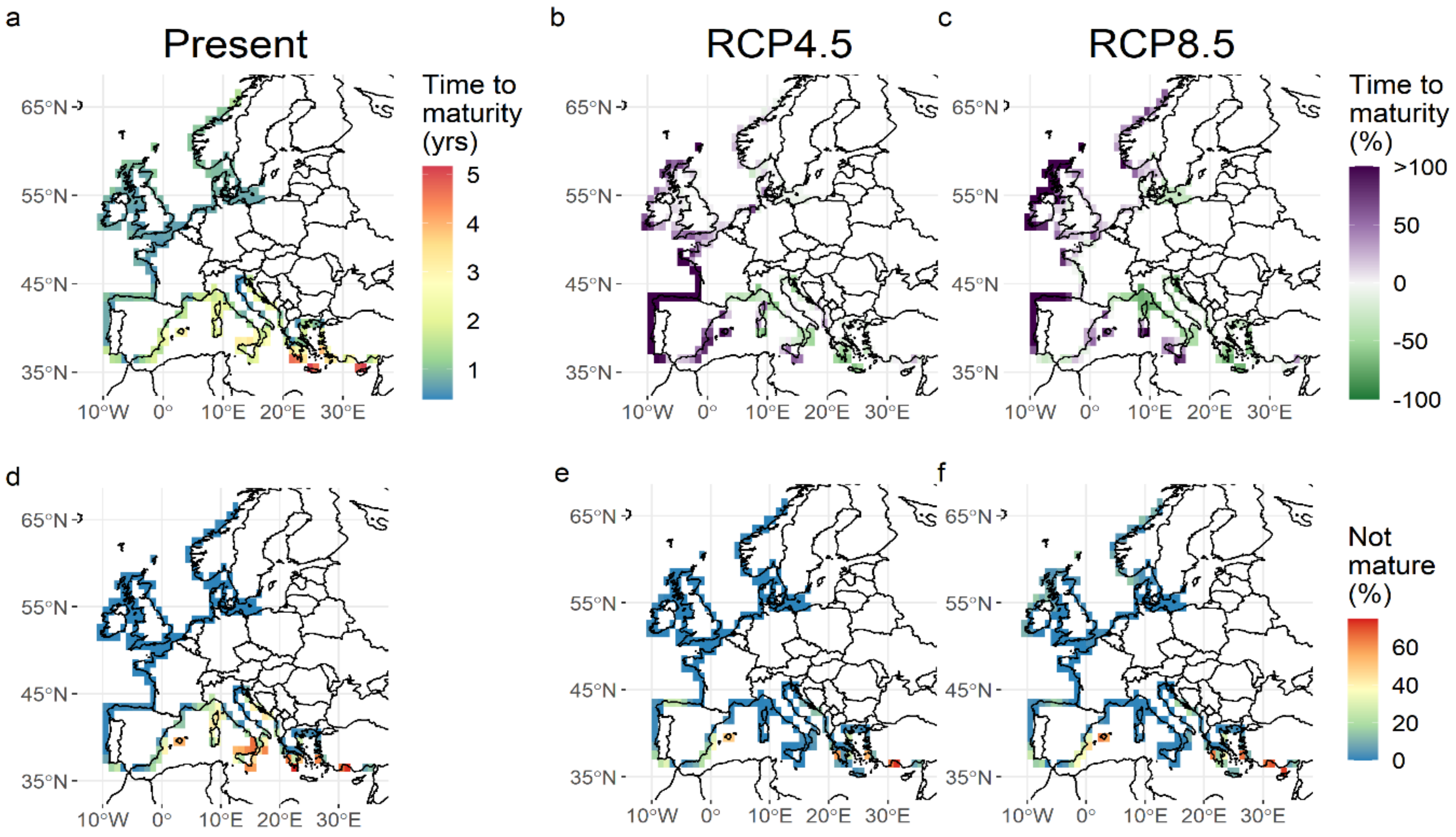

Figure 4.9 Present day maturation time (a) and the percentage change in the time to maturity of *Magallana gigas* between the present day and RCP4.5 (b), and RCP8.5 (c). The proportion of *M. gigas* which did not reach sexual maturity (d-f) under each scenario. Results are based on the median time at which oysters reached volume at maturity V_P, and the proportion in each grid cell that did not reach V_P by the end of a 10-year DEB simulation.

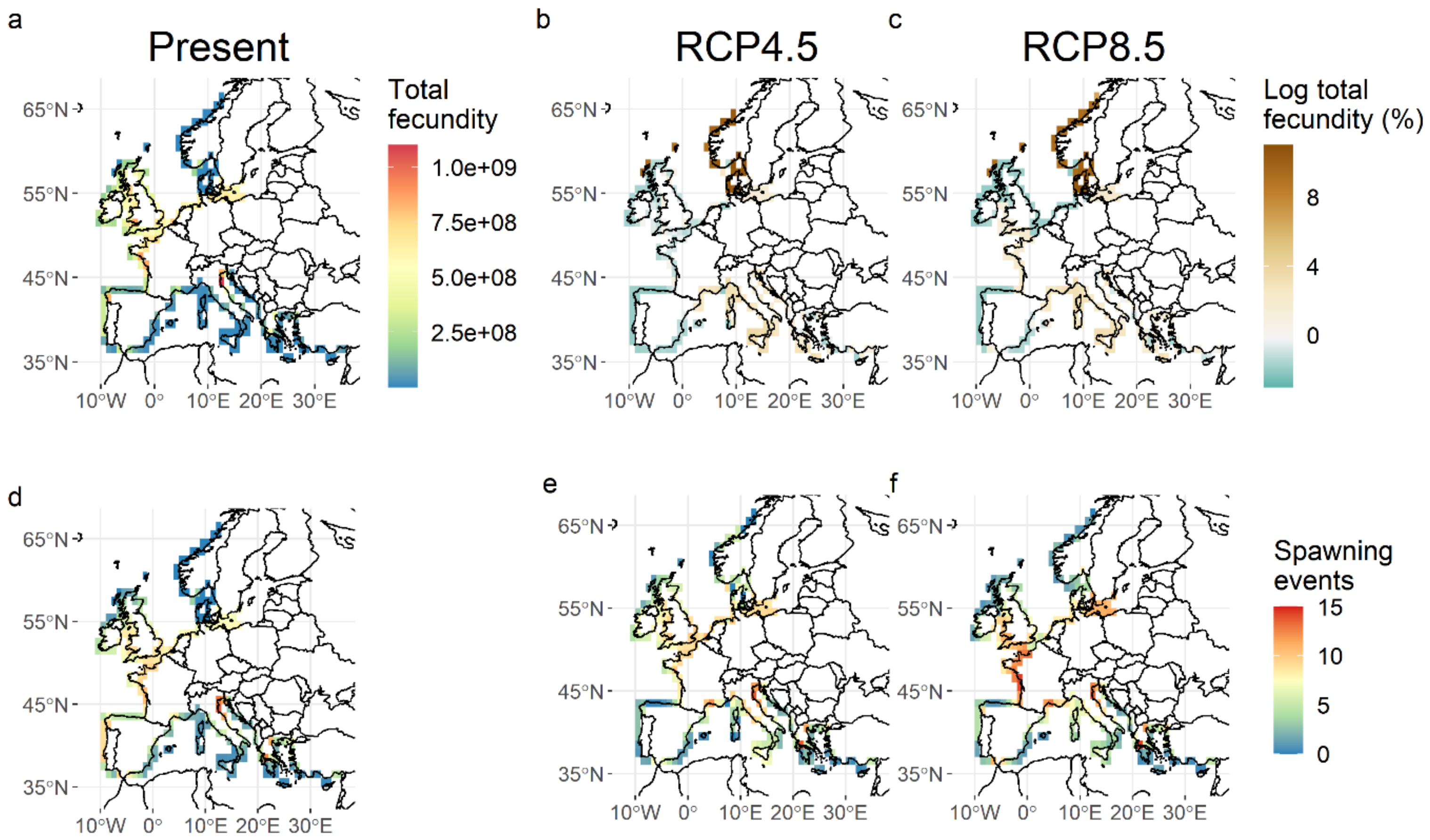

Figure 4.10 Present day total fecundity (a) and the percentage change in total fecundity of *Magallana gigas* between the present day and RCP4.5 (b), and RCP8.5 (c). The total number of spawning events over 10 years under each scenario (d-f). Results are based on the median cumulative fecundity and median number of spawning events at the end of a 10-year DEB simulation.

4.3.3.1 Variability across individuals

Although the models predicted a decrease in median oyster length on the north coastlines of Europe, the UK, and the west coast of Scandinavia by the end of the century (Figure 4.8), the estimated variability across individuals shows that future changes may not be readily observed in the field in these locations (Figures 4.11, 4.12). Time to maturity was predicted to increase around Scandinavia under RCP8.5, however, this change is small relative to the variation across the simulated cohort (Figure 4.11). The decreases in length coincided with an increase in energy invested into reproductive effort, with more eggs being produced in total and more spawning events occurring across the majority of individuals (Figures 4.11, 4.12). In the southwest of the UK and France a shift in the number of spawning events is expected to occur, with a large proportion of individuals experiencing more than one spawning event per year under the RCP8.5 scenario but with fewer eggs released during each spawning event (Figure 4.12).

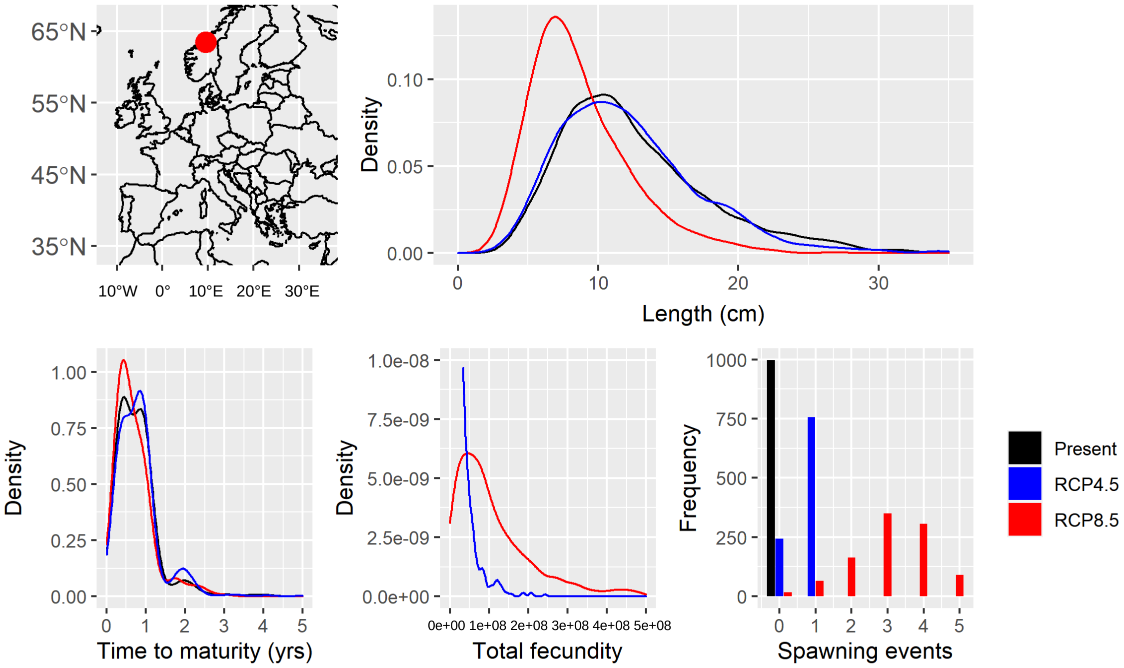

Figure 4.11 Variability in DEB outputs for 1000 simulated individuals of *Magallana gigas* at a representative location on the coast of Norway (63.5°N, 9.5°E). Density for length, time to maturity and total fecundity, and the frequency of the number of spawning events over a 10-year simulation are shown for the present day, and two end-of-the-century scenarios.

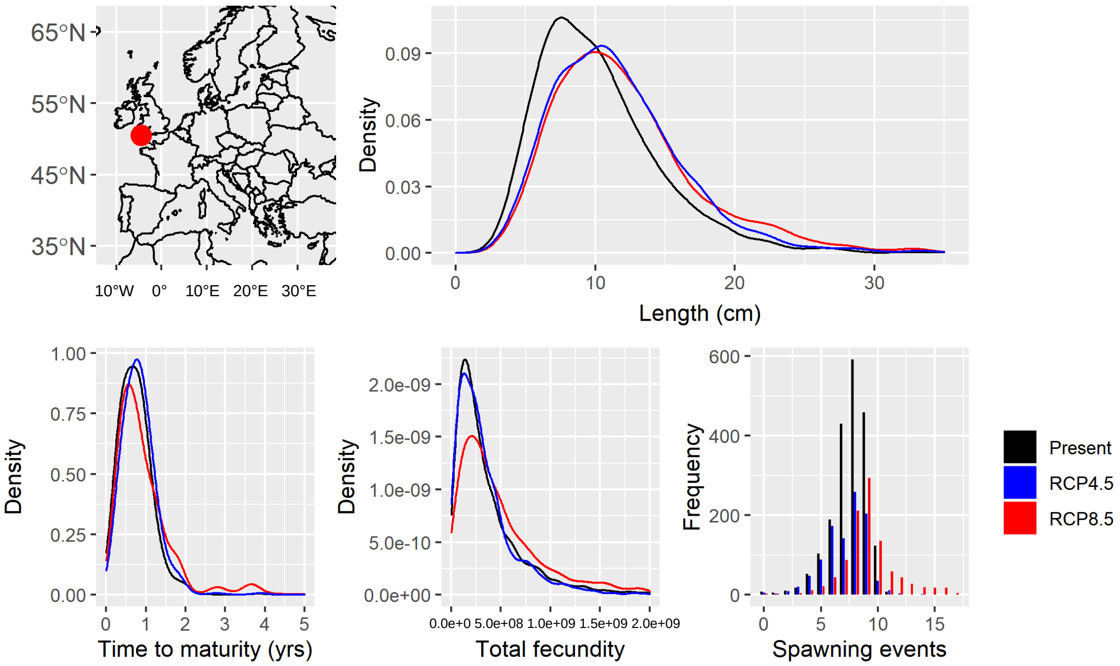

Figure 4.12 Variability in DEB outputs for 1000 simulated individuals of *Magallana gigas* at a representative location on the southwest of the UK (50.5°N, 4.5°W). Density for length, time to maturity and total fecundity, and the frequency of the number of spawning events over a 10-year simulation are shown for the present day, and two end-of-the-century scenarios.

In the Mediterranean, particularly the coasts of southern France, Italy and Sicily, length was predicted to increase by the year 2100 and, relative to the estimated variability across individuals, it is much more likely that changes will be observable in the field (Figure 4.13). This coincided with a decrease in maturation time across the simulated cohort and an increase in total fecundity. There was a substantial increase in the number of spawning events between present day and both end-of-the-century scenarios across most of the individuals (Figure 4.13). In present day scenario there was an apparent seasonal influence on time to maturity in the Mediterranean Sea, with peaks in *M. gigas* reaching maturity just before the summer months of years one, two and three.

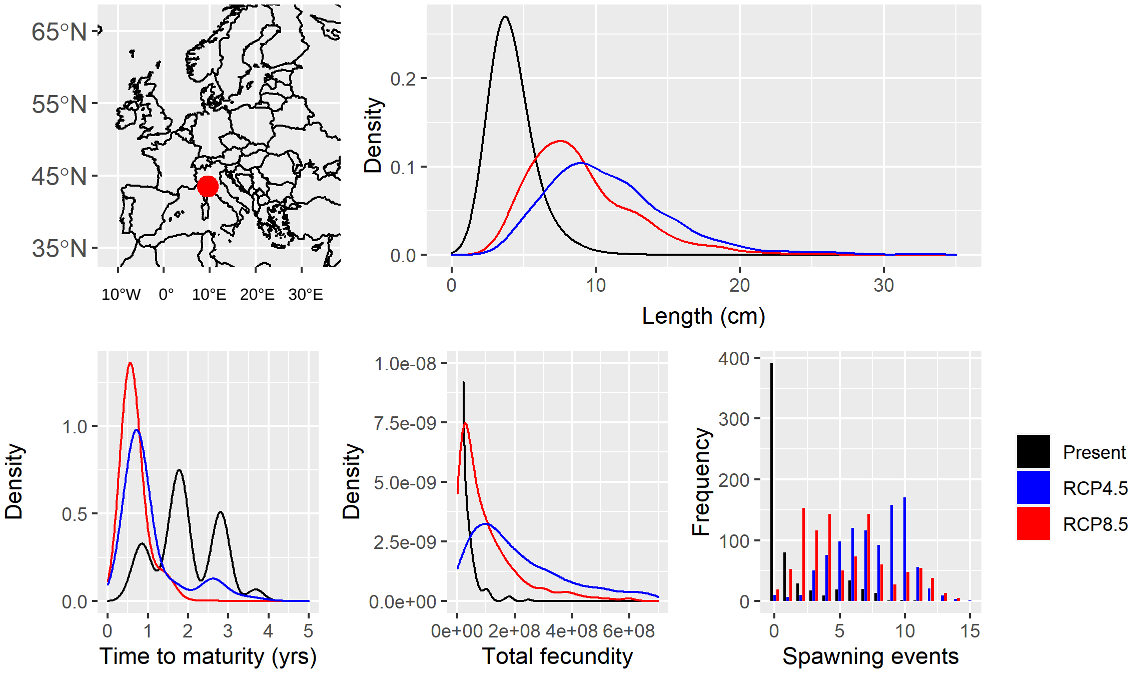

Figure 4.13 Variability in DEB outputs for 1000 simulated individuals of *Magallana gigas* at a representative location in the Mediterranean Sea (43.5°N, 9.5°E). Density for length, time to maturity and total fecundity, and the frequency of the number of spawning events over a 10-year simulation are shown for the present day, and two end-of-the-century scenarios.

The coast of Spain will likely experience a noticeable decrease in *M. gigas* lengths by the end of the century (Figure 4.14). The number of spawning events is expected to decrease across the simulated cohort and although spawning is still predicted to occur in most years, a much smaller proportion of *M. gigas* will be able to successfully spawn out. This may lead to a decrease in abundance of *M. gigas* in these areas with CCC. Smaller oyster lengths coincided with increases in time to maturity, with a large proportion of *M. gigas* not reaching maturity until after 5 years under the RCP4.5 scenario, and to a lesser extent under the RCP8.5 scenario.

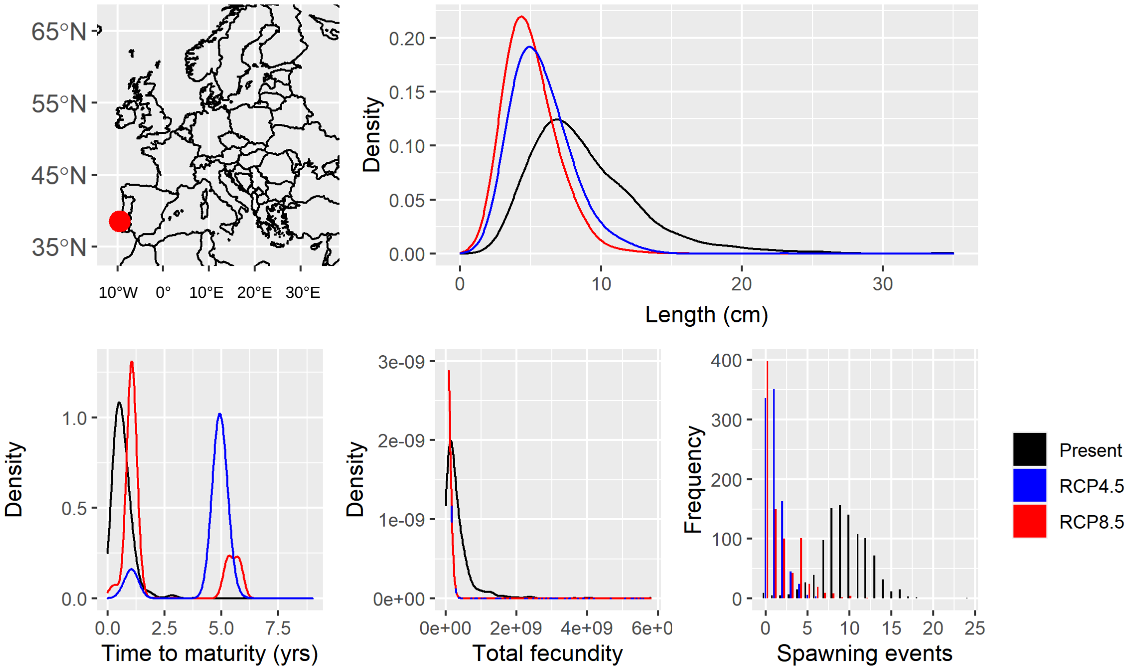

Figure 4.14 Variability in DEB outputs for 1000 simulated individuals of *Magallana gigas* at a representative location on the coast of Spain (38.5°N, 9.5°W). Density for length, time to maturity and total fecundity, and the frequency of the number of spawning events over a 10-year simulation are shown for the present day, and two end-of-the-century scenarios.

4.3.4 Parameter importance and model sensitivity

The assimilation rate of food, P_{Am}, was the most influential parameter in the model. Randomization of P_{Am} across oysters led to the largest percentage increase in MSE of between 20 – 25% across the life-history traits (Figure 4.15). Volume-specific maintenance cost, P_M, led to high percentage increases in MSE for length. Overall, random variation in dry mass ratio of structure, d_v, maximum storage density, E_m, and volume specific cost of growth, E_G, led to relatively small or no increases in MSE (Figure 4.15).

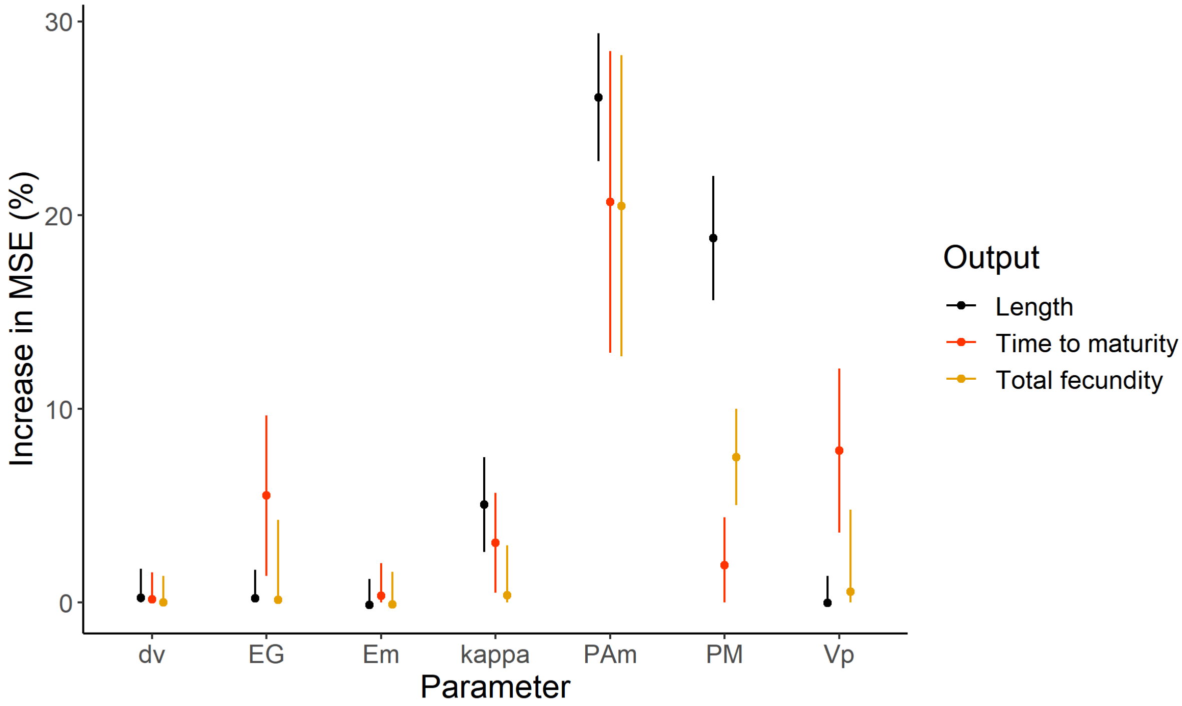

Figure 4.15 Decrease in model accuracy using random forest for seven DEB parameters on the median values of length, time to maturation and total fecundity of *Magallana gigas*. Decrease in accuracy was determined by the percentage increase in mean squared error (MSE) between the original and randomised models.

An overall ±10% shift in the mean of P_{Am}, κ and P_M led to the largest percentage changes in the DEB outputs both in the present day and RCP8.5 models (Figure 4.16). The largest changes were observed under a 10% increase in P_{Am} which increased total fecundity by up to 40%, and length to a lesser extent, whilst decreasing time to maturity by up to 20%. All model outputs were generally less sensitive to changes in V_p, d_v, E_m and E_G. Sensitivity results were similar for both the present and end-of-the-century models (Figure 4.16) and are in line with the parameters identified from parameter importance (Figure 4.15). This sensitivity analysis illustrated that small to moderate changes in key parameters can produce changes in model outputs which are large relative to the average changes predicted under CCC scenarios. This reinforces the value of the inter-individual simulation adopted in the present study.

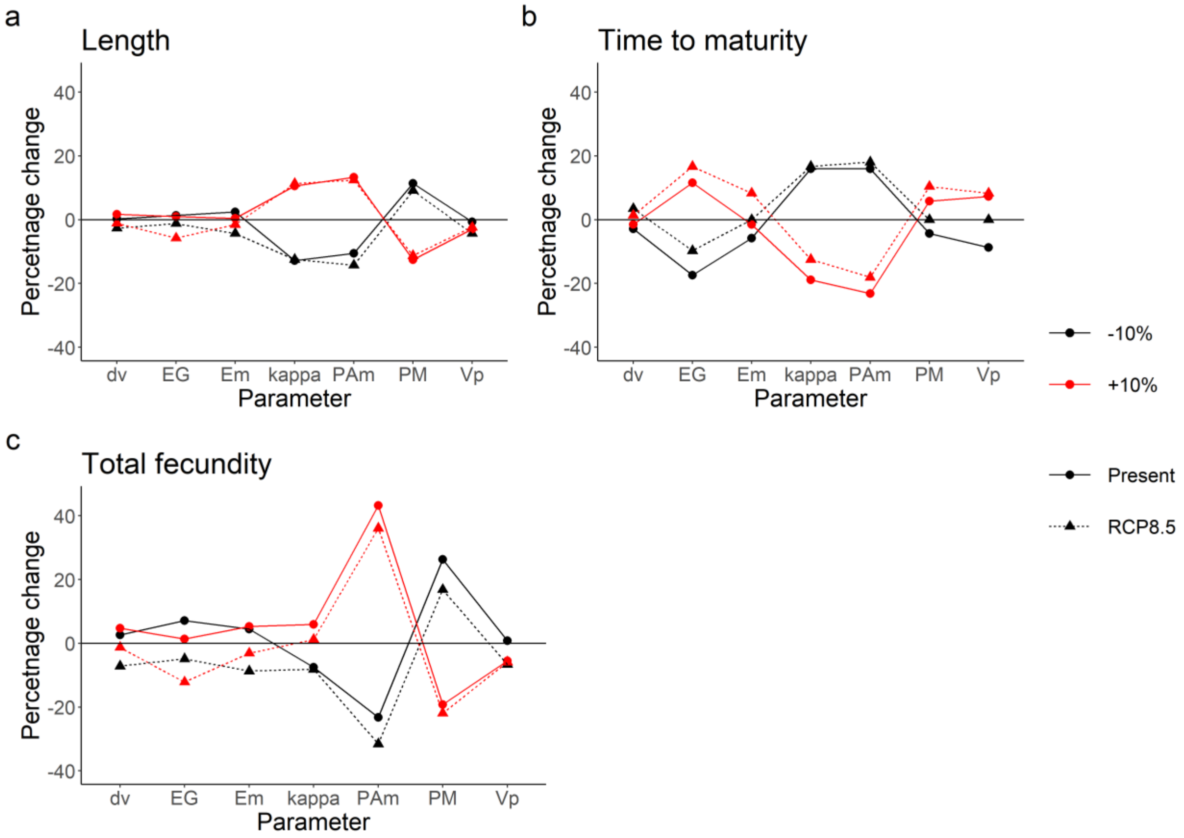

Figure 4.16 Percentage change in the median length (a), time to maturity (b) and total fecundity (c) of *Magallana gigas* over a 10-year DEB simulation after modifying each parameter by ±10% in the present day and RCP8.5 scenario. Results are based off environmental conditions at a representative location on the southwest of the UK (50.5°N, 4.5°W).

4.4 Discussion

Overall, patterns in growth, maturity, and reproduction of *M. gigas* across the northeast Atlantic, Mediterranean Sea and North Sea were predicted to vary spatially in response to the impact of CCC conditions on underlying physiological rates. Under CCC conditions, the DEB-IBM forecasted an increase in the number of spawning events and fecundity at high latitudes in line with increasing SST, implying that predicted warming could promote the spread of *M. gigas* poleward. Local chlorophyll concentration was identified as a key driver for determining the spatial patterns of life-history traits and, by the end of the century, increase in food availability enhanced the growth of *M. gigas* in regions such as the northern Mediterranean Sea, northwest France and southwest UK. Across the study area, the proportion of oysters reaching maturity was predicted to increase under CCC scenarios, and thus may indicate increased survival to adulthood in the future. In the first study to investigate the effects of both inter-individual variability and large-scale region-specific variability on *M. gigas* life-history traits, we found that the model provided a complex understanding of the responses of individuals relative to the predicted average changes across a cohort in life-history traits with CCC. In addition, the model produced robust estimates of real-world variability within observed *M. gigas* populations. Overall, this study significantly advances the understanding of how both internal and external variability involved in growth, maturity and reproduction interact.

Presently, localised populations of *M. gigas* are already established in Norwegian waters as far north as Nordmøre (63°N) due to anthropogenic introductions from aquaculture and/or shipping (Anglès d'Auriac *et al.*, 2017; Rueness *et al.*, 2019). The DEB model predicted that, whilst *M. gigas* are able to survive and grow at higher latitudes such as the north of the UK and Norway, reproduction is currently limited by lower temperatures. Under CCC conditions, this study agrees with previous work which predicted that future warming will provide more favourable conditions for spawning and settlement of *M. gigas* at their northern distribution limits, such as on the Skagerrak coast of Norway (Rinde *et al.*, 2017). Similarly, King *et al.* (2020) forecasted a poleward advancement of the proportion of years where settlement and spawning thresholds are exceeded along the European shelf at the end of the century. Mechanistic hindcast approaches have found that warming and increased food concentrations over the last 50 years have already led to a poleward expansion in geographical range of *M. gigas* due to a northward shift in the northern boundary of *M. gigas*' reproductive niche from 47° N to 60° N (Thomas *et al.*, 2016). The predicted increase in fecundity and spawning events at northern latitudes with CCC may therefore facilitate the poleward shift *M. gigas* distributions by the end of the century.

Chlorophyll concentration, and thus food availability, was the main factor influencing the growth, maturity and reproduction of *M. gigas* under present day and end-of-the-century conditions. This is in agreement with Thomas *et al.* (2011) and Thomas & Bacher (2018) who also found that spatial and temporal trends in other marine bivalve life-history traits were strongly linked to chlorophyll concentrations. Dutertre *et al.* (2010) also found that chlorophyll concentrations promoted feral *M. gigas* recruitment in Bourgneuf Bay, on the west coast of France. The present study found that although reproduction of *M. gigas* at high latitudes was limited by temperature, changes in structural growth were not strongly linked to temperature throughout the study area. *M. gigas* have been observed to grow under a broad range of temperatures, between 10 – 40°C (Mann, 1979; Rico-Villa *et al.*, 2009) and thus, the temperatures in the study area were unlikely to substantially limit growth. Identifying the effects of fine-scale environmental fluctuations on energy expenditure has applications in oyster aquaculture planning and management such as site selection by predicting time to reach commercial size (Sarà *et al.*, 2012; Cheng *et al.*, 2018). For example, DEB has been used to assess site suitability and total annual production of *M. gigas* in shallow lagoons around the east coast of Sardinia by modelling oyster growth rate under local environmental conditions (Graham *et al.*, 2020).

The results in this study were in agreement with recent smaller-scale DEB studies. Firstly, Bertolini *et al.* (2021) used a DEB model to predict present day *M. gigas* lengths on the eastern Italian coast of the Adriatic sea. They found a gradient in oyster lengths with smaller to larger oysters from the southern to the northern regions in the Adriatic Sea. The present results also found similar average oyster sizes and gradient in this region. This gradient along the coast was attributed to the southern region experiencing summer temperatures exceeding *M. gigas* critical temperature limit coupled with low chlorophyll concentrations. Secondly, Thomas & Bacher (2018) used the DEB model to predict the percentage change in *M. gigas* lengths between present day and end of the century CCC conditions along the northwest coast of France and southwest of the UK. They found that final lengths in this region increased by 7-15% by the year 2100, similar to percentage change predicted for this region in this study (10-20%). Comparable results between these smaller-scale DEB modelling studies provides a form of validation for the results of the present large-scale study. The simulation of 1000 individuals in the present study, however, provides a unique insight into the inter-individual changes in life-history traits under CCC conditions. Modelling inter-individual variability allowed the magnitude of these changes to be put into context of real-world changes. For example, the average length of oysters may increase on the southwest coast of the UK, however the spread of lengths across the simulated cohort implies that the likelihood of observing this change on the coast would likely be low. The simulations have also shown interesting features in oyster growth, such as the potential seasonal effects of environmental variables on time to maturity, however, further investigations would be required to determine effects of seasonality on growth.

The present model was calibrated in part using physiological measurements of oysters from the Yealm estuary. Whilst this has allowed for real-world input to the model, variation in physiology between separated populations around the northeast Atlantic and surrounding waters cannot be ruled out and may have led to a lack of fit of the simulated to observed data at La Rochelle. Sensitivity analysis in the present study highlighted that relatively small shifts in mean parameter values can have large impacts on the outputs from a DEB model and thus potential differences between separated populations requires more consideration. Parameterisation of a DEB model for New Zealand *M. gigas* by Ren & Schiel (2008) found considerably different parameter values compared to a DEB model for French oysters by van der Veer *et al.* (2006), highlighting the likelihood of intra-specific differences in physiology from differences in environmental conditions and genetics or variability of measuring DEB parameters under laboratory settings. Physiological variability has also been observed in *M. gigas* from different geographic areas, with French individuals having higher respiration rates than those from Japan, Taiwan and Spain (Goulletquer *et al.*, 1999). These intraspecific differences between populations can lead to phenotypic and trait variation which ultimately impacts fitness of the species and may have implication when investigating species responses to environmental change (Des Roches *et al.*, 2018; Ghaffari *et al.*, 2019). For example, Monaco *et al.* (2019) showed that using DEB parameters from native populations of *Mytilus galloprovincialis* led to the model overestimating the growth of introduced populations. Incorporating local adaptation into ENMs has been shown to affect forecasts of distributional changes under CCC, for example, predicting both expanded and restricted distributions than models only considering occurrences (Oney *et al.*, 2013; Valladares *et al.*, 2014; Lecocq *et al.*, 2019). Accounting for this variation is also important to consider when studying NIS as intraspecific variability can be positively correlated with establishment and success of NIS in novel environments (González-Suárez *et al.*, 2015). Combining mechanistic modelling with intraspecific variability across geographic scales requires significant effort in physiological laboratory experiments, however, this commitment will ultimately improve mechanistic understanding of the effects of environmental change on species functioning (Jung *et al.*, 2010) and more accurately predict future distributions on larger spatial scales.

As expected, given the formulation of the DEB model, parameter importance and sensitivity analysis showed that variation of maximum assimilation rate, P_{Am}, resulted in the largest changes in growth and reproduction in the DEB model. In addition, the sensitivity analysis illustrated that small-moderate changes in P_{Am}, and the other key parameters, can produce changes in model output that are large relative to the changes produced by CCC. This is an important finding in terms of putting the CCC predictions into context. Duarte *et al.* (2012) performed sensitivity analysis on a DEB model parameterised for mussels and found that the model was most sensitive to ±10% changes in P_{Am}, P_M, and κ. Similarly, Duarte *et al.* (2010) found that out of 20 simulated parameters, mussel growth was sensitive to ±10% changes in the carbon fraction in food items (a measure of food energy availability) and the allometric coefficient for feeding. The sensitivity of the DEB model to changes in these parameters justifies the simulation approach used in the present study to explore climate induced change relative to inter-individual variation. On a similar note, if local/separated populations of *M. gigas* vary in their average parameter estimates, this may have substantial effects on the predictions of life-history traits in the area using bioenergetic models. Evaluation of the magnitude and sensitivity of the predicted changes in relation to inter-individual variability therefore supports the value gained from the IBM approach used in this study and highlights that studies which use static values are likely to underestimate model uncertainty.

DEB is a useful and widely applicable tool for examining the changes in life-history traits with spatial and temporal environmental variability. However, it is still challenging to validate model outputs with independently observed data (Thomas & Bacher, 2018). Validation steps in the present study focused on the ability of the model to simulate and reproduce variability in length over time at four locations on the northern European coast. These locations were chosen due to the availability of species-specific growth data in the literature with which DEB outputs can be compared. Whilst an overall good fit was observed for *M. gigas* growth, there remains a limited understanding of whether the model can make robust predictions of growth throughout the entire study area, for example regions in Scandinavia and the Mediterranean Sea. Similarly, interannual data of other life-history traits such as fecundity and timing of spawning events are scarce. Future research should endeavour to gather such data on local scales to test mechanistic models (Alunno-Bruscia *et al.*, 2011; Thomas & Bacher, 2018), and doing so will greatly improve the validity of these models.

To incorporate inter-individual variability into the present DEB model, parameters were randomly sampled independently from log-normal distributions. This univariate approach assumed there are no correlations between the parameters in the model. Covariation between life history parameters cannot be ruled out (Sibly *et al.*, 2000; Klok *et al.*, 2007) and is an important aspect of modelling at a population level, however, few if any studies have measured the relationships between primary DEB parameters in individual organisms. Ideally, as described by Sibly *et al.* (2000), models which have unknown correlations between variables should use variables which are independent of each other. The DEB model contains many parameters, the majority of which are difficult or impossible to directly measure in the laboratory. Furthermore, estimating multiple parameters for individual organisms, necessary to determine a correlation structure, would be extremely challenging. Where relationships between parameters can be estimated in laboratory experiments these should be incorporated within DEB-IBMs, which could reduce the variability in the output in DEB-IBMs.

4.5 Conclusion

The present work builds upon the wealth of *M. gigas* DEB studies found in the literature (Pouvreau *et al*., 2006; Alunno-Bruscia *et al*., 2011; Bernard *et al*., 2011; Thomas *et al*., 2011; Thomas *et al.*, 2016) by being the first bioenergetic model to combine inter-individual variability and large-scale environmental variability to investigate species responses to CCC. Using a DEB-IBM approach, this study identified varying interactions between the life-history traits of *M. gigas* with end-of-the-century environmental conditions across the northeast Atlantic, Mediterranean Sea and North Sea. Food concentration is an important driving force in the DEB model and thus changes in chlorophyll concentrations predicted under CCC were largely responsible for the changes in spatial patterns in life-history traits in the study area. By the end of the century, it is predicted that *M. gigas* will shift its reproductive range to higher latitudes in line with projected warming and thus may ultimately shift its leading range edge poleward. Further, this study demonstrated that simulation approaches incorporating inter-individual variability can make robust predictions of species responses to environmental change at large spatial scales and provide estimates of the potential establishment and spread of non-indigenous species under CCC.

Chapter 5 Overview and synthesis

This thesis advances knowledge of the complex interactions determining the effects of contemporary climate change (CCC) on non-indigenous species (NIS) distributions. Additionally, it emphasises the importance of assessing how different experimental and modelling approaches can affect the results and overall conclusions of the studies. In this final chapter the main findings of the thesis are discussed and put into context of the wider literature. Studies reviewing the results of both correlative and mechanistic model on the same species are rare (Rougier *et al.*, 2015), therefore I provide a review of the two ecological niche modelling (ENM) techniques used in this thesis to model the effects of CCC on *Magallana gigas* spatial pattern. The results from this thesis and the implications for future research into species physiology and distributions are summarised throughout.

5.1 Main findings and implications

It is well known that physiological tolerances constrain the fundamental niches of species which in turn determine their geographical distribution (Hutchinson, 1957). In this thesis, quantifying niches in environmental and geographical space, and examining the long-term impacts of CCC on physiology and life-history traits has shown that *M. gigas* can tolerate CCC conditions and CCC will likely facilitate the poleward range expansion of *M. gigas* by the end of the century. Modelling of native and introduced niches in Chapter 2 showed *M. gigas* have rapidly shifted their niche in analog and non-analog climates since their introduction in the mid-1900s. Identification of niche shifts demonstrated the capability of *M. gigas* to thrive in novel environmental conditions as a result of anthropogenic introduction, a finding that is likely pivotal to the current success of this widespread NIS. Equally, niche shifts coupled with ENM forecasts provided an important insight into the potential for *M. gigas* to continue to survive and spread under CCC conditions predicted for the end of the century.

Investigations into long-term exposure of *M. gigas* to CCC conditions in Chapter 3 showed that adult oysters were tolerant to seasonal long-term warming and ocean acidification predicted for the end of the century which may increase their competitive dominance over native species in introduced communities. In addition, future temperature and pH conditions did not interact with reduced salinity which had a significant effect on physiology. Whilst tolerance to warming and ocean acidification may not affect *M. gigas* survival and spread under future conditions, Chapter 4 demonstrated that life-history traits were linked to chlorophyll concentrations (i.e. food availability) and low concentrations may limit growth and reproduction on *M. gigas.* Environmental variability led to predictions of complex spatial changes around the coastlines in the northeast Atlantic and Mediterranean Sea and North Sea under CCC. These changes included increased length and reproduction in the Mediterranean Sea, multiple spawning events per year along the northwest coast of France and southwest of the UK and decreases in length and reproductive outputs along the coast of Spain. The results of Chapters 2 and 4 both predicted a poleward expansion in *M. gigas* distributions by the year 2100 due to increased habitat suitability and reproductive potential at higher latitudes, respectively, under two CCC emission scenarios.

Aquaculture already acts as a significant pathway for the introduction of invasive species in the northeast Atlantic (Castro *et al.*, 2017). Currently, *M. gigas* are farmed in northern regions too cold for reproduction, such as along the coasts of Scotland and Norway. Thus, the establishment of wild oysters is uncommon at these higher latitudes with only a handful of oysters having been reported outside of aquaculture locations (Herbert *et al.*, 2012; Cook *et al.*, 2014). The successful aquaculture of *M. gigas* but limited spread from these locations is reflected in the mechanistic modelling in Chapter 4. These models showed that present day environmental conditions are suitable for growth but the temperature threshold for spawning is not exceeded, thus they do not reproduce and are unlikely to spread. The results presented in Chapters 2 and 4 are in agreement with previous studies suggesting warming will increase the spread of *M. gigas* to more northerly locations (Thomas *et al.*, 2016; Rinde *et al.*, 2017). It is therefore likely that CCC will promote the spread of *M. gigas* from these northerly sites of introduction. The extent of spread will depend on limitations of larval dispersal but as *M. gigas* have the capability to disperse large distances (approximately 50km), and larvae remain in the water column for long time periods times (2 – 4 weeks) (Brandt *et al.*, 2008; Wood *et al.*, 2021), it is likely that spread from sites of introduction will occur at higher latitudes by the year 2100 (King *et al.*, 2020). Aquaculture at higher latitudes may also be enhanced in the future as Chapter 2 predicted increases in habitat suitability, and warming is expected to facilitate faster growth rates to marketable sizes (Palmer *et al.*, 2021). As new sites become suitable for oyster farming, the socio-economic benefits of aquaculture and wild harvesting coupled with the concern for conservation of habitats will likely cause challenges for policy and management of NIS (Herbert *et al.*, 2016).

Shellfish are considered some of the most vulnerable organisms to ocean acidification and there are concerns that CCC may overall negatively impact shellfish rearing and harvesting globally (Clements & Chopin, 2017). Shellfish aquaculture is of significant economic importance to coastal aquaculture and fishing communities (Herbert *et al.*, 2016) with the global production of *M. gigas* being worth between $1.2 – $1.4 billion per year (Chapter 3). Although the clearance and oxygen consumption rates of adult *M. gigas* exhibited tolerance to ocean acidification (Chapter 3), other important biological functions could be affected by ocean acidification (Tan & Zheng, 2020). For example, a one month study by Gazeau *et al.* (2007) showed that net calcification in *M. gigas* can decrease under ocean acidification predicted for the end of the century (although it was acknowledged that long-term studies are needed to assess for potential acclimation and adaptation). Chapter 2 also found that CCC may decrease habitat suitability at the tropical range edge, and Chapter 4 showed that warming coupled with low chlorophyll concentrations under CCC conditions could limit *M. gigas* growth, maturity and reproduction. There is therefore a suggestion that aquaculture of *M. gigas* in some regions could be negatively impacted by CCC and lead to substantial economic loss in unfavourable areas.

The evidence of widespread occurrence and niche shifts in Chapter 2, plus the minimal effect of CCC conditions on physiology in Chapter 3 emphasises that *M. gigas* can tolerate a broad range of environmental conditions. This supports the growing consensus in the literature that NIS tend to be generalists and are more likely to tolerate or adapt to changes in climates than native species (Dukes & Mooney, 1999; Lenz *et al.*, 2011; Zerebecki & Sorte, 2011). Meta-analyses have shown that marine NIS which are widely established are more heat tolerant than other NIS which colonise but fail to establish and display similar tolerances to native species (Bates *et al.*, 2013). Similar to *M. gigas*, other highly successful widespread NIS such as the green shore crab *Carcinus maenas* (Tepolt & Somero, 2014), green mussel *Perna viridis* (McFarland *et al.*, 2015) and European carp *Cyprinus carpio* (Koehn, 2004) have all demonstrated a broad temperature tolerance, thus providing them a potential competitive advantage under warmer CCC conditions. Under stressful conditions, NIS have also shown less pronounced deviations from normal performance compared to native species (Lenz *et al.*, 2011), which may allow them to perform better and outcompete native species with CCC.

It is important to note that this thesis predominately focussed on adult individuals whereas changes in *M. gigas* distributions will equally depend on the fragility of early life-history stages to CCC conditions. As highlighted in Chapter 3, there are conflicting results in the literature with regards to the tolerance of early life-history stages of *M. gigas*. For example, Parker *et al.* (2010) found ocean acidification had a negative effect on fertilisation success, however this result was not observed in other studies which found neutral effects, even under extreme pH conditions predicted for the year 2300 (Kurihara *et al.*, 2007; Havenhand & Schlegel, 2009). Early evidence in the literature suggested that larval stages of invertebrates are less tolerant to environmental change than adults (Byrne, 2011; Byrne &

Przeslawski, 2013). However, most experiments are conducted on single life-history stages and it is important to understand the potential carry-over effects across generations (Ross *et al.*, 2016). Studies suggest that after long-term acclimation of adult individuals, offspring can be more resilient to ocean acidification and carry-over will potentially buffer the effects of CCC over multiple generations (Donelson *et al.*, 2011; Parker *et al.*, 2015; Ross *et al.*, 2016). Parental exposure of the Hong Kong oyster *Magallana honkongenesis* to ocean acidification showed enhanced growth and survival of larvae compared to non-exposed adults in estuarine conditions (Lim *et al.*, 2021). It could therefore be the case that the tolerance of *M. gigas* to warming and ocean acidification found in Chapter 3 has the potential to carry-over to other generations. Transgenerational studies remain uncommon in the literature, but a better understanding of the potential carry-over effects is vital and will significantly further knowledge of species responses to CCC.

5.2 Importance of modelling methodologies

In ecology, the interactions of environmental changes with species physiology and distributions have been widely studied. This thesis has advanced current understanding by incorporating novel methods into each chapter and highlighting areas where careful consideration is needed when interpreting results. Firstly, studying potential niche shifts in NIS is increasingly popular in the studies on invasive species. However, it was relatively unknown how different popular niche change frameworks can influence the results of niche dynamics between introduced and native niches. Chapter 2 addressed this by directly comparing the two-dimensional Centroid, overlap, unfilling and expansion framework and the multi-dimensional space *n*-dimensional hypervolume framework. Contrasting results showed evidence of niche shift only at higher dimensions. It was demonstrated that previous studies investigating niche changes using only the first two principal components of the environmental data space likely do not account for a sufficiently high percentage of the variability in the data to capture the key features and thus the results should be interpreted with caution.

Secondly, long-term multiple stressor experiments are rare in the literature, particularly on NIS. In Chapter 3, the 10-month multiple stressor experiment on adult *M. gigas* was presented, which is the longest reported mesocosm experiment on *M. gigas*. The results showed tolerance to warming and ocean acidification predicted for the end-of-the-century conditions. This experiment contrasted with the results of previous short-term experiments on adult *M. gigas* (Lannig *et al.*, 2010; Lemasson *et al.*, 2018). It is likely that short-term experiments reflect the acute responses of the organism to environmental change and do not allow for the initial acclimation and potential seasonal cycles which influence physiology (Suckling *et al.*, 2015). Seasonality, which is often not incorporated into mesocosm experiments due to their generally short duration, was found to have a potential role in determining physiological rates and should be incorporated into future CCC laboratory experiments. This study therefore provides arguably more realistic results on the effects of CCC on *M. gigas* physiology. Whilst the present experiment incorporated multiple stressors, seasonality and long-term exposure, further research is still required into the long-term effects of CCC on NIS. For example, long-term experiments examining effects of CCC on different life-history stages, physiological mechanisms, and life-history traits, are fundamental for more complete understanding of how CCC will affect *M. gigas.* Equally, studies should strive to investigate interactions with other potential stressors which are less well studied, for example immersion time, hypoxia, eutrophication and predation.

Lastly, dynamic energy budget (DEB) modelling has traditionally been limited by the lack of studies both incorporating intraspecific variability to simulate the effect of environmental variables on species life-history traits, and measuring the uncertainty created by DEB parameter variability. The modelling of *M. gigas* in Chapter 4 is unique, combining both large-scale region-specific environmental variation and an inter-individual variability simulation varying multiple DEB parameters. It was demonstrated that individual-based modelling is an effective way of producing robust, biologically realistic estimates of species energetics and spatial patterns of life history traits under environmental change. Importantly, examining the spread of simulated data across present and future conditions allowed for the magnitude of potential changes in life-history traits to be put into context of natural individual variability. This study therefore significantly advances the understanding of how different sources of variability interact and influence life-history traits in the present day and under CCC conditions. Variability in the parameters also allowed an investigation into the uncertainty in model estimates, showing that small changes in parameter means can have a considerable effect on the life-history traits under current and future environmental conditions. Measuring this uncertainty is something which is fundamentally important when modelling but is uncommon in mechanistic ENMs.

5.3 Correlative versus mechanistic ENMs

One of the main aims in this thesis was to model species distributions using both correlative and mechanistic approaches and to compare the usefulness and robustness of the models when forecasting NIS distributions with CCC. Overall, the combination of ENM modelling techniques in this thesis has shown that different approaches can produce complementary results. It is evident that both models have a practical role when predicting species distributions, with the correlative model highlighting areas of potentially suitable habitat and the mechanistic model predicting how these habitats may influence the species life-history traits.

The two models characterize niches different and as such ultimately provide different predictions on how the species is likely to be distributed. Mechanistic models typically predict distributions based on the fundamental niche of the species as the models are parameterised using abiotic variables. In contrast, correlative models implicitly incorporate biological interactions and physical barriers by using occurrence data and thus predict the realised niche of the organism (Pearson & Dawson, 2003). The realised niche of a species is therefore smaller than the fundamental niche due to these constraints. As already discussed in this thesis, non-climatic factors such as dispersal, competition and predation play an important role in determining species distributions, particularly at local and regional scales and under finer spatial resolutions (Elith *et al.*, 2006; Kissling *et al.*, 2012). Models which do not incorporate these limiting factors are likely to over-predict the actual distribution of the species (Václavík & Meentemeyer, 2009). However, Elith *et al.* (2010) used correlative models to estimate the distribution limits of a non-indigenous cane toad and found that there were few biotic interactions limiting their distribution and the toads have a range which reflects environment conditions. The success of invasive species through factors such as outcompeting natives and the absence of predators may mean the lack of biotic data is not a major influence on predicting invasive species' distribution and that invasive species distributions may more often than not reflect physical conditions (Elith *et al.*, 2010). Results from models incorporating only physical factors on invasive species (thus characterizing their fundamental niche) could therefore provide a reasonable estimate of their distributions. Jiménez-Valverde *et al.* (2011) described that although biotic factors may cause absences of the species in a particular area, models for invasive species should aim to estimate the complete area at risk from invasion. This is particularly the case as biological interactions are likely to change with CCC (Blois *et al.*, 2013), as well as changes to physical barriers over time. Overall, both correlative and mechanistic models should ideally be used together to examine the differences in modelled distributions. Examining these differences could be useful for the management of NIS with CCC where potential spatial and temporal changes in biotic factors could affect the realised niche.

In Chapter 2, the correlative model predicted a poleward shift in suitable habitats for *M. gigas* under end-of-the-century conditions globally. This prediction of a poleward shift was further validated in Chapter 4 where the mechanistic model predicted an increase in number of eggs and spawning events at higher latitudes around the northeast Atlantic under future

CCC conditions. It is therefore suggested that wild populations of *M. gigas* may become more abundant at higher latitudes by the end of the century. Congruent results between modelling approaches agrees with other studies which have produced similar predictions from both approaches (Kearney *et al.*, 2010b; Rougier *et al.*, 2015). For example, Rougier *et al.* (2015) found correlative and mechanistic models produced similar trends between the habitat suitability and population dynamics of the allis shad, *Alosa alosa*. There is a general consensus that correlative and mechanistic models should be used in a complementary way rather than making a preferential choice (Morin & Thuiller, 2009; Serra-Diaz *et al.*, 2013; Rougier *et al.*, 2015). Equally, the use of both models may provide a useful way to offset model uncertainty as both models rely on different assumptions. Variations between the two predictions may identify areas where differences between the realised and fundamental niche might be significant (Morin & Thuiller, 2009; Serra-Diaz *et al.*, 2013). Combining both model outputs could be considered an 'ensemble' approach in the general sense and will provide greater insights into the potential distributions of species and changes with CCC.

The two models did produce contradictory results in the northeast Atlantic region and Mediterranean Sea. The correlative model predicted a decrease in habitat suitability in the Mediterranean Sea under both emission scenarios. The mechanistic model, however, predicted *M. gigas* will undergo increased growth and reproduction with CCC, suggesting these areas may become more favourable. As well as differences between models arising from the characterisation of different niches, it is important to note that the models in Chapters 2 and 4 did not use the same variables. The correlative model included temperature, salinity, chlorophyll concentration, pH and calcite, whereas the mechanistic model only used temperature and chlorophyll concentration for the DEB simulations. This could be responsible for divergences between model predictions. Other factors which may have led to differences are, firstly, the mechanistic model used finer-scale temporal environmental data as opposed to long-term means to assess how this environmental variation will affect their success with CCC. Secondly, the correlative model was trained on global occurrence data and not on only northeast Atlantic populations, which the mechanistic model is based upon. Whilst a direct comparison of these two models is not possible, two diverging predictions in the Mediterranean Sea implies that forecasting the effect of CCC in this region could be more difficult. Some additional data and different modelling approaches are likely required to see if a consensus forms.

A species' response to environmental change is not necessarily uniform across its biogeographic range due to individual-level interactions, with the local environment leading to local-scale adaptations (Valladares *et al.*, 2014). It remains relatively unknown, however, how the inclusion of locally adapted populations of the same species may impact correlative and mechanistic ENMs. Investigation of native and introduced niches in Chapter 2 showed that separated populations of the same species (native and introduced) can have different niches which may ultimately lead to inaccurate predictions of species distributions. The importance of examining differences between local populations was highlighted in Chapter 4 where small shifts in DEB parameter means (which could symbolise changes between populations) led to substantial shifts in the life-history traits of *M. gigas*. Local adaptation can lead to increased model sensitivity and significant differences in current and future predictions in species distributions (Hällfors *et al.*, 2016; Lecocq *et al.*, 2019). Overall, few ENMs have incorporated potential differences between local populations but their inclusion could greatly benefit the robustness of ENMs (Kolbe *et al.*, 2010; Hällfors *et al.*, 2016; Chapman *et al.*, 2017). However, collecting a range of physiological data from multiple populations would be a very time consuming and costly undertaking. Chapman *et al.* (2017) used phenological experimental data between southerly and northerly ragweed populations to predict the introduced ranges of individual populations. They found that the northern populations had lower thermal requirements for bud development than southern populations due local adaptation during invasion and thus, the mechanistic ENM predicted this would extend the introduced range northwards and increase average habitat suitability in current and future climates. Exclusion of intraspecific data when modelling NIS could substantially underestimate the extent of biological invasions both in the present day and with CCC (Chapman *et al.*, 2017). Overall, understanding how intraspecific variability affects both correlative and mechanistic ENM predictions requires much further investigation.

The mechanistic ENM incorporated environmental data at a finer temporal resolution than the correlative model, for example daily or seasonal compared to long-term (decadal) averages, which could lead to a more accurate and detailed predictions of spatial patterns both in the present day and under CCC conditions. Long-term environmental averages, which are often used in correlative ENMs, exclude natural climate fluctuations which species experience over short time scales (Redfern *et al.*, 2006; Robinson *et al.*, 2011). These natural fluctuations in climate over months, weeks or days are important for determining or limiting species distributions and abundance (Parmesan *et al.*, 2000; Chan *et al.*, 2016; Montalto *et al.*, 2014). Daily and seasonal fluctuations to unfavourable conditions and the frequency of extreme events, such as marine heat waves, are likely to increase with CCC and models using long-term averages could therefore underpredict the effects of CCC (Bateman *et al.*, 2012). This may especially be the case at range edges where species are likely living close to their physiological limits and may be more sensitive to environmental changes (Parmesan *et al.*, 2000). Using correlative ENMs, Fernandez *et al.* (2017) found SST to be the main variable determining the spatial patterns of cetaceans when using coarse temporal resolutions (monthly to yearly averages), but the importance of other limiting variables, such as distance to frontal areas, was detected at finer resolutions (daily to weekly averages). Pennino *et al.* (2019) observed that environmental data at weekly, monthly and seasonal resolutions provided better predictive power and estimation of the relationship between benthic fish species and their habitats than yearly averages. Scales *et al.* (2017) found similar results showing that seasonal and climatological time scales, as opposed to daily or weekly scales, increased model error in marine predator habitat models. Using mechanistic ENMs, Montalto *et al.* (2014) found that temporal averaging can lead to the underestimation of the number of eggs, reproductive events and time to maturation in the bivalve *Mytilus galloprovincialis.* The selection of temporal resolution therefore plays an important role in predicting species distributions and finer resolutions are likely needed to detect the effects and interactions between environmental variables (Montalto, *et al.,* 2014; Fernandez *et al.*, 2017). Coarser temporal resolutions may be more appropriate on mesoscales/global scales (Fernandez *et al.*, 2017), however, the interaction between temporal and spatial resolutions when using ENMs remains relatively unclear.

In general, ENMs heavily depend on the availability of environmental data which can be a major limiting factor in predicting species distributions. Global climate models have greatly advanced the use of ENMs for predicting past, present and future distributions under variable climates and have enabled investigations using multiple environmental variables. Accessible forecasts of end-of-the-century environmental conditions in marine systems tend to have coarse spatial resolutions (such as 1° x 1° HadGEM-ES used in this thesis) and limited temporal resolutions. As a result, predictions of species distributions in the marine environment under CCC are likely to be coarse. Whilst coarse resolutions are useful for predicting large-scale distributions and general biogeographic trends in species distributions, such as in Chapter 2, they may not be useful for conservation planning and management where fine-scale, regional or local estimates are required (Reid, 1998; Hess *et al.*, 2006). The accessibility of high-resolution environmental data is necessary for the advancement and application of marine ENM predictions. It is important to note, however, that biological interactions and topography will play a larger role in predicting species' distributional patterns at fine scales (Pearson & Dawson, 2003; Montoya *et al.*, 2009; Robinson *et al.*, 2011).

Predicting the distributions of target species has vast potential to influence conservation, management and policy (Guisan *et al.*, 2013; Marshall *et al.*, 2014). Although prevention of NIS introduction is a priority, early detection and subsequent early eradication is recognised as the most cost-effective mechanism for biosecurity (Tidbury *et al.*, 2016). Invasion risk mapping requires robust predictions in potential growth, reproductive potential and habitat suitability for efficient and targeted management to increase the chances of identifying potential establishment and areas of spread (Jiménez-Valverde *et al.*, 2011). The significance of physiological understanding for conservation has been recognised in the literature (Carey, 2005; Cooke & O'Connor, 2010; Evans *et al.*, 2015). As such, 'conservation physiology', described as an integrative approach using mechanistic responses to environmental changes to understand biological diversity and functioning, could be used for tackling conservation problems (Wikelski & Cooke, 2006; Cooke *et al.*, 2013). Chapter 4 identified areas of concern at northern latitudes in the northeast Atlantic and in the Mediterranean Sea where *M. gigas* are predicted to have increased spawning events, potentially facilitating their spread. This novel insight into areas of potential future proliferation has applications in the development of targeted environmental conservation and management decisions with the aims to limit NIS spread on the coastlines. It is likely that localised, ecosystem-based modelling will be needed in targeted areas to more fully understand the ecological consequences of *M. gigas* spread under CCC.

5.4 Concluding remarks

This thesis found, using a combination of approaches, that the highly successful *M. gigas* can tolerate CCC conditions and will likely undergo a poleward range expansion towards end of the century. Robust estimates provided evidence for the growing consensus in the literature that CCC will facilitate the spread and competitive dominance of NIS. The novel methods presented in this thesis have emphasised best practices which should act as a basis for future investigations into NIS physiology and distributions. This included firstly, the wider use of hypervolumes, or other alternatives to principal components analysis, to estimate and visualise niche shifts. Secondly, the use of long-term, seasonal mesocosms to understand the effects of multiple stressors on species biological functions, and lastly, the development of mechanistic ENMs which incorporate inter-individual variability to examine species life-history traits across large spatial scales. From comparing two competing types of ENMs, it is clear that they provide slightly different but often complementary insights into how species niches may change with CCC. Running multiple types of ENMs, particularly when undertaking the collection of physiological data, requires significant investment. However, their combination will allow for more robust predictions of NIS distributions and a greater understanding of how large-scale patterns in biodiversity will rapidly change under CCC.

Chapter 6 Appendices for Chapter 2

Table 6.1 Table of the environmental variables used to for modelling *Magallana gigas* niches in environmental and geographical space from Bio-ORACLE v2.0 (Tyberghein *et al.*, 2012; Assis *et al.*, 2018) and HadGEM-ES along with a justification of their biological importance for *M. gigas*.

Environmental Variable	**Units**	**Variable importance**
Temporal mean from monthly sea surface temperature	°C	The geographic range boundaries of marine ectotherms are limited by the species' thermal tolerance, affecting fundamental biological functioning (Sunday *et al.*, 2012)
Interpolated mean of *in-situ* salinity	PSS	Salinity is a key range limiting factor for marine species, impacting species physiology and survival (Cognetti & Maltagliati, 2000; Paavola *et al.*, 2005)
Interpolated mean of *in-situ* pH	-	The pH of seawater is influenced by CO_2 in the atmosphere and can have a significant effect on shell growth and dissolution in marine calcifying organisms (Doney *et al.*, 2009)
Temporal mean from seasonal calcite concentration	mol/m^3	Calcite concentration serves as a proxy for the carbonate chemistry in the water which is important for the calcification rates and the formation of oyster shells, which are predominately made of calcite (Stenzel, 1963; Fabry *et al.*, 2008)
Temporal mean from monthly chlorophyll *a* concentration	mg/m^3	Chlorophyll *a* concentration is a measure of primary productivity and thus a proxy for food availability for suspension feeders, such as oysters (Tyberghein *et al.*, 2012; Rodil *et al.*, 2014).

Table 6.2 Weightings of the environmental variables in the first and second axes for the principal components analysis and partial least squares.

Environmental variable	Principal component eigenvectors		Partial least squares loadings	
	Axes 1	Axes 2	Axes 1	Axes 2
Calcite	-0.35	0.65	-0.53	-0.29
Chlorophyll	-0.43	-0.40	0.04	0.44
pH	0.40	-0.31	0.32	-0.58
Salinity	0.56	-0.15	0.19	-0.44
Temperature	0.47	0.55	0.76	0.54

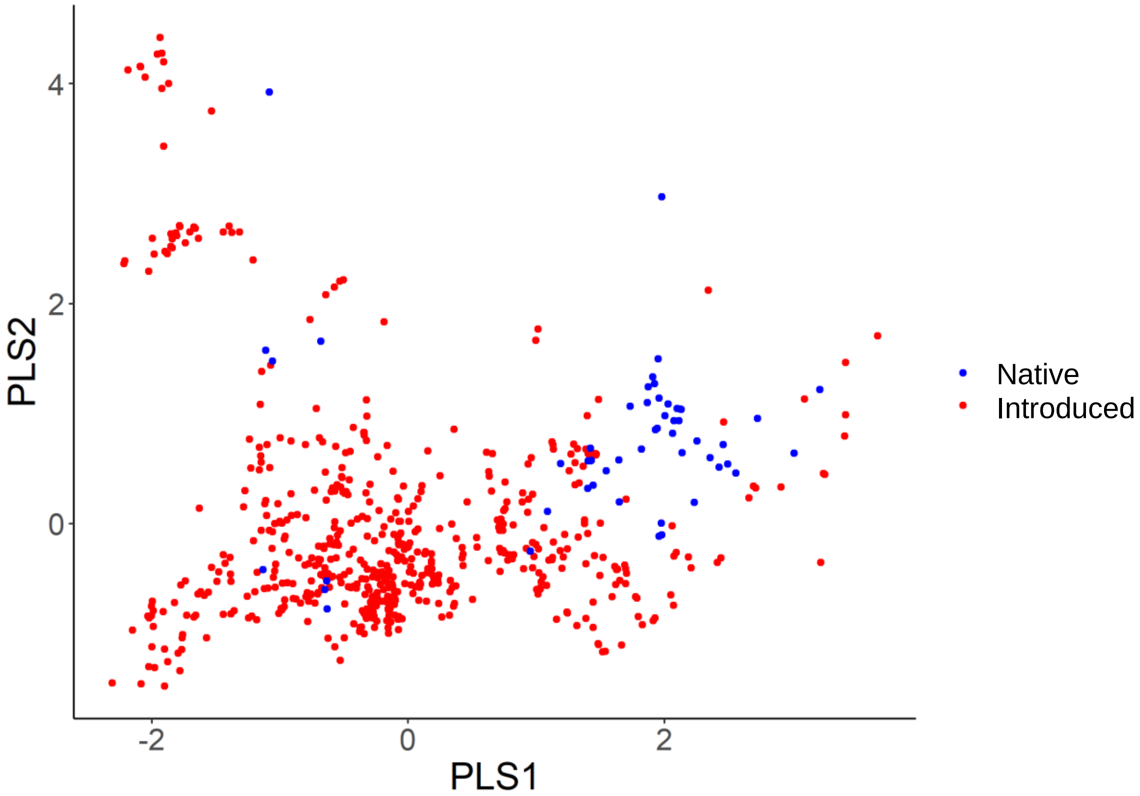

Figure 6.1 Partial least squares analysis in two-dimensional space of the native (blue) and introduced (red) niches. The native points overlay the introduced.

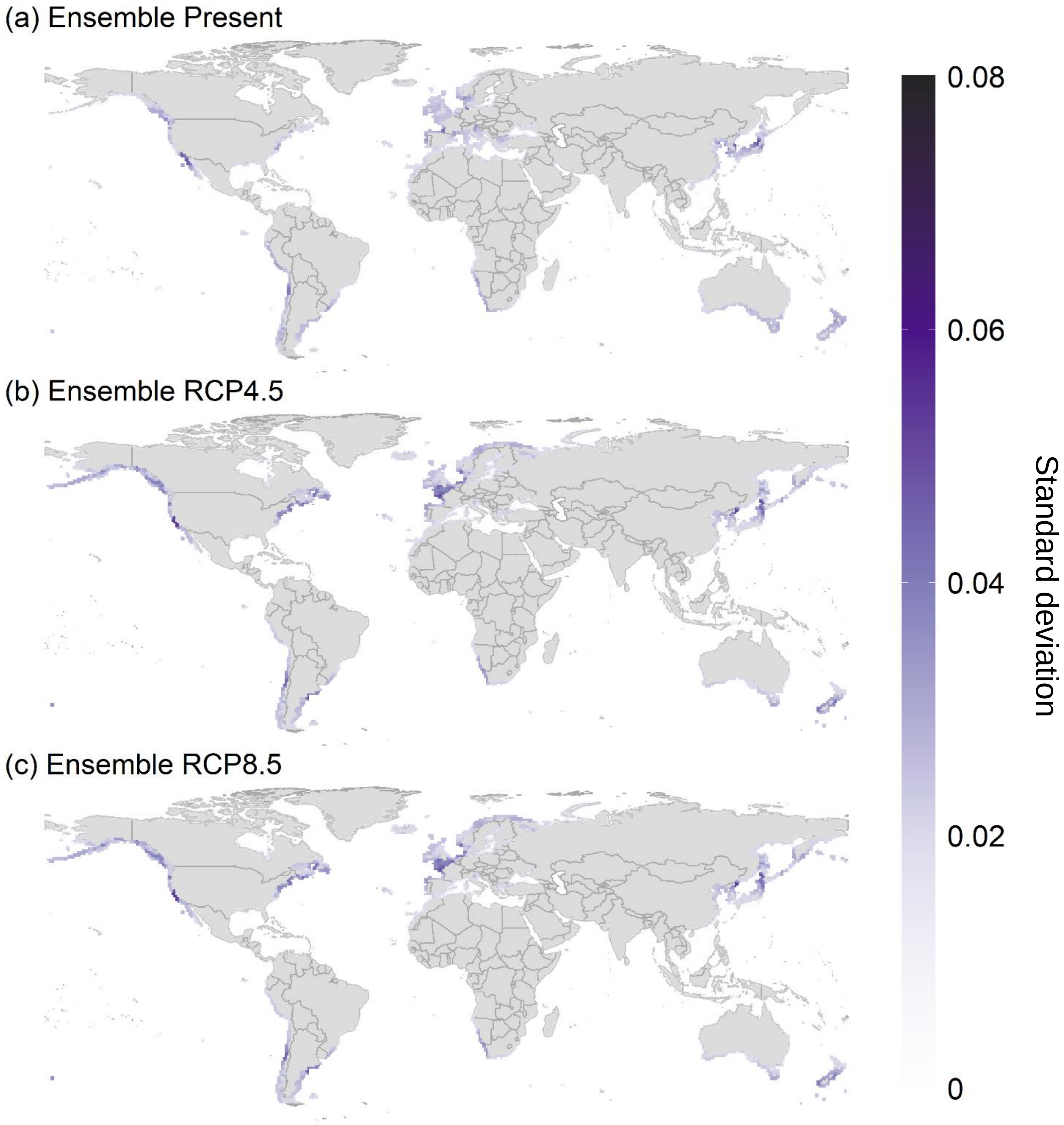

Figure 6.2 Standard deviation of habitat suitability for the *Magallana gigas* ensemble model along the global coastline for the present day (a) and the end of the century based on RCP4.5 (b) and RCP8.5 (c) scenarios.

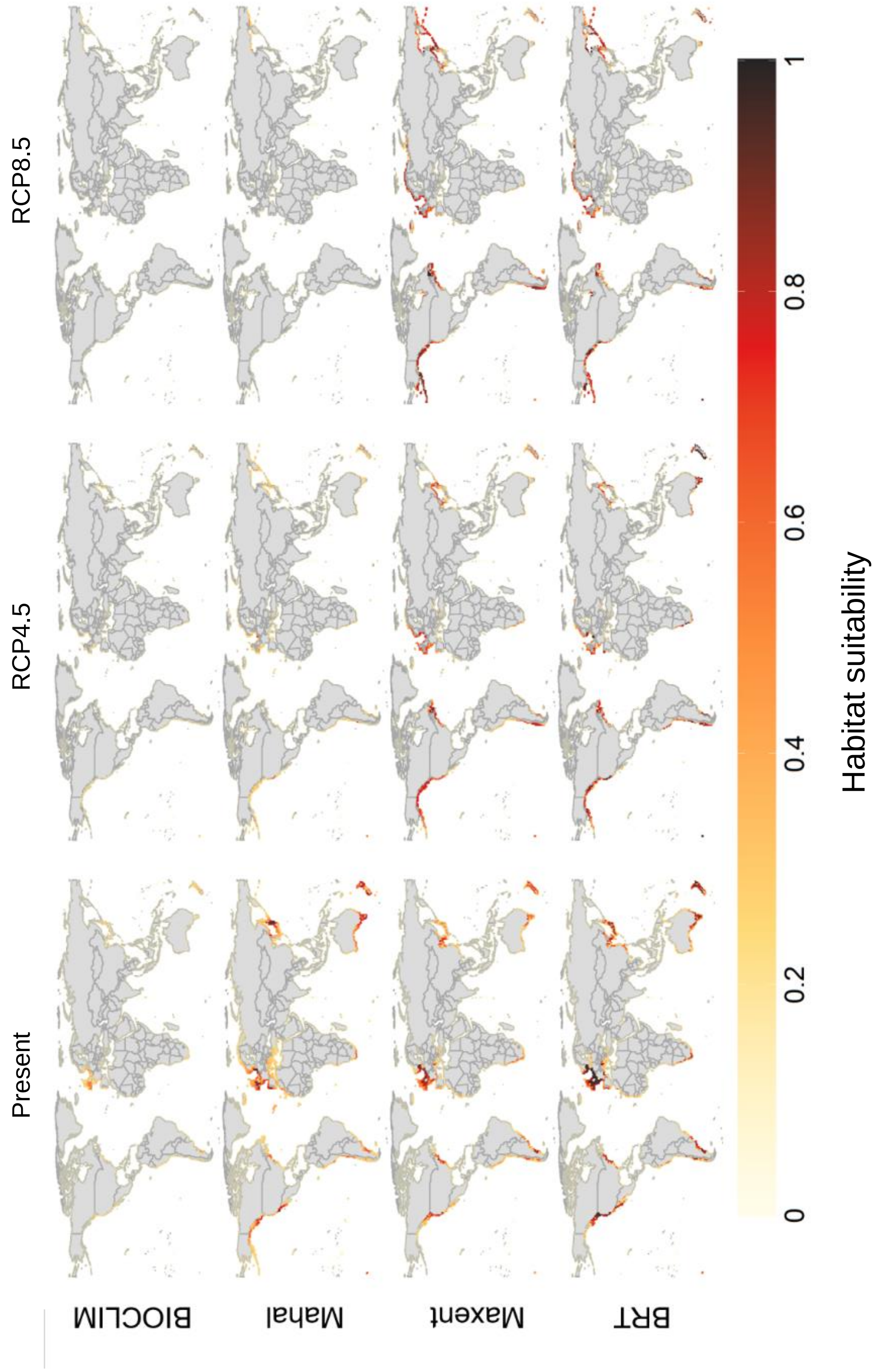

Figure 6.3 Habitat suitability for *Magallana gigas* for BIOCLIM, Mahalanobis distance, Maxent and Boosted Regression Trees models in the present and predicted for the end of the century. Each model was run 100 times and the median determined.

Chapter 7 Appendices for Chapter 3

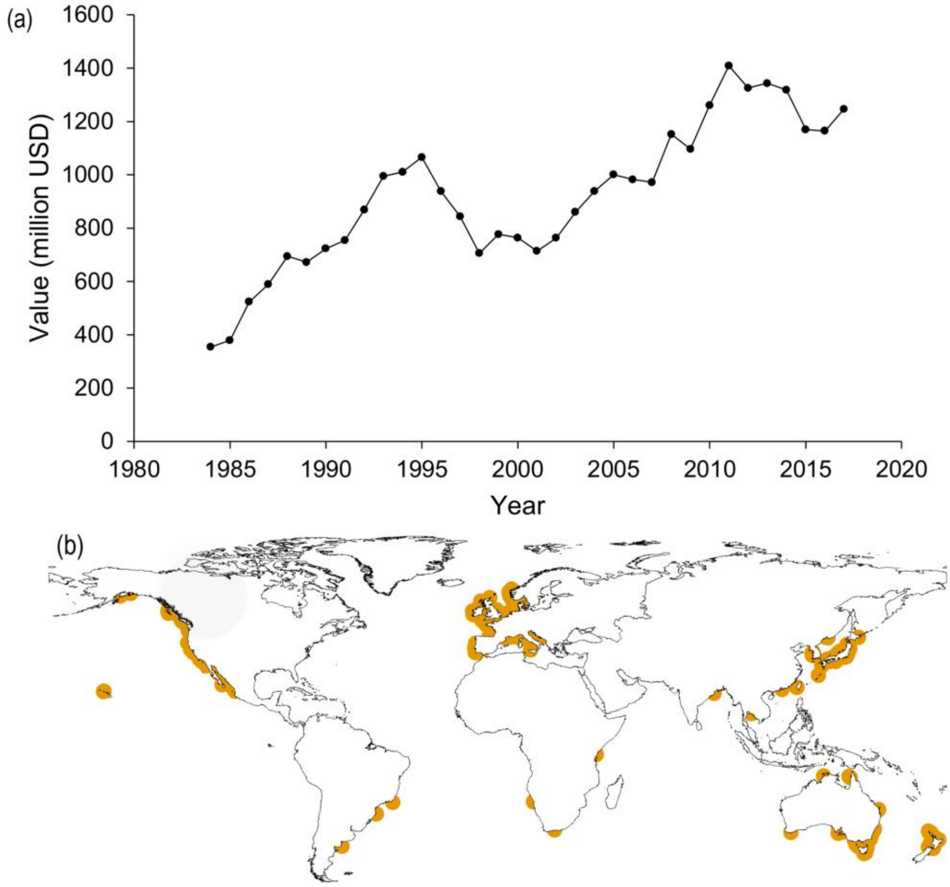

Figure 7.1 (a) The global aquaculture value of *Magallana gigas* between 1984 and 2017 (FAO, 2019) and (b) the global distribution of wild *M. gigas* from Global Biodiversity Information Facility (GBIF, accessed: 7th October 2019).

Table 7.1 Mean (± standard deviation) salinity, pH and total alkalinity for each of the 12 treatments over 10 months. Salinity and pH were monitored every 1-2 days, and total alkalinity measured every 2 weeks for the duration of the experiment.

Treatment temperature (°C) - salinity - pH	Salinity	pH	Total alkalinity (umol kg-1)
Ambient - 20 - 7.5	19.9 ± 0.9	7.54 ± 0.05	1835.4 ± 81.4
Ambient - 20 - 7.7	20.2 ± 1.1	7.70 ± 0.04	1828.0 ± 81.5
Ambient - 20 - 8.1	21.2 ± 1.6	8.05 ± 0.04	1807.4 ± 98.4
Ambient - 34 - 7.5	33.5 ± 1.8	7.54 ± 0.04	2317.0 ± 93.1
Ambient - 34 - 7.7	33.0 ± 1.4	7.72 ± 0.03	2293.9 ± 15.4
Ambient - 34 - 8.1	33.9 ± 1.2	8.01 ± 0.03	2302.6 ± 95.3
+4 - 20 - 7.5	20.4 ± 1.1	7.51 ± 0.06	1833.4 ± 102.9
+4 - 20 - 7.7	21.3 ± 1.1	7.72 ± 0.04	1810 ± 105.1
+4 - 20 - 8.1	20.5 ± 1.3	8.10 ± 0.06	1838.5 ± 88.2
+4 - 34 - 7.5	34.3 ± 0.9	7.53 ± 0.06	2332.7 ± 92.1
+4 - 34 - 7.7	34.1 ± 1.9	7.72 ± 0.03	2304.6 ± 92.0
+4 - 34 - 8.1	34.0 ± 1.8	8.07 ± 0.05	2334.6 ± 95.2

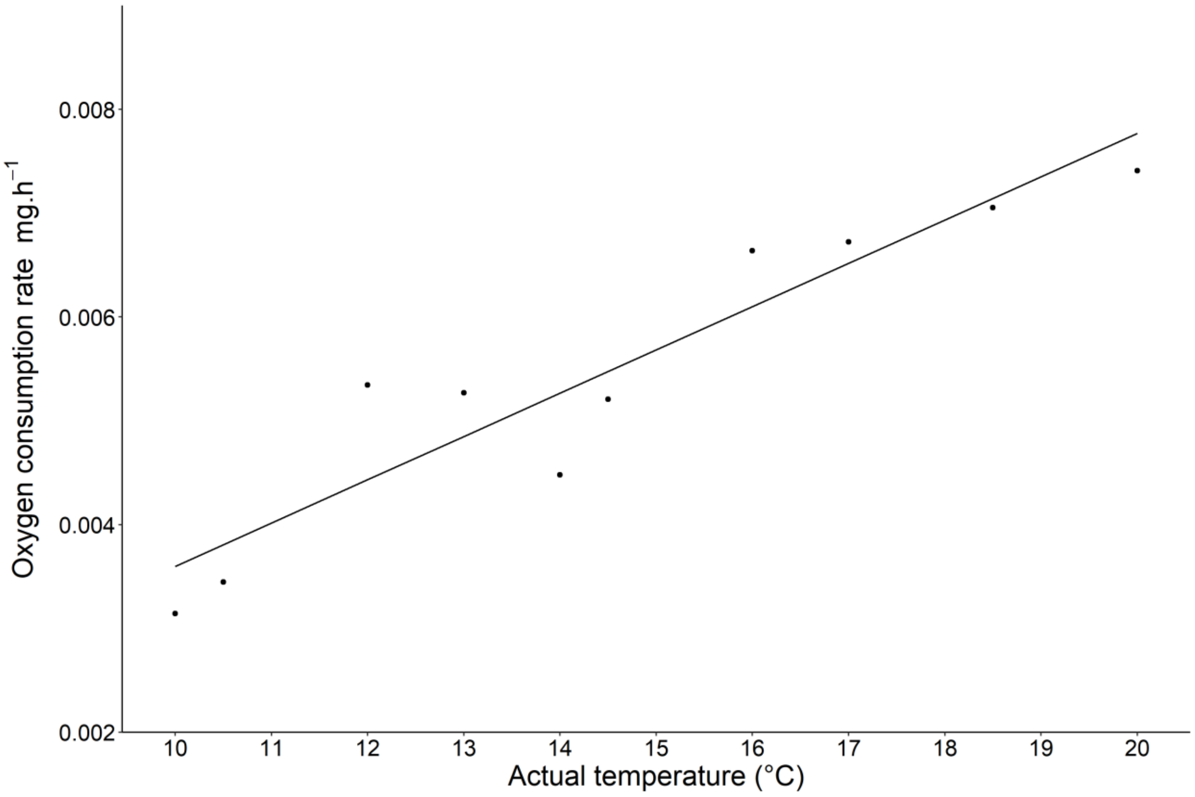

Figure 7.2 Mean oxygen consumption rates (mg hr^{-1}) of *Magallana gigas* across all treatments against average monthly temperature of the water. Temperature was based on mean monthly SST from the Western Channel Observatory L4 station data. Data were weighted by sample size and standardised to 1g oyster ($R^2 = 0.87$).

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