University of Strathclyde

A unified population model of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic

Robert Wilson

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Abstract

A fundamental challenge of marine ecology is to understand climate change induced range shifts. At the level of individual ecosystems, the impacts of these range shifts will result from the complex changes in community composition. This forces us to consider not simply individual species, but the species that may replace them and play similar roles in an ecosystem.

Here we consider the important zooplankton species *Calanus finmarchicus* and *C. helgolandicus*. Recent climate change has resulted in the gradual replacement of *C. finmarchicus* by *C. helgolandicus* in the North Sea. However, the ability of *C. helgolandicus* to fully replace *C. finmarchicus* has been questioned by some researchers. We therefore sought to fill a key knowledge gap. The comparative differences between the two species have never been critically reviewed. Further, the relative geographic distributions of both species have never been related to inter-species differences in biology or ecology.

This thesis has two key elements. First, we critically review and synthesize existing knowledge of inter-species differences between *C. finmarchicus* and *C. helgolandicus*, overturning many assumptions common in the literature. Second, we produce a unified population model of both species across the North Atlantic, which relates differences in geographic distribution to inter-species differences in biology. This model is then used to highlight the limits of current understanding of mortality, and of the vital importance of improved quantitative knowledge of overwintering if we are to understand the future evolution of both species' distributions.

Acknowledgements

First things first. I must thank my supervisors Dr. Douglas Speirs and Prof. Mike Heath. Without them to constrain me, my tendency to wander down some garden path may have resulted in me never returning. I particularly thank Dougie for his insistence on applying Occam's razor to modelling problems. I hope this advice shows.

Thanks must also go to Dr. Neil Banas, who kindly sat in on many fruitful discussions in the final months when the elements of the thesis finally came together. Ian Thurlbeck provided much needed technical help throughout my PhD. If I had to work with a black box, it was always with Ian's help that I was able to use it.

I shared an office for three years with Andisheh Bakhshi, Alan MacDonald, and Ruaraidh McPike. They were all surprisingly tolerant of me borrowing their computers almost every night of the week for half a year. Alessandro Sabatino provided useful advice about ocean circulation and temperatures, and also helped to make it impossible to keep track of who drank what from the office espresso machine. Thanks also to Vannesa Trijoulet for providing valuable advice about the display of figures.

Despite having an absolutely hellish time during it, I wish to thank John Dunne and the crew of FRS Scotia for allowing me to spend two weeks on board a research cruise in the North Sea in December 2011. It may have been a rather uncomfortable two weeks, but the unwelcome confirmation that I lack sea legs was more than made up for by the crash course I received in how challenging marine biology can be.

Finally, I want to think the Marine Alliance for Science and Technology Scotland and the University of Strathclyde whose funding made this thesis possible.

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Abbreviations

C1-C5	Copepodite stages of *Calanus*
C6	Adult stages of *Calanus*
CPR	Continuous Plankton Recorder
EPR	Egg production rate
DT	Development time
GAM	General Additive Model
TAG	Triacylglycerol
NEMO	Nucleus for European Modelling of the Ocean
N1-N6	Naupliar development stages of Calanus
OGCM	Oceanic General Circulation Model
OSV	Oil sac volume
OWS I	Ocean Weather Ship India
OWS M	Ocean Weather Ship Mike
PL	Prosome length
Q_{10}	Factor a physiological trait increases with each 10°C increase in temperature
SST	Sea Surface Temperature
WE	Wax ester

Part I

Introduction

Chapter 1

Introduction

1.1 The need for comparative ecology

The zooplankton species *Calanus finmarchicus* and *C. helgolandicus* share a lot in common. Both develop from egg to adult through six naupliar and five copepodite stages; cannot be distinguished using morphology at stages before the final copepodite stages; have very strong genetic similarities; and were thought for decades by some scientists to be the same species. Yet, *C. finmarchicus* lives no further south than the North Sea in the eastern Atlantic, while *C. helgolandicus* lives no further north than the North Sea and does not live in any oceanic regions. In spatial terms they do not share much in common at all.

But why?

This thesis marks the first attempt at providing an in depth answer. However, a simple question must be asked. What is the difference between *C. finmarchicus* and *C. helgolandicus*? This is the question that motivates everything that follows. The answers

are surprising, and they challenge some of the commonly expressed views in the scientific literature. But first things first: Why should we being asking such questions in the first place?

Ongoing climate change is resulting in large changes to zooplankton communities in the North Atlantic (Beaugrand et al., 2002; Chust et al., 2013). As oceans warm, species are moving north, tracking the changes in favourable environmental conditions (Reygondeau and Beaugrand, 2011). These changes take many forms, from alterations to total biomass, size and species composition to the energy available to higher trophic levels. In turn these can have significant impacts on many fish species, which have life cycles dependent on the annual or seasonal availability of certain classes of zooplankton (Beaugrand et al., 2003; Nicolas et al., 2014; van Deurs et al., 2009; Frederiksen et al., 2013). The changes relating to *C. finmarchicus* are of particular importance.

C. finmarchicus is one of the most ecologically important zooplankton species in the North Atlantic. It dominates the mesozooplankton biomass in large regions (Head et al., 2003), and is vital prey for many commercial fish, including cod, haddock and herring (Loeng and Drinkwater, 2007; Helle and Pennington, 1999; Gaard and Reinert, 2010; Prokopchuk and Sentyabov, 2006). Declines in the population of *C. finmarchicus* are likely to have significant influences on populations of important commercial species such as cod (Beaugrand et al., 2003) and herring (Broms et al., 2012). Yet, evaluations of the impact of changes of *C. finmarchicus* on higher trophic levels often involve a mischaracterization of *C. helgolandicus*, the congeneric species replacing *C. finmarchicus*. For example, it has been claimed that *C. helgolandicus* cannot be a full replacement of *C. finmarchicus*, in part because it is smaller and has lower lipid levels. However, there appears to be little scientific evidence to back up this assumption (Wilson et al., 2015). A fuller accounting of interspecies differences is therefore necessary.

Both species overlap in the North Sea, but their distributions have little else in common. *C. finmarchicus* has a population covering most of the North Atlantic from the

Labrador Sea to the Norwegian Sea (Melle et al., 2014). In contrast, *C. helgolandicus* lives from the Mediterranean Sea to the North Sea, but is essentially absent from oceanic regions (Bonnet et al., 2005). However, the reasons for these spatial disparities have not received much attention in the scientific literature.

The differences in the geographic distribution of both species must result from interspecies differences. These can take many forms. However, the most probable involve responses of physiological traits to temperature. Interspecies differences in the response of growth, development time, fecundity, metabolism and metabolism could explain the different geographic distributions between each species. In fact, differences in the response of development time to temperature have been proposed as the lead cause of their different geographic distributions (Møller et al., 2012).

We therefore take a two pronged approach to our problem. First, we critically evaluate the interspecies differences between each species. This involves a comparative review of the ecology and biology of both species. This review has been published in revised form in the journal Progress in Oceanography (Wilson et al., 2015). In addition, we perform a statistical analysis of Continuous Plankton Recorder data to highlight the different ecological niches of both species and to consider their recent geographic shifts (Chapter three).

Differences in interspecies will result in different emergent behaviours on a large geographic scale. The only way to understand this is to model it. We therefore set out with the ambitious goal of modelling both species under the assumption that the only interspecies differences were those revealed by our comparative review. The large scale geographic differences would then be emergent properties solely of known differences.

1.2 The Life Cycle of *Calanus*

C. finmarchicus and *C. helgolandicus* develop through 13 development stages: egg, 6 naupliar (N1-N6), 5 copepod (C1-C5), and a male or female adult stage (C6m/C6f). C5 of *C. finmarchicus* are known to diapause during winter, and sometimes this is viewed as a separate sub-stage (C5d). The first feeding stage is N3 for both species. Lipids play an important role in the life cycle of *C. finmarchicus* (Hirche, 1996), and lipid accumulation mostly begins in stage C3. *C. helgolandicus* accumulates lipids, however their importance in its life cycle are less clear.

Throughout most of its geographic range *C. finmarchicus* has an annual life cycle (Heath et al., 2000a; Irigoien et al., 2000a). However, in its colder extremes generations can exceed 1 year (Heath et al., 2008), whereas in warmer environments there can be multiple generations each year (Hirche et al., 2001). Reflecting its warmer temperature regime *C. helgolandicus* typically has multiple generations each year (Bonnet et al., 2005).

1.3 An outline of prior expectations

At its foundation, science is about the proposal of ideas and theories, and the testing of them against data. However, these ideas are normally presented in the scientific literature in a much tidier fashion than the manner in which they came to the researchers involved. Initial hypotheses and ideas are quickly or gradually disregarded. Yet, this process of the development of a clearer view cannot be laid out in a scientific paper. A thesis is slightly different.

I will therefore outline the ideas I held before I first reviewed the ecology and biology of both species. These views were consistent with much of the opinion expressed in the scientific literature; however they appear to be wrong. As I am human, these views

were clung too in the face of contradicting data for much longer than they should have been, and some of them may still creep into the sentences you are about to read. Here then is a simple outline of my prior beliefs, or hopes, about the two species.

C. finmarchicus, a cold water species, will have significantly longer development times at warmer temperatures than *C. helgolandicus*, and this should show up clearly in development time studies. A stark difference in the response of development time and egg production rate to temperature should explain why one species does not exist south of the North Sea, while the other does not exist to the north of it. Similarly, I assumed that *C. helgolandicus* was much smaller than *C. finmarchicus* and to have lower lipid levels. The persistence of *C. finmarchicus* in oceanic regions is heavily dependent on its ability to diapause, which is in turn heavily dependent on large reserves of lipid. This lower lipid level was therefore expected to explain why *C. helgolandicus* is restricted to continental shelf regions; it simply does not have enough energy reserves to survive a long period without food during winter.

This was the basic story that I hoped to give quantitative form in a population model. The story appears to be wrong.

Published development time studies do not show *C. finmarchicus* taking longer to develop than *C. helgolandicus*. And there is no evidence that *C. finmarchicus* is larger than *C. helgolandicus* when they are grown under the same conditions. Likewise, there is no clear evidence that the species accumulate different levels of lipid.

A new story was needed. This story came in two parts. In 2012, Møller et al. (2012) published evidence that there were clear interspecies differences in the relationship between ingestion rate and temperature. This implied that *C. finmarchicus* takes longer to develop at temperatures above 12°C than *C. helgolandicus*. Before this study was published there were no known interspecies differences that could potentially explain their geographic distributions. There was no way to create a population model of both

species where their geographic distribution emerged from known properties of their biology. A key barrier was overcome.

The second part of the story came with the realisation that smaller individuals appear to be able to acquire much less lipid, relatively speaking. Therefore *C. helgolandicus* does appear to have lower lipids, but not as a result of interspecies differences, but of apparent allometric scaling of lipid levels. This results in a view of the biology of both species that potentially could explain both the relative geographic distributions of both species and the fact that *C. helgolandicus* is restricted to the continental shelf.

1.4 A comment on linguistic conventions

The requirement to write about a subject in a stylistically consistent manner forces you to make decisions about the use of language (Pinker, 2014). Word choice often reveals biases where none should exist. The way the use of "he" and "she" often highlights sexist attitudes springs to mind.

And here we have to address the apparent superiority the phrase "*C. finmarchicus* and *C. helgolandicus*" appears to give to *C. finmarchicus*. Throughout I follow the convention of writing "*C. finmarchicus* and *C. helgolandicus*". Likewise, this thesis has inevitable lists of facts, and throughout I will list the facts for *C. finmarchicus* first. This is a convention followed by almost all of the literature which considers both species at the same time. However, some literature either reverses the convention (Cook et al., 2007) or varies the ordering throughout the text (Jønasdøttir et al., 2005; Jønasdøttir and Koski, 2011).

The ordering of the phrase is almost certainly a reflection of the relative importance granted by researchers to *C. finmarchicus* compared with *C. helgolandicus*. Here I hope to put both species on equal footing.

In addition, I will occasionally use *Calanus* as shorthand for *C. finmarchicus* and *C. helgolandicus*.

1.5 Software and programming languages used

All statistical analysis was performed using the statistical software R. Plots were produced using the R package ggplot2 (Wickham, 2009). The population model was coded in C, while calculation of transition matrices for physical transportation was carried out in Python.

This thesis was typeset using LaTeX 3.14, which is available through the TeX Live distribution (`http://tug.org/texlive/`).

1.6 Thesis summary

Chapter 2 provides an extensive critical review of the ecological and biological differences between the two species. This chapter has been published in Progress in Oceanography (Wilson et al., 2015). The underlying purpose of this review was to provide the ecological and biological foundation for the population modelling of both species.

Against expectations, this chapter shows that there are very few known differences between the two species. Body size and lipid levels appear to be indistinguishable where the two species coexist. The only known biological difference between the two species is the relationship between development time and ingestion rate and temperature. This indicates that at temperatures of 12 °C and below, *C. finmarchicus* has shorter development times. However, there is a dome-shaped response of development time with temperature for each species. This results in *C. finmarchicus* having a longer development time than *C. helgolandicus* at higher temperatures. Importantly, this chapter

develops new models of growth and development for both species. These models will then be used in later chapters to formulate the population models for both species, with egg production rate being related to growth.

Chapter 3 carries out a statistical analysis of long term trends in abundance of both species throughout the North Atlantic using Continuous Plankton Recorder data. The goal of this chapter is to understand the extent to which environmental variables can explain the known distributions of both species. General Additive Models were the principle method used. We find that temperature and salinity are the key drivers of the distribution of *C. finmarchicus*. Importantly, we find that the distribution of *C. helgolandicus* cannot be credibly reproduced without using bathymetry as a predictive variable. Finally, we reconstruct recent trends in *C. helgolandicus* abundance in the eastern Atlantic. In contrast to a recent study which used GAM models to show that *C. helgolandicus* is expanding in every direction, our reconstructions indicate that *C. helgolandicus* abundance has declined significantly at the southern edge of its distribution on the eastern Atlantic.

Chapter 4 and 5 outlines the population model and formulation. The population model is an extension of the work of Speirs et al. (2006). We modelled both species using biological assumptions derived from the review in chapter 2. Our review indicates that there are minimal biological differences between the two species. We therefore started with the assumption that the only differences between the two species should be the relationship between development time and temperature and also egg production rate. To credibly model the geographic distributions of both species we had to assume that mortality scaled more steeply with temperature in *C. finmarchicus* than in *C. helgolandicus*.

A new model of diapause duration is outlined. This model relates prosome length of diapausing animals to temperature at birth, and in turn diapause duration. This allows us to model diapause duration of both species in an integrated manner, and

we assume that there are no interspecies differences in diapause behaviour. Chapter 2 proposes that *C. helgolandicus* only exists on continental shelf regions due to an inability to diapause. Our modelling tests whether this is a result of interspecies differences in diapause behaviour.

Chapter 6 shows the results of the model. We show that the baseline model can successfully reproduce the geographic distribution of both species in the North Atlantic. Both models are reasonably successful at reproducing the seasonal cycle of abundance at times series locations in comparison with field data. Population density estimates of *C. finmarchicus* diapausers are credible. Comparisons of modelled prosome length with field data shows that our simplified model of prosome length provides realistic predictions of body size. Comparisons of egg production rate with field estimates indicates that our model is reasonably successful, however they indicate that our model is not fully incorporating all key environmental effects on fecundity.

The baseline model was driven by the NEMO OCGM. We tested the sensitivity of the *C. finmarchicus* model to OCGM by driving it with the surface temperatures from the OCCAM OCGM. This showed significant differences. In particular, model performance in the Norwegian Sea was significantly better using OCCAM due to a more realistic representation of temperature. The sensitivity of *C. finmarchicus*'s distribution to assumptions related to diapause exit were tested by running the model assuming that diapause duration was also triggered by photoperiod. This provides some evidence that there is an environmental cue for *C. finmarchicus* diapause exit, with model predictions of *C. finmarchicus* abundance improving significantly at OWS Mike in the Norwegian Sea when a photoperiod cue is assumed.

Model results show that *C. helgolandicus*'s distribution is very sensitive to assumptions about diapause duration. Small (10%) increases to potential diapause duration results in *C. helgolandicus* becoming an oceanic species. This provides evidence for the key role in lipid levels play in determining the distribution of *C. helgolandicus*. Finally, we show

that autumn bloom of *C. helgolandicus* in the North Sea is potentially largely a result of the advection of populations into the North Sea.

Chapter 7 then outlines the challenges faced if we want to forecast the future geographic distribution of *C. helgolandicus* under climate change. Two major sources of uncertainty are highlighted: the actual ability of *C. helgolandicus* to diapause and mortality. We use a simplistic climate change scenario to show that whether *C. helgolandicus* remains a shelf species is highly dependent on model assumptions about potential diapause duration and mortality. This chapter shows that deep water temperatures are predicted to stay relatively unchanged in the Norwegian Sea this century, whereas surface temperatures will warm significantly under future projections from the NEMO model. This indicates that *C. helgolandicus* may possibly become an off-shelf species in this region in future.

Chapter 8 provides a general discussion of the population model. We highlight the significant uncertainties surrounding modelling mortality in *Calanus*. Our model of mortality is arguably largely ad hoc. However, understanding of mortality in zooplankton remains a difficult, if not insurmountable problem. We highlight two key weaknesses in our model, which can possibly be resolved by further research. *C. helgolandicus* has a spring bloom in the North Sea. However, our model fails to reproduce this. We argue that the spring bloom is inconsistent with what we know about the relationship between development time and temperature.

Our model limits the southern extent of *C. finmarchicus* to realistic locations by having an extremely high relationship between mortality and temperature. This is unsatisfying. However, this may possibly be resolved by future research that considers why *C. finmarchicus* does not exist in the Celtic Sea, whereas *C. helgolandicus* does. An understanding of the mechanisms behind this may allow us to credibly model both species distributions without unsatisfying temperature dependent mortality. We close the discussion by considering the limits of known experimental studies, and where key

knowledge gaps can be closed. Our model assumes that growth and egg production rate have dome-shaped responses to temperature. This may not be the case in reality, or the turning points may be different. Experimental knowledge over a wider range of temperatures may result in much improved Calanus models. But most importantly, they will allow us to better understand the impacts of climate change.

Part II

Biology and ecology

Chapter 2

A review of the ecology and biology of *Calanus finmarchicus* and *C. finmarchicus*

2.1 Introduction

The calanoid copepod species *Calanus finmarchicus* and *C. helgolandicus* play critical roles in marine food webs. Historically, research has focused mostly on *C. finmarchicus*. This is largely a result of the important role it plays in the subpolar North Atlantic ecosystem (Heath et al., 2000b; Aksnes and Blindheim, 1996), with it being a key prey species for many commercially important fish (Lynch et al., 2001). The number of papers published with titles including the words "*C. finmarchicus*" (582) and "*C. helgolandicus*" (192) that were published until 2013 (Web of Science) reflects this focus. However, significant changes in both species geographic distribution in recent decades, and the potential impacts of these changes, have resulted in a large increase in interest in the comparative ecology and biology of *Calanus*.

C. finmarchicus has a geographic distribution covering a large part of the subpolar North Atlantic from eastern Canada to the North Sea. The North Sea demarcates the northern extent of the range of *C. helgolandicus*, which extends as far south as the Mediterranean Sea. During recent decades, the geographic range of *C. finmarchicus* has shifted northwards (Barnard et al., 2004), while a recent analysis of Continuous Plankton Recorder data provided evidence that *C. helgolandicus* is expanding in every direction (Chust et al., 2013). These range shifts are understood to have largely been driven by increased oceanic temperatures (Reygondeau and Beaugrand, 2011), and they are likely to continue as a result of future climate change (IPCC, 2007). Evidence also indicates that neither species has undergone significant thermal adaptation to changing oceanic temperatures in recent decades (Hinder et al., 2013).

The primary region where both species overlap is the North Sea, and this region has seen a significant regime shift in recent decades. *C. helgolandicus* abundance now exceeds that of *C. finmarchicus*, a reversal of the situation in the 1960s (Reid et al., 2003b). Debate remains over the precise causes of this regime shift (Reid et al., 2003b; Beaugrand, 2004), however the change in temperature regime appears to be the most influential factor (Beaugrand, 2012).

A long term shift from *C. finmarchicus* to *C. helgolandicus* in the North Sea and other regions may have significant ecosystem impacts. The specific suitability of *C. finmarchicus* to act as prey for individual fish species is strongly influenced by its body size, lipid stores and seasonality (Frederiksen et al., 2013; van Deurs et al., 2014, 2009). Consequently, interspecies differences in these traits are important determinants of the suitability of *C. helgolandicus* to replace *C. finmarchicus* in terms of ecosystem function.

Due to their morphological similarities, *C. finmarchicus* and *C. helgolandicus* were originally thought to be the same species, until Sars distinguished them in 1901. This was disputed for many decades (Frost, 1974), but was resolved in the 1990s when molecular techniques were used to confirm them as separate species (e.g. Bucklin et al.

(1995)). They are generally thought to be morphologically indistinguishable, except for the C5 and adult stages (Fleminger and Hulsemann, 1977). As a result, interspecies behavioural and morphological differences are expected to be subtle. The inability to distinguish between each species in earlier stages is reflected by long term time series, such as the Continuous Plankton Recorder, only reporting species specific abundance for C5 and adult stages.

The biology and ecology of *C. finmarchicus* (Melle et al., 2014) and *C. helgolandicus* (Bonnet et al., 2005) have been separately reviewed in recent studies. The review of the ecology of *C. helgolandicus* Bonnet et al. (2005) carried out a short comparison of the differences between each species. However, the summary statistics for each species were arguably not very comparable and, in particular, may provide an incomplete reflection of the relative growth rates and development times for both species when they co-occur. This review is the first extensive comparative review of the key differences between *C. finmarchicus* and *C. helgolandicus*.

Geographic distributions of zooplankton populations are largely driven by the response of species to different temperature regimes, food levels and the role of ocean circulation in transporting populations (Speirs et al., 2006). Our a priori assumption is that differences between *C. finmarchicus* and *C. helgolandicus* are a result of different quantitative responses of life cycle traits to environmental conditions. Latitudinal differences in the range of each species indicate that temperature is a key determinant of interspecies differences in geographic distribution (Bonnet et al., 2005; Helaouët and Beaugrand, 2007). Some researchers (e.g. Møller et al. (2012)) suggest that interspecies differences in the response of growth to temperature explain these large scale differences. Here we provide a critical quantitative comparative review of the relationship between temperature and the following key life cycle traits: growth, development and egg production. In addition to differences in development, we hypothesize that possible differences in diapause behaviour are a significant determinant of the two species geographic

distributions. In particular, the potential inability to diapause for significant periods of time may limit *C. helgolandicus* populations largely to continental shelf regions.

2.2 Surface Development

2.2.1 Body Size

Quantitative aspects of key life cycle traits such as ingestion (Wirtz, 2013), metabolism (Saiz and Calbet, 2007) and fecundity (Campbell and Head, 2000) are strongly influenced by body size. Interspecies differences in body size are therefore expected to influence the respective population dynamics of *C. finmarchicus* and *C. helgolandicus*. Differences in body size may also result in different ecosystem function, with a recent paper (Frederiksen et al., 2013) invoking lower body size of *C. helgolandicus* as a reason it cannot be a full replacement for *C. finmarchicus* as prey for some fish.

Growth experiments have shown a clear negative relationship between adult body size and temperature (Campbell et al., 2001), which we expect to be reflected in geographic patterns of body size. To quantify this relationship we reviewed published female prosome lengths for each species and compared them with mean annual sea surface temperature (SST) in the regions studied (Figure 2.1). We have excluded laboratory studies which used fixed temperatures during experiments because our proxy for the temperature at which individuals developed, mean annual SST, is not fully comparable with the temperatures of laboratory experiments. Our comparison shows that the relationship between annual SST and female prosome length across both species is approximately linear, indicating that temperature is the most significant influence on geographic patterns of body size in both species.

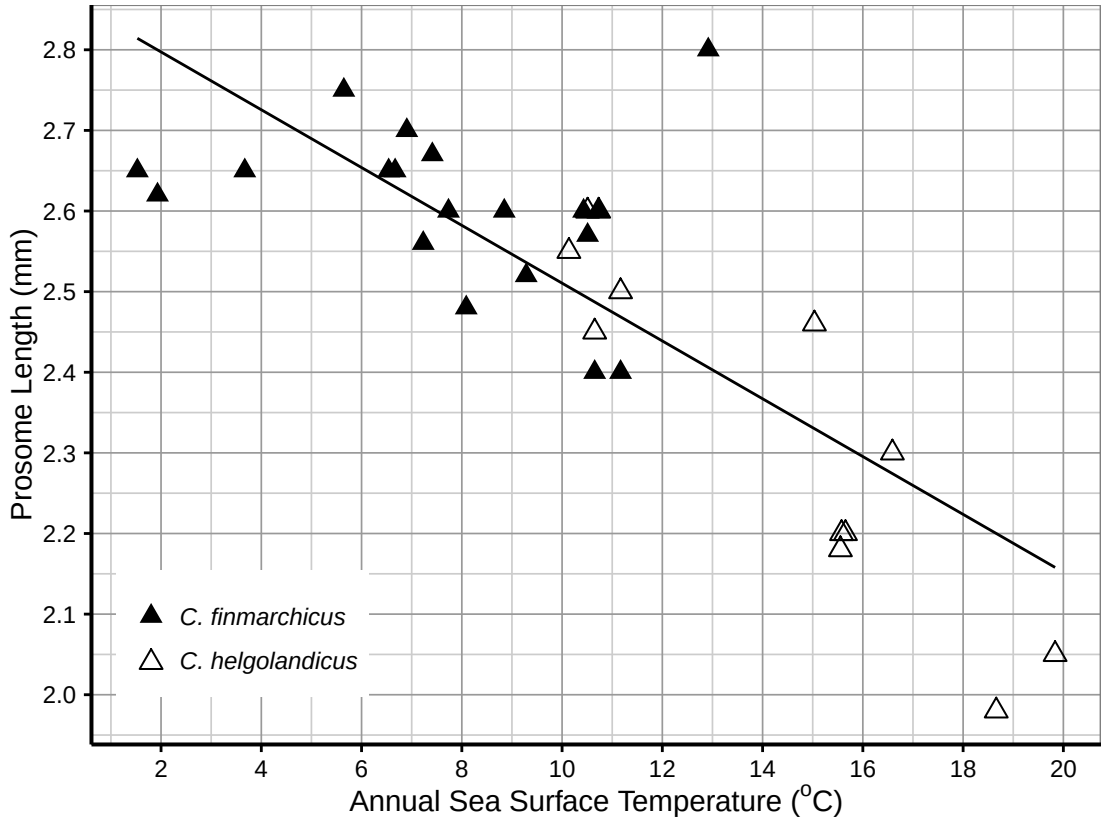


FIGURE 2.1: Comparison of published female prosome lengths of *C. finmarchicus* and *C. helgolandicus* with annual sea surface temperature. *C. finmarchicus* references: Tande 1982; Richardson et al. 1999; Runge and Plourde 1996; Ohman and Runge 1994; Kjellerup et al. 2012; Svensen and Tande 1999; Niehoff et al. 1999; McLaren et al. 2001; Niehoff 2004; Runge et al. 2006; Munk et al. 2003; Madsen et al. 2008a; Jønasdøttir et al. 2008; Stenevik et al. 2007; *C.helgolandicus*: Jønasdøttir et al. 2005; Ceballos et al. 2004; Ceballos and Álvarez Marqués 2006b; Rey-Rassat et al. 2002c; Jønasdøttir and Koski 2011; Yebra et al. 2011; Bonnet et al. 2009

Prosome lengths of females in co-occurring populations have been reported in the North Sea by two studies (Jønasdøttir et al., 2005; Jønasdøttir and Koski, 2011). Comparison of these results (Figure 2.2) indicates a very close relationship between female prosome lengths of each species. No biologically significant differences in body size are discernible, with *C. helgolandicus* having a marginally larger mean female prosome length (2.58 mm) than *C. finmarchicus* (2.56 mm). We therefore conclude that existing evidence is consistent with both species developing to the same body size under identical environmental conditions.

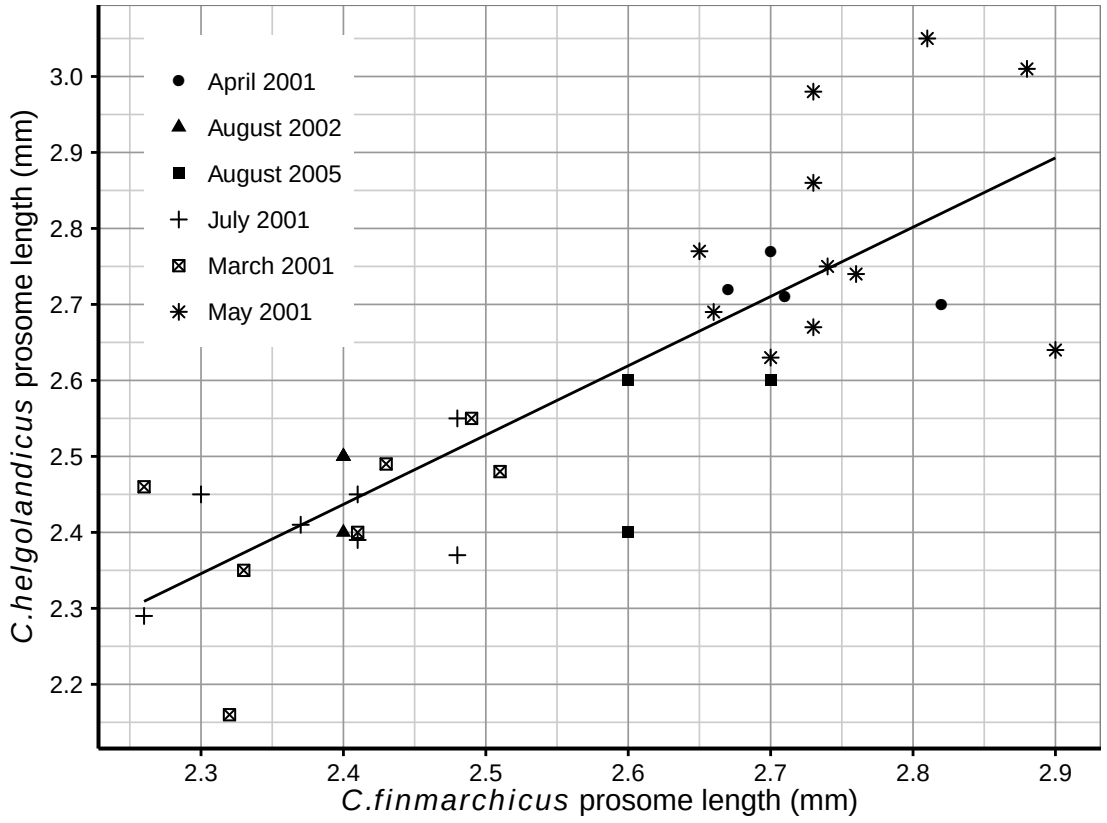


FIGURE 2.2: Comparison of female prosome lengths for co-occurring *C. finmarchicus* and *C. helgolandicus* published in Jønasdøttir et al. (2005) and Jønasdøttir and Koski (2011).

2.2.2 Influence of temperature and development and growth

Interspecies differences in growth rate and development time are likely to be strong determinants of differences in the viability of each species in a particular environment. Here we critically review published development times for each species to see if there are interspecies differences.

2.2.2.1 Comparison of published development times

The most extensive study of growth and development in *C. finmarchicus* is the classic work of Campbell et al. (2001), which has been used in a number of population models (Melle et al., 2014). A key finding was that *C. finmarchicus* follows the equiproportional rule of development (Corkett et al., 1986). This important rule states that the relative duration of each stage is independent of temperature. A notable departure from equiportionality was observed for the C5 stage, which was prolonged at a temperature of 4°C, however the reasons for this were unclear. Additional evidence that *C. finmarchicus* undergoes equiproportional development is given by the laboratory study of Hygum et al. (2000a). Tande (1988) concluded that *C. finmarchicus* does not undergo equiproportional development. However, they compared individuals from different geographic regions, and did not control for food conditions. Campbell et al. (2001) found that between 4 and 12°C, the relationship between development time and temperature followed a Belehrádek function (Belehrádek, 1935). Development time from egg to adult was approximately 91, 45 and 32 d at 4, 8 and 12°C respectively. Comparison with other published estimates of *C. finmarchicus* development time from egg to adult (Corkett et al., 1986; Tande, 1988) show very close agreement in development times across studies. The work of Campbell et al. (2001) therefore appears to be a solid basis for the many modelling studies that have used it.

Development and growth of *C. helgolandicus* has been studied less extensively. The first published study of its growth from egg to adult was that of Thompson (1982), which concluded that *C. helgolandicus* does not develop equiproportionally. However, they did not perform species identification checks (Thompson, 1982), which possibly resulted in a large number of *C. finmarchicus* individuals being used. Apart from this, the recent work of Bonnet et al. (2009) is the only laboratory study of *C. helgolandicus* growth from egg to adult to consider the influence of temperature on stage duration. Analysis of stage durations at temperatures of 9, 12 and 15°C indicated that naupliar stages

develop equiproportionally, but they concluded that copepodite stages did not. A comparison of stage durations of this study with two others (Rey et al., 2001; Cook et al., 2007) showed very consistent relative stage durations for naupliar stages across each study, providing further confirmation that naupliar stages develop equiproportionally.

We plotted published relationships between egg to C5 development time and temperature for both species (Figure 2.3). This illustrates apparently clear differences between each species at temperatures at and below 12°C. All development times from egg to C5 for *C. helgolandicus* (Bonnet et al., 2009; Thompson, 1982; Diel and Klein Breteler, 1986) are longer at the relevant temperature than would be expected for *C. finmarchicus* based on the classic work of Campbell et al. (2001). Development times for naupliar stages of *C. helgolandicus* were also found to be longer at 8 and 12°C by Cook et al. (2007) in comparison with published naupliar development times for *C. finmarchicus* (Campbell et al., 2001; Cook et al., 2007).

However, published development times for *C. helgolandicus* are not consistent with each other. This makes inferring the quantitative differences between each species problematic. The experimental results of Bonnet et al. (2009) indicate that at 12°C, *C. helgolandicus* takes approximately 10 d longer to develop from egg to adult than *C. finmarchicus* (Campbell et al., 2001), and that development time from egg to adult for *C. helgolandicus* at 15°C is approximately 5 d longer than for *C. finmarchicus* at 12°C. These differences are not consistent with other published results. Cook et al. (2007) found that *C. helgolandicus* had a shorter development time from egg to final naupliar stage at 15°C than *C. finmarchicus* did at 12°C. *C. helgolandicus* development time from egg to C1 was also 4 and 6 d shorter at 12 and 15°C respectively in Cook et al. (2007) than in Bonnet et al. (2009). Similarly, Rey et al. (2001) reported *C. helgolandicus* development times from egg to C1 under multiple food regimes at 15°C, finding development time under 10 d for all regimes. This is in contrast to the 14 d reported in Bonnet et al. (2009).

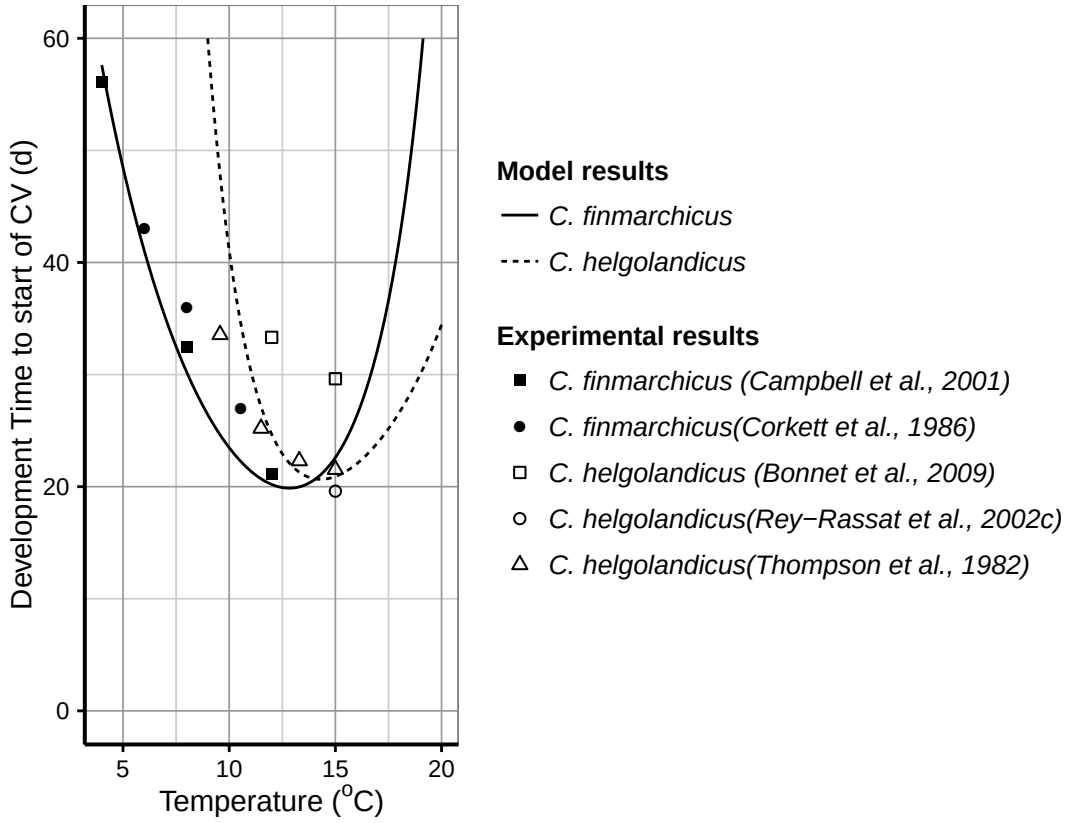


FIGURE 2.3: Development time for *C. finmarchicus* and *C. helgolandicus* from egg to start of C5 stage. Model was parameterized for *C. finmarchicus* using Campbell et al. (2001). Solid lines are modelled development times assuming that the only interspecies difference is the relationship between ingestion rate and temperature, whereas symbols are published experimental development times for each species.

After comparing their results with those of Thompson (1982), Bonnet et al. (2009) concluded that the experiment of Thompson (1982) probably contained significant numbers of *C. finmarchicus* individuals. However, the development time to final naupliar stage at 12°C recorded by Thompson is very similar to those reported for *C. helgolandicus* by Cook et al. (2007) and Rey et al. (2001). Similarly, the development time from egg to adult reported by Thompson (1982) (26.21 d) is similar to the time (24.4 d) reported by Rey et al. (2001). The difference between the development times to adult reported by Rey-Rassat et al. (2002c) and Bonnet et al. (2009) is 12 d, and this is particularly anomalous given that the same food regime was used in both studies (*Prorocentrum micans*). The development time reported by Diel and Klein Breteler (1986)

at 10°C (39 d) is also reasonably consistent with that reported by Thompson (1982) at 9.57°C (41.72 d).

This suggests that the development times published by Thompson (1982); Rey et al. (2001); Cook et al. (2007); Diel and Klein Breteler (1986) are broadly consistent. In contrast, Bonnet et al. (2009) appears to be an outlier, reporting significantly longer development times than the other studies.

After reviewing the methodology in these studies it appears that differences in dietary regimes are probably the reason for the diaparities in published *C. helgolandicus* development times. As shown by Diel and Klein Breteler (1986), diet can have a significant influence on the development time of *Calanus* species. Bonnet et al. (2009); Cook et al. (2007); Rey et al. (2001); Rey-Rassat et al. (2002c) all reported development times under the same dietary regime (*Prorocentrum micans*). However, Bonnet et al. (2009) appear to have grown individuals at below food saturated conditions. Total volume of water was 0.5 mL/individual in Bonnet et al. (2009) in contrast to 6.25 (Cook et al., 2007), 4 (Rey et al., 2001) and 6 mL/individual (Rey-Rassat et al., 2002c) in the other studies. Bonnet et al. (2009) replenished food supply every 12 hours, however clearance rates for stages N1-N6 are approximately 3 ml/individual/day (Rey et al., 2001) when fed on a *P. micans* diet. In addition, the mean prosome length of females reported by Bonnet et al. (2009) at 15°C was 1.95 mm, significantly lower than the mean of 2.59 mm reported by Rey-Rassat et al. (2002c). It therefore appears probable that the lower development times reported by Bonnet et al. (2009) are a direct result of the dietary regime used.

If we accept that the *C. helgolandicus* development times reported by Bonnet et al. (2009) cannot be compared directly with the published times for *C. finmarchicus* then we can draw the following conclusions. *C. finmarchicus* has shorter development times than *C. helgolandicus* at and below temperatures of 12°C. However, a lack of published data means we do not know if there are interspecies differences above 12°C.

We are therefore faced with two questions. First: What explains the interspecies differences in development times? Second: Are there interspecies differences at temperatures above 12°C? We consider these questions by developing a model of the growth and development of each species. In turn, we are asking a third question. Can known differences in development time between the two species be explained by known differences in the key drivers of growth rate?

Growth in *Calanus* species in essence is the net change in body weight that results from the following key processes: ingestion and assimilation of food, egestion, excretion and metabolism. Differences in development time for each species must result from quantitative differences in how one or more of these processes are influenced by temperature and/or diet, or in absolute differences at each temperature.

Before detailing our growth and development model we will review existing knowledge of interspecies differences in these life cycle traits.

2.2.2.2 Metabolism and excretion

Metabolism plays a key role in determining the thermal niche and the potential to diapause of each species (Ingvarsdøttir et al., 1999). Recently, Maps et al. (2014) summarized published metabolic rates for *Calanus* species. In total, five papers have reported respiration rates for *C. finmarchicus* (Hirche, 1983; Marshall and Orr, 1958; Saumweber and Durbin, 2006; Ingvarsdøttir et al., 1999; Ikeda et al., 2001). These studies provide valuable quantitative insight into the metabolism of *C. finmarchicus* in both a diapausing and non-diapausing state. Only one of these papers (Hirche, 1983) is sometimes referenced as reporting *C. helgolandicus* respiration rates. Hirche (1983) reported *C. finmarchicus* respiration rates which were based exclusively on *C. finmarchicus* individuals. However, *C. helgolandicus* individuals were not distinguished from *C. finmarchicus* in the experiments sometimes referred to as showing *C. helgolandicus* respiration rates. A knowledge gap therefore exists in our understanding of metabolism in

C. helgolandicus. However, the strong relationship between body size and metabolism (Ikeda et al., 2001) suggests that metabolic rates for *C. finmarchicus* and *C. helgolandicus* should be very similar. In addition, Maps et al. (2014) concluded that there was an almost identical interspecies pattern in allometric scaling of metabolism with body size across *Calanus* species. However, apparent interspecies differences in response of ingestion to temperature (Møller et al., 2012) suggests that the energetics of each species differ, which may result in different metabolic rates.

Assimilation and excretion play critical roles in determining growth rate in zooplankton. A number of studies have reported assimilation efficiencies for *Calanus* species under different dietary regimes (summarized in Mayor et al. (2011)). However, the lack of directly comparable data means that interspecies comparisons are currently not possible and remain an open question.

2.2.2.3 Influence of food on growth

A small number of studies have considered the influence of food concentration on growth in each species, however discerning the existence of interspecies differences from these studies is difficult. The laboratory study of Campbell et al. (2001) considered the relationship between relative stage duration and carbon and nitrogen growth rates and food concentration. Stage durations were only recorded for low, medium and high food concentration; however there was a clear trend, with both nauplii and copepodite stages exhibiting longer stage durations at lower food concentrations. Carbon and nitrogen specific growth rates were found to saturate at high food concentrations.

The influence of food concentration on *C. helgolandicus* development time from egg to naupliar stages (Cook et al., 2007) and from egg to adult stages (Rey-Rassat et al., 2002c) have been studied experimentally. Both studies only considered diets that could be described as having low and high food concentration, and they indicated that development is significantly slower at lower food concentrations.

Influences of both diet (Rey et al., 2001) and food concentration (Rey-Rassat et al., 2002c) on *C. helgolandicus* growth have been studied experimentally. Low food concentration has a significant negative influence on *C. helgolandicus* carbon and nitrogen growth rate (Rey-Rassat et al., 2002c). Growth rates also appear to be influenced by dietary composition, with Rey et al. (2001) reporting different carbon and nitrogen growth rates under varying dietary regimes. These studies only considered growth at the temperature of 15°C, therefore due to the influence of temperature and body size on ingestion growth rates in each species cannot be reliably compared.

We are therefore only able to make general descriptions of the relationship between growth and food concentration for each species. The nature of the functional response (Gentleman et al., 2003) of growth rate to food concentration in each species is uncertain. However, global patterns (Hirst and Bunker, 2003) and that for *C. finmarchicus* (Campbell et al., 2001) indicates that this functional response may follow a Michaelis-Menten relationship. Further study is necessary to provide evidence of interspecies differences.

Similarities in feeding behaviour were indicated by the study of Meyer et al. (2002), which found that neither *C. finmarchicus* or *C. helgolandicus* fed selectively on different algal groups of the same size, concluding that only size selective algal feeding occurred in each species. Harris (1996) also studied *C. finmarchicus* and *C. helgolandicus* in the field and concluded that size-selective feeding predominated. However, in general, non-size selective-feeding has been observed in both species (e.g. Meyer-Harms et al. (1999) and Irigoien et al. (2000b)).

Temperature and body size both have significant influences on ingestion rates in *Calanus* species (Harris, 1996)). A consequence is that quantitative comparisons of individuals of each species from different geographic regions need to be interpreted carefully. This difficulty is raised by the two existing comparative studies of feeding in each species

(Meyer et al., 2002; Møller et al., 2012), with both studies raising each species at significantly different temperatures. The smaller size of *C. helgolandicus* than *C. finmarchicus* in existing feeding studies is likely to partially explain any interspecies differences in absolute ingestion rate, due to allometric scaling of ingestion rate (Wirtz, 2013). The results of Meyer et al. (2002) showed higher ingestion rates for nauplii, copepodite and adult female *C. finmarchicus* than for *C. helgolandicus*. However, the temperature at which individuals were raised and feeding experiments conducted, 10°C for *C. finmarchicus* and 15°C for *C. helgolandicus*, means that differences between the two species ingestion rates cannot be confidently related to interspecies differences rather than the influence of temperature on body size and ingestion.

The recent study of Møller et al. (2012), which measured clearance rate over a wide temperature range for both species, provides a more accurate quantification of the differences between each species ingestion rates. Clearance rate for females, normalized to the fraction of its maximum clearance rate, was higher for *C. finmarchicus* below 11°C, but higher for *C. helgolandicus* above 11°C (Figure 2.4). A dome shaped response of ingestion rate to temperature was found for both species, with optimum temperature for *C. finmarchicus* being approximately 11°C and *C. helgolandicus* being 13°C. The significant differences of the temperature at which individuals were raised; 5°C for *C. finmarchicus* and 15°C for *C. helgolandicus* would have resulted in *C. finmarchicus* females being significantly larger than *C. helgolandicus*. This, coupled with potential acclimatization effects, means that future study of clearance rates of individuals raised under identical conditions is needed to clarify our understanding of interspecies differences.

It was generally assumed that *Calanus* species do not consume small cells, i.e. those that are “filtered” (Meyer et al., 2002). However, evidence indicates that *C. helgolandicus* consumes small cells (Meyer et al., 2002), and has been raised to adult stages on a diet of *Isochrysis galbana* (Irigoien et al., 2000b). Naupliar stages of *C. helgolandicus*

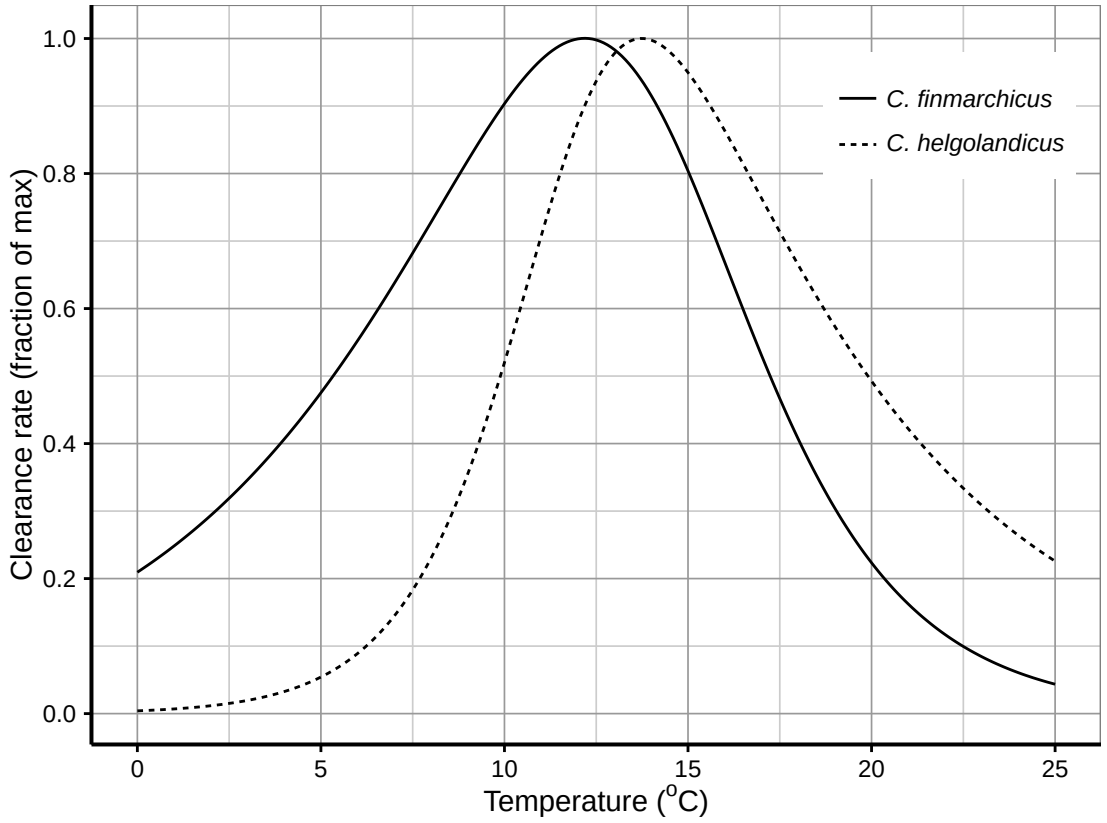


FIGURE 2.4: The relationship between clearance rate and temperature for *C. finmarchicus* and *C. helgolandicus*. Reproduced from Møller et al. (2012), an experimental study which estimated clearance rates for both species at a number of temperatures.

appear to require higher food concentrations and develop more slowly when feeding on smaller cells (Cook et al., 2007). *C. finmarchicus* is also known to consume small cells (Harris, 1996; Båmstedt et al., 1999). Feeding studies of both species grown under the same environmental conditions will be needed to confirm if there is an interspecies difference in ingestion rate when feeding on small cells.

2.2.2.4 Growth and development model

Reviewing published studies of ingestion, ability to assimilate food and metabolism indicates that we can only make direct quantitative comparisons of the relationship between ingestion rate and temperature. We therefore hypothesized that interspecies differences in the response of ingestion rate to temperature alone can explain a large part of the difference in published development times, and we tested this by creating a new development model. Published development times for *C. finmarchicus* (Campbell et al., 2001; Corkett et al., 1986) and *C. helgolandicus* (Bonnet et al., 2009; Rey-Rassat et al., 2002c; Thompson, 1982; Diel and Klein Breteler, 1986) were used for parameterization and model testing purposes.

Allometric scaling of key functions with body size suggests that stage based development can be dispensed with and replaced with a more simplified view of development that will maintain the key quantitative aspects of development. Ingestion and metabolic rates are therefore assumed to be stage independent in our model, i.e. they only depend on body size and temperature. Molting between stages is influenced strongly by body weight, and we assume that molting body weight is pre-determined, referring to this as the critical molting weight (Carlotti et al., 1993). Consideration of published body sizes (Figure 2.1) indicates that terminal body size is the same for both species under identical environmental conditions, and that body size under food saturated conditions is determined by temperature (Campbell et al., 2001). We therefore assume that terminal adult body weight is determined by temperature. Carbon weight was used as our measure of body weight. Development in stage C5 of *C. finmarchicus* is a combination of structural growth and lipid accumulation. Lipid accumulation occurs on a large scale in C5 of *C. finmarchicus* as a precursor to diapause, however *C. helgolandicus* may not accumulate lipids on the same scale. Consequently, we have parameterized our development model only up to the start of C5. As a result of a lack of comparable experimental data on the relationship between development time and food concentration

for each species we assume food-saturated conditions throughout.

Ingestion of carbon is governed by two processes: the relationship between maximum carbon ingestion rate (units: μ C h^{-1}) and body size (units: μg C), f_1, and the relationship between carbon ingestion rate and temperature, f_2. Ingestion rate in zooplankton is understood to be strongly influenced by body size (Wirtz, 2013). Saiz and Calbet (2007) showed that maximum ingestion rate has approximately 3/4 power scaling with body size, therefore we set f_1 to be $\mu w^{0.75}$, where w is carbon weight (μg C) and μ is a parameter to be fitted within boundaries estimated from Saiz and Calbet (2007). The form of f_2 is a dome shaped response (Figure 2.4) taken from Møller et al. (2012). Some of the food ingested is egested or excreted and therefore not assimilated into body carbon. We define the assimilation efficiency, AE, as the percentage of food ingested that is assimilated, and this is parameterized within boundaries derived from Mayor et al. (2011). This is then applied to the ingestion rate to give us the rate at which food is assimilated into body carbon.

Metabolic costs are understood to have approximately 3/4 power scaling with body weight in general (Gillooly et al., 2001) and the review by Maps et al. (2014) indicates that this holds for *Calanus*. Metabolism also increases with temperature, and this relationship follows a Q_{10} relationship, i.e. each increase in temperature of 10°C will result in respiration rates increasing by a factor of Q_{10}. Therefore we use the equation $Q_{10}^{T/10}\lambda w^{0.75}$ to represent metabolic costs (units: μg C h^{-1}), where T is temperature (°C) and with Q_{10} and λ being parameterized within reasonable bounds derived from the literature review contained in (Maps et al., 2014). Minimum and maximum published Q_{10} are 2.3 (Marshall and Orr, 1958) and 3.4 (Hirche, 1983) respectively.

Thus our growth model is a differential equation of the form:

$$\dot{w} = f_2 AE\mu w^{0.75} - Q_{10}^{(T/10)} \lambda w^{0.75} \tag{2.1}$$

where $\dot{w}$ is the rate of growth of carbon weight (μgC h^{-1}) and

$$f_2 = \frac{P_5}{[1 + exp(P_3/T - P_3/P_1) + exp(P_4/P_2 - P_4/T)]} \tag{2.2}$$

For *C. finmarchicus* $P_1 = 293, P_2 = 284, P_3 = 13,282, P_4 = 29,725$, and $P_5 = 6.05$, and for *C. helgolandicus* $P_1 = 289, P_2 = 275, P_3 = 39,429, P_4 = 14,123$ and $P_5 = 12.12$ (Møller et al., 2012). P_5 is a typo corrected from Møller et al. (2012) (Møller, personal communication).

Individuals are assumed to molt to the next stage when their carbon weight reaches the respective critical molting weight. We estimated the relationship between molting weight for C5 individuals and temperature using published data on length-weight (Hygum et al., 2000b) and temperature-length relationships (Campbell et al., 2001). C5 molting weight was therefore assumed to relate to temperature using the equation $C_m = 2.307 * 10^{-10} * (-27.4 * T + 2084)^{3.52}$, where C_m is the C5 molting carbon weight (μg), and T is temperature (°C).

First we parameterize our model completely for *C. finmarchicus*, using the development times at 4, 8 and 12°C under food-saturated conditions reported by Campbell et al. (2001). The parameterization of development to C5 was performed by minimising the least squares of our model fit. This provides a general parameterization of growth to C5 for *C. finmarchicus*, and our parameter values are $AE = 0.488$, $Q_{10} = 3.19$, $\mu = 0.0415$, $\lambda = 0.000101$. The relationship between development time and temperature given by the model (Figure 2.3) departs from the conventional Belehrádek function, which sees development time decrease monotonically with temperature. In contrast, our model

indicates that there is a U-shaped relationship between development time and temperature. This U-shape is a result of the differing relationships between ingestion rate and metabolism and temperature. Ingestion rate appears to decrease with increasing temperatures above a temperature of approximately 12°C for *C. finmarchicus* (Møller et al., 2012). However, metabolic costs will continue to increase with temperature. As a result, carbon-specific growth rate will have a dome-shaped response to temperature, and development time will have a U-shaped response in turn.

We then changed the ingestion rate parameters to model *C. helgolandicus* and compared the results with published development times for *C. helgolandicus* (Figure 2.3). Modelled *C. helgolandicus* developments times are reasonably consistent with those of (Thompson, 1982) and (Rey-Rassat et al., 2002c). However, as expected, they are considerably shorter than those reported by Bonnet et al. (2009); approximately 8 d at 12 and 15°C. This implies that the development times published by Thompson (1982); Cook et al. (2007); Rey et al. (2001) and Rey-Rassat et al. (2002c) are more directly comparable with those of *C. finmarchicus* published by Campbell et al. (2001).

Published differences in ingestion rate therefore appear to able to explain most of the known interspecies differences in development time. However, future study is needed to clarify these issues. Quantitative understanding of interspecies differences in absolute ingestion and respiration rates is currently lacking, along with knowledge of the influence of temperature on respiration rate. Dietary regime can have a significant influence on growth (Rey et al., 2001), and therefore future studies of potential interspecies differences in the influence of food quality on development appears to be useful.

In addition, the *C. helgolandicus* individuals captured by (Møller et al., 2012), were from a geographically identical region, L4 English Channel, to those used by Bonnet et al. (2009). However, Møller et al. (2012) (Gullmar fjord, Norway) captured individuals from a geographically distinct region from those in Campbell et al. (2001) (Gulf

of Maine). Genetic differentiation exists between eastern and western North Atlantic populations (Unal and Bucklin, 2010). Whether this differentiation results in significant quantitative differences in aspects of the Calanus life cycle, such as development time, remains an open question (Melle et al., 2014).

The relationship between development time and temperature produced here is unconventional; however it is consistent with that produced by Møller et al. (2012)), who used the same ingestion rate-temperature relationship to model development in *C. finmarchicus* and *C. helgolandicus*. Currently, there is no data to test whether, as predicted, this relationship departs from the conventional Belehrádek function. This is because development time has yet to be measured at temperatures above the turning points implied by our model. However, there is considerable evidence that this may be the case. Experimental evidence indicates that the relationship between egg production rate and temperature appears to be dome-shaped for most zooplankton species where egg production rate is reported at a broad enough temperature range (e.g. Halsband-Lenk et al. (2002); Holste and Peck (2006), and Pasternak et al. (2013)). In addition to Møller et al. (2012), a dome-shaped response has been found between ingestion rate and temperature in other zooplankton species (e.g. Garrido et al. (2013) and Alcaraz et al. (2013)). This indicates that a dome-shaped response of growth to temperature may be a regular occurrence in zooplankton species.

Our model also indicates that there is an upper temperature limit, above which *Calanus* species cannot exist. At around 18°C, the development time for *C. finmarchicus* is lengthened extremely. High metabolic costs and lowered ingestion rates in this temperature region are likely to result in high mortality rates and an inability of *C. finmarchicus* populations to persist. This temperature range coincides with that seen in regions just south of the southerly latitudinal extent of *C. finmarchicus*. Similarly, development time for *C. helgolandicus* is extremely protracted at temperatures below 9°C. We therefore hypothesize that the inability of Bonnet et al. (2009) to raise *C. helgolandicus* to adult at

9°C results from ingestion being too low at that temperature to offset metabolism. This suggests that both species may only be able to exist within particular thermal windows. These windows are of particular interest in the context of climate change. Alcaraz et al. (2013) recently synthesized research on thermal thresholds and concluded that differences in the temperature response of positive and negative elements of metabolic balance can result in an upper temperature threshold for zooplankton. Further quantification of these relationships will provide useful insights into the likely impacts of climate change on *Calanus* species.

2.2.3 Egg Production

Environmental influences on egg production rate play a significant role in influencing the population dynamics of zooplankton. Therefore interspecies differences in egg production rate are a candidate mechanistic explanation of the large geographic differences in populations of *C. finmarchicus* and *C. helgolandicus*.

Spawning time of each species has been reported by a small number of papers. *C. finmarchicus* and *C. helgolandicus* have been reported to spawn at midnight and midday (Laabir et al., 1995), and midday and dawn (Marshall and Orr, 1955; Runge, 1987) respectively. Whether these studies indicate interspecies differences in spawning behaviour remains inconclusive.

2.2.3.1 Environmental influences on egg production

Environmental variations are known to have a significant influence on egg production rate (EPR) of *Calanus* species. Temperature (Hirche et al., 1997), body size (Campbell and Head, 2000), and food quantity and quality (Diel and Tande, 1992; Jønasdøttir et al., 2002) all influence EPR. Importantly, comparisons of EPR in different geographic regions is made challenging by the complex influence of temperature. In broad terms

temperature has two key influences. Higher temperatures result in smaller females, and this has a negative influence on EPR (Campbell and Head, 2000). In contrast, for a given female EPR will increase with temperature (Hirche et al., 1997).

2.2.3.2 Comparison of egg production rate in both species

We reviewed published studies of maximum EPR for *C. finmarchicus* and *C. helgolandicus* (Figure 2.5). The studies indicate that EPR for *C. finmarchicus* is in general higher than for *C. helgolandicus* at each species optimal temperature for growth. However, this is not evidence of biological differences in egg production rate. Body size is significantly lower in *C. helgolandicus* than *C. finmarchicus* at optimal temperatures, therefore the strong positive relationship between body size and egg production rate (Campbell and Head, 2000; Jønasdøttir et al., 2005) possibly explains a large part of the difference between each species in these studies. The apparent reduction in maximum EPR with increased annual temperature indicates that body size variation explains a significant part of the large scale geographic variation in EPR across both species. However, the large scale relationship between temperature and egg production rate is still a matter of debate.

A recent study (Bonnet et al., 2005) compared EPR for *C. helgolandicus* at four separate stations, finding that temperature did not have a discernibly large influence. This inability to predict the influence of temperature on egg production over large geographic scales has also been demonstrated by a multi-station analysis of *C. finmarchicus* EPR (Melle et al., 2014). In contrast, laboratory studies have found that temperature does have a significant influence on egg production rate (Runge and Plourde, 1996; Hirche et al., 1997; Jønasdøttir et al., 2005; Jønasdøttir and Koski, 2011). This lack of quantitative understanding of the influences on geographic variations in egg production rate within species means that comparison of individuals living in very similar, or identical,

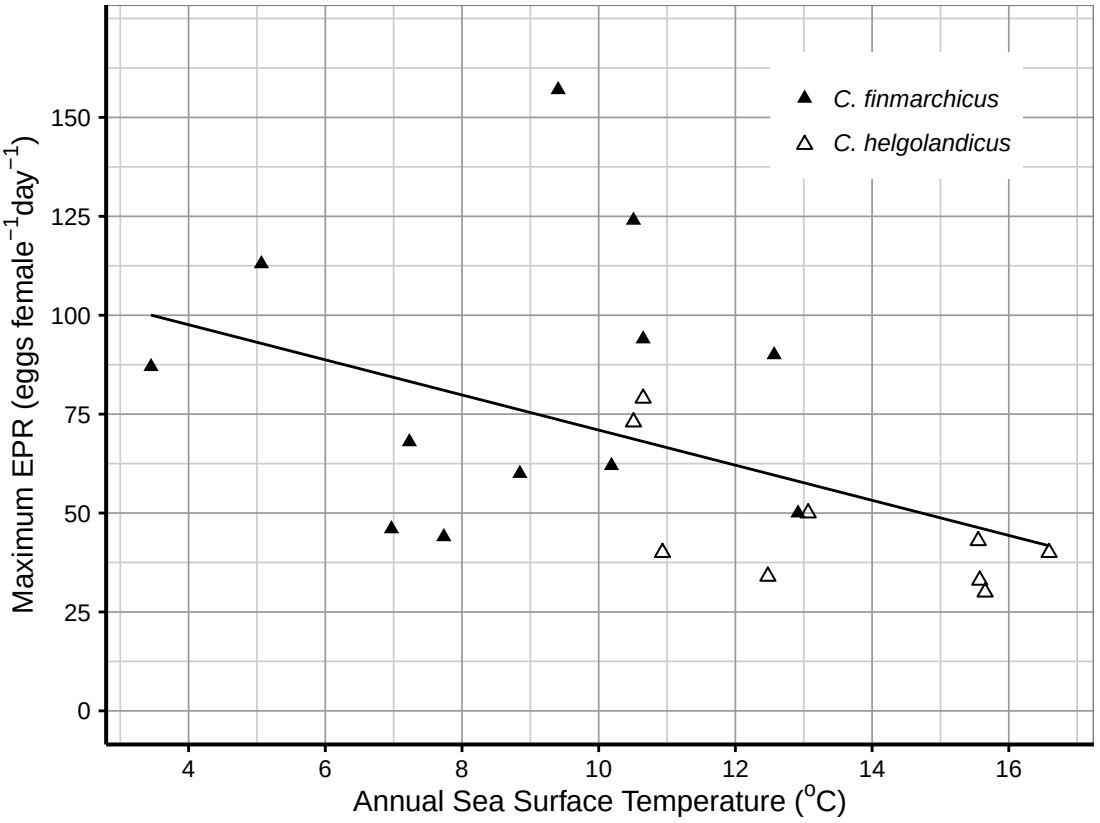


FIGURE 2.5: Comparison of published maximum egg production rates and annual average SST. *C. finmarchicus*: Head et al. (2000); Diel and Tande (1992); Jønasdøttir et al. (2008); Niehoff et al. (1999); Niehoff (2004); Durbin et al. (2003); Jønasdøttir et al. (2005); Jønasdøttir and Koski (2011); Gislason and Astthorsson (2000); Hay (1995); Runge et al. (2006); Campbell and Head (2000). *C. helgolandicus*: Fileman et al. (2010); Harris (1988); Tiselius et al. (2012); Ceballos et al. (2004); Ceballos and Álvarez Marqués (2006b); Ceballos et al. (2006); Jønasdøttir and Koski (2011); Jønasdøttir et al. (2005). Line shows linear model: Max. EPR = 115.35 - 4.438 * Temperature ($R^2 = 0.175$).

environments is needed if we are to draw inferences about interspecies differences in egg production rate.

Rigorous comparison of egg production rates of co-occurring *C. finmarchicus* and *C. helgolandicus* faces a number of difficulties. Ages of co-occurring females may be significantly different as a result of interspecies differences in development time. This can have an impact on relative EPR of each species for multiple reasons: young females can take a significant time to reach full reproductive maturity (Plourde and Runge,

1993; Niehoff et al., 1999), older females can have lower EPR (Diel and Tande, 1992; Hirche et al., 1997), and feeding history can have a significant impact on EPR (Rey-Rassat et al., 2002b; Hirche et al., 1997; Niehoff, 2000; Ceballos and Álvarez Marqués, 2006b).

To date two studies, both carried out in the Dogger Bank, North Sea, have recorded EPR for co-occuring *C. finmarchicus* and *C. helgolandicus* (Jønasdøttir et al., 2005; Jønasdøttir and Koski, 2011). These studies show that interspecies differences, if they exist, do not follow a clear pattern. Jønasdøttir and Koski (2011) reported egg production rates for the years 2001, 2002 and 2005, finding no statistically significant differences between the two species EPR. Jønasdøttir et al. (2005) reported that *C. finmarchicus* had higher per capita EPR in March, April and June 2001, whereas it was higher in *C. helgolandicus* in May and September of that year. This lack of a clear seasonal pattern is in contrast to what we would expect from the apparent relationship each species ingestion rate has to temperature (Møller et al., 2012). EPR and ingestion rate are positively correlated for calanoid species (Peterson and Dam, 1996), which we would expect to result in a discernable pattern of interspecies differences in EPR.

These results should also be interpreted in the light of their respective development times. Our development model (Figure 2.3) indicates that at the temperatures reported in these studies both species will have very similar growth rates. Processes governing EPR and growth are very similar (Mclaren and Leonard, 1995), therefore we may expect the relationship between EPR and temperature to follow a similar pattern to that between development time and temperature. EPR is conventionally viewed as increasing with in situ temperature, however our growth model suggests that at high temperatures the trade off between ingestion and respiration will result in a dome shaped response of EPR with temperature. This dome shaped response has been shown for other zooplankton (e.g. Holste and Peck (2006)), however studies of EPR at a wider

range of temperatures is needed to confirm if it exists for *C. finmarchicus* and *C. helgolandicus*. This potential temperature response may also be a further influence on the thermal niche of each species.

We conclude that at its optimal temperatures of 15 °*C. helgolandicus* will have significantly lower egg production rate than for *C. finmarchicus* at its optimal temperature of 12 °C. However, based on studies of co-occurring individuals there is no evidence of clear interspecies differences.

2.2.4 Vertical population structuring and diel vertical migration

Both *C. finmarchicus* (Heath et al., 2004) and *C. helgolandicus* (Andersen et al., 2001) display vertical population structuring where the seasonal thermocline has developed. Studies in the Irish Sea (Williams, 1985) and the Dogger Bank, North Sea (Jønasdøttir et al., 2005) indicate a distinct pattern of vertical structuring in each species. Prior to the development of the seasonal thermocline there is no evidence of differences in vertical structuring. In contrast, the development of the thermocline results in *C. finmarchicus* largely living in cooler deep waters, with *C. helgolandicus* remaining at the surface. Gowen et al. (1997) found that there appeared to be no preference for stratified or non-stratified regions of the Irish Sea by *C. finmarchicus* or *C. helgoldandicus*, which they argue suggests that there was no spatial separation between the two species. Irigoien et al. (2004) also found no significant difference between the vertical positioning of *C. finmarchicus* and *C. helgolandicus* in the water column in the Irish Sea. However, the temperatures in this study region were significantly lower than for Williams (1985) and Jønasdøttir and Koski (2011), where living in deeper waters may be necessary for *C. finmarchicus* to survive. The extent of vertical separation between the two species may therefore be strongly influenced by the temperature profile of the water column.

These differences can be interpreted using our development model for each species. The differences in vertical distribution are likely a reflection of each species different metabolism-ingestion trade off. At temperatures of approximately 17 °C, *C. finmarchicus* may be incapable of offsetting metabolic costs through ingestion, therefore existence in colder deeper waters may be a necessary life cycle adaptation.

Diel vertical migration plays an important role in *Calanus* species, allowing individuals to avoid predation, and to feed at optimal times (Lampert, 1993). Comparisons of vertical structuring during the day and night show clear evidence that both species undertake diel vertical migration (Jønasdøttir and Koski, 2011; Andersen et al., 2004). The only study of diel vertical migration of co-existing *C. finmarchicus* and *C. helgolandicus* (Irigoien et al., 2004) found no significant difference between each species diel vertical migration behaviour in the Irish Sea. Both species migrated to the surface at night in the central part of the Irish Sea, but at coastal regions this pattern was reversed. No significant differences were found between the diel vertical migration amplitude of each species.

2.2.5 Diapause Behaviour

A key life cycle adaptation of *C. finmarchicus* is a long non-feeding period during winter which is spent in deep waters with reduced respiration rates. This behaviour is commonly referred to as diapause, dormancy or overwintering in the literature (reviewed in Hirche (1996)). The reasons for this period of diapause are thought to be multiple, including the need to survive long periods of low food supply and avoiding high predation rates (Ji, 2011). Individuals normally enter diapause during the fifth copepodite stage (Heath and Jønasdøttir, 1999), however significant numbers of C4 copepodites have been observed in some diapause populations (Head and Pepin, 2008).

Diapause usually begins in summer and autumn when individuals swim to depths (Hirche, 1996) and remain there for a period of up to six months. Median diapause

duration has been estimated as 200 d in the western North Atlantic and 250 d in the eastern North Atlantic (Melle et al., 2014). Exit from diapause normally occurs in the second half of winter, but significant geographic variations in timing exists (Jønasdøttir et al., 2008). This diapause period is known to occur at a temperature range of -1-11 °C (Dupont and Aksnes, 2012) and a depth range of 500-1500 m (Heath and Jønasdøttir, 1999).

Some uncertainty persists in our understanding of the causes and mechanisms behind diapause in *C. finmarchicus*, however a large body of evidence (synthesized in Irigoien (2004)) now indicates that lipids play a fundamental role in diapause for *C. finmarchicus*. Before diapause commences individuals build up significant lipid reserves. These lipid reserves are primarily composed of wax esters (WE), the proportion of which is normally in excess of 80% (Kjellerup et al., 2012). Lipids then act as the primary energy reserve for respiration during diapause (Ingvarsdøttir et al., 1999), with lipid sacs often taking up in excess of 60% of body volume (Perrin et al., 2012), but being continuously depleted as diapause proceeds.

Diapause requires individuals to maintain neutral buoyancy at depths for a significant period of time. Visser and Jønasdøttir (1999) proposed that the thermo-physical properties of lipids enable *C. finmarchicus* to attain neutral buoyancy in deep waters. This ability however has been challenged due to its sensitivity to the relative biochemical composition of individuals (Campbell and Dower, 2003). The model of Visser and Jønasdøttir (1999) was also based on the properties of the lipids in the Pacific species *Neocalanus plumchrus*, and it is unclear if the properties of lipids in *C. finmarchicus* are the same (Wilson et al., 2013; Pond and Tarling, 2013).

Recently the level of unsaturation in lipids has been proposed as a partial determinant of the neutral buoyancy depth of zooplankton (Pond, 2012). The temperature at which lipids can undergo liquid-solid phase transitions is dependent on the level of unsaturation (Pond and Tarling, 2011), and selective catabolism of saturated and unsaturated

wax esters may play a key role in aiding neutral buoyancy during diapause (Clark et al., 2012). The physical properties of *C. finmarchicus* lipids in general, and in terms of their relationship to unsaturation level needs further study, and so the relative importance of lipids to buoyancy regulation remains unclear.

After exiting diapause, individuals molt to the next development stage, primarily from C5 to adult. C5 individuals that are to become female predominantly exit diapause after males (Heath, 1999) and then lay eggs in proportion to food supply, however there is some evidence that remaining lipid reserves may fuel pre-spring bloom egg production (Richardson et al., 1999).

It remains unclear what triggers diapause entrance and exit. Photoperiod was proposed as a potential trigger for diapause initiation and exit (Miller et al., 1991), however this failed to reproduce the observed geographic variations in diapause onset and duration (Hind et al., 2000). Current debate centres on whether diapause initiation is related specifically to the amount and composition of lipids, with the Lipid Accumulation Window hypothesis (Maps et al., 2012b) and wax ester unsaturation level (Pond, 2012) having been proposed as triggers for diapause initiation.

In contrast to *C. finmarchicus*, the diapause behaviour of *C. helgolandicus* remains less clear. The study of Hirche (1983) is sometimes cited as showing that *C. helgolandicus* undergoes diapause. This showed reduced respiration rates during winter, a key piece of evidence for diapause, however *C. finmarchicus* and *C. helgolandicus* were not distinguished, therefore its conclusions about the behaviour of *C. helgolandicus* remain unclear. However, the only other study reporting respiration rates for *C. helgolandicus* during winter (Williams and Conway, 1988) concluded that it did not undergo true diapause in the Irish Sea. Further evidence of differences in diapause behaviour is provided in the North Sea, where *C. finmarchicus* largely retreats to deeper water by November, in contrast to *C. helgolandicus* which mostly remains in shallower waters

(Bonnet et al., 2005), indicating that *C. helgolandicus* may not diapause in the North Sea.

Differences in diapause behaviour in each species could also be inferred from first principles, assuming that lipids are the principle driver of diapause, by comparative analysis of lipid content of both species. These differences may also have broader ecological impacts. A recent study argued that *C. helgolandicus* would not be a full replacement for *C. finmarchicus* as part of the diet for some fish species (Frederiksen et al., 2013) partly as a result of its lower lipid content.

Reported values of wax ester content of *C. helgolandicus* are significantly lower than those for *C. finmarchicus* (Tables 2.1 and 2.2). For example a laboratory study found that C5 of *C. finmarchicus* had 3 times more wax ester than those of *C. helgolandicus* (Rey-Rassat et al., 2002a). However, individuals were raised at different temperatures in this study: *C. finmarchicus* at 8 °C and *C. helgolandicus* at 15 °C. A consequence is that the *C. finmarchicus* individuals would have been significantly larger, and there is very strong evidence that smaller *C. finmarchicus* individuals have lower lipid levels (Miller et al., 2000). The same difficulty exists for comparison of other studies of lipid levels in both species.

TABLE 2.1: Published papers reporting lipid levels of stage C5 *C. finmarchicus*

Reference	Location	Maximum WE (μg C)
Kattner and Krause, 1987	North Sea	30
Kattner and Krause, 1989	North Sea	49.8
Ohman and Runge, 1994	St. Lawrence	11.4
Heath and Jønasdøttir, 1999	Faroe-Shetland Channel	100
Clark et al., 2012	Loch Ewe	100
Marker et al., 2003	Bergen	77
Marker et al., 2003	Tromso	82
Hygum et al., 2000a	Mesocosms	60
Hygum et al., 2000b	Mesocosms	72
Rey-Rassat et al., 2002a	Mesocosms	142
Jønasdøttir, 1999	Faroe-Shetland Channel	200

TABLE 2.2: Published papers reporting lipid levels of stage C5 *C. helgolandicus*

Reference	Location	Maximum WE (μg C)
Gatten et al., 1980	English Channel	50.3
Kattner and Krause, 1989	North Sea	36
Ceballos and Álvarez Marqués, 2006b	Cantabrian Sea	21.3
Sargent et al., 1977	English Channel	19.9
Rey-Rassat et al., 2002a	Mesocosms	55

We therefore have two possibilities: there is an interspecies difference in lipid accumulation in each species, or that observed differences between the two species is largely because smaller individuals have lower lipid values. The relationship between body length and wax ester content in *C. finmarchicus* is very significant with C5 individuals of prosome length 2 mm having total wax ester content over 5 times lower than those of individuals with prosome lengths of 2.7 mm (Miller et al., 2000; Pepin et al., 2011; Saumweber and Durbin, 2006). The majority of reported wax ester levels for *C. helgolandicus* C5 have been in the English Channel, and these values were 55 (Rey-Rassat et al., 2002a), 50.31 (Gatten et al., 1979) and 19.9 μg C (Sargent et al., 1977). *C. finmarchicus* C5 have on average 50 μg C of wax ester (Pierson et al., 2013) when their prosome lengths are 2 mm. This is approximately the size of *C. helgolandicus* C5 in the English Channel. Therefore the recorded wax ester levels for *C. helgolandicus* are not significantly different to those in *C. finmarchicus* of the same size. This indicates that there are no significant interspecies differences in lipid accumulation ability.

Comparison of the lipid composition of co-occurring *C. finmarchicus* and *C. helgolandicus* populations is currently lacking, however a study of lipid composition of both in relatively similar regions of the North Sea (Kattner and Krause, 1989) concluded that there was no evidence of interspecies differences, and that observed differences can probably be explained by environmental differences. Existing data is therefore consistent with lipid accumulation rate being consistent across both species.

An open question is the actual behaviour of *C. helgolandicus* during winter. Populations exist in regions with sea bed depths ranging from 1,000 to 4,000 m (Bonnet et al.,

2005; Stöhr et al., 1996; John et al., 1998; Andersen et al., 2001). It has been observed living predominantly at depths of 2,000 m in June in the Levantine Sea (Bonnet et al., 2005) which indicates a seasonal vertical migration may occur. This oversummering behaviour is probably a necessary life cycle adaptation given *C. helgolandicus*s possible metabolism-ingestion trade off. Temperatures at the surface during summer are potentially too high for *C. helgolandicus* to offset metabolic losses by ingesting food, therefore a seasonal migration to deeper, cooler waters may be necessary.

There are currently no studies of the duration and timing of any possible diapause period for *C. helgolandicus*. However, consideration of our knowledge of the duration of diapause for *C. finmarchicus* can be used to make some credible predictions about the maximum duration of diapause for *C. helgolandicus*. Diapause can be seen as an extended period of low respiration rates without feeding (Ingvarsdøttir et al., 1999), therefore diapause must end before an individual starves. The two main influences on time to starvation are total lipid content at the start of diapause and in situ temperature (Saumweber and Durbin, 2006). Throughout most of its geographic range *C. helgolandicus* would diapause at temperatures greater than 10 °C, and C5 individuals would have body size below 2 mm. Extension of the diapause duration model of Saumweber and Durbin (2006) (updated by Pierson et al. (2013)) to *C. helgolandicus* would indicate a maximum diapause duration of less than 60 d, more than 3 times shorter than for *C. finmarchicus*. Respiration rates for *C. helgolandicus* are not available in the literature; therefore this is a preliminary prediction.

Importantly, an inability to survive without food for longer than 2 months may be an explanation for *C. helgolandicus* largely being restricted to continental shelf regions. Oceanic regions experience more prolonged periods of low food supply than shelf regions, and an inability of *C. helgolandicus* to diapause may result in low viability of populations in off-shelf regions.

2.3 Mortality

Estimates of mortality in stage-structured *Calanus* populations face many problems and uncertainties. Advection, patchiness of populations, and uncertainties in estimates of stage duration, among other factors, has led to the general view that the problem is intractable (Ohman, 2012). As a result there has been relatively little attempt to quantify the impact of mortality on populations. However, some recent research has attempted to provide a clearer direction for the rigorous quantification of mortality in *Calanus* (Ohman, 2012; Gentleman et al., 2012).

A limited number of studies have made field-based estimates of mortality in *C. finmarchicus* (e.g. Eiane et al. (2002); Eiane and Ohman (2004); Ohman and Hirche (2001); Ohman et al. (2002) and Ohman et al. (2004)) and *C. helgolandicus* (Hirst et al., 2007). These estimates of *Calanus* mortality have been used in population models of *C. finmarchicus* (Speirs et al., 2006) and *C. helgolandicus* (Maar et al., 2013). Both species see significantly higher mortality in egg and early naupliar stages than in later stages. However, inferring interspecies differences from these studies is very difficult. The only existing studies of each species have been in distinct geographic regions, with distinct predation and temperature regimes. Mortality can vary significantly with predation regime (Eiane et al., 2002) and temperature (Hirst et al., 2007). Therefore, published mortality estimates are not directly comparable and we cannot make particularly credible conclusions about interspecies differences.

We can however infer some general differences between each species, given the apparent response of their development times to temperature. Below 12°C *C. finmarchicus* develops faster than *C. helgolandicus*. As a result, we would expect mortality pressures to be stronger on *C. helgolandicus* at these temperatures. Similarly, our development time model indicates that the converse is true for temperatures above 13°C, where *C. finmarchicus* is likely to see more significant mortality pressures. *C. finmarchicus* also appears to have significantly lower egg survival rates at higher temperatures (Preziosi

and Runge, 2014). The dome-shaped response of each species ingestion rate to temperature (Møller et al., 2012) implies that starvation mortality will be different in each species. The low ingestion rates of *C. helgolandicus* at temperatures of around 7°C and below imply that it will have very high levels of mortality at these temperatures, and that this will be particularly pronounced during periods of low food. Similarly, *C. finmarchicus* is likely to see pronounced levels of mortality at temperatures close to 20°C because the lowered ingestion rates are likely to fail to offset increased respiratory costs at these temperatures. Mortality may therefore play a key role in limiting the geographic extent of each species.

2.4 Biogeography and environmental niches of *C. finmarchicus* and *C. helgolandicus*

Interspecies differences can be discerned by evaluating the ecological niches of species in relation to the environment. A recent study (Helaouët and Beaugrand, 2007) considered the environmental niches of *C. finmarchicus* and *C. helgolandicus* in relation to a range of environmental variables. They found that the most influential factors on the abundance of each species, as recorded by the Continuous Plankton Recorder, are temperature and its correlates, and bathymetry. An additional question is the ability of environmental variables to explain the large scale geographic distribution of each species. We consider this question here, restricting our analysis to those variables considered by Helaouët and Beaugrand (2007) which have high quality spatial coverage in the North Atlantic, that is temperature, bathymetry and salinity. We used the statistical modelling method of general additive modelling (GAMs) to relate average monthly abundance of *C. finmarchicus* and *C. helgolandicus* to average annual sea surface temperature, monthly salinity and bathymetry during the period from 1958 to

2002, with seasonality, when considered, accounted for by including a monthly component in GAM models. Monthly sea surface temperature is from the HadISST dataset (Rayner et al., 2003). Bathymetry was taken from the General Bathymetric Chart of the Oceans. Monthly salinity data is taken from the World Ocean Atlas (2009) (Antonov et al., 2010).

Biological and environmental data was resolved to a 1°resolution, with *Calanus* abundance averaged in each cell by month. We used monthly CPR data from 1958 to 2002. Initially there were 170, 149 observations, which are then reduced to 85,007 after resolving to a 1 by 1°resolution. Abundance data was then log transformed, i.e. we used $\log_{10}(abundance + 1)$. We then considered the success of these models in predicting the geographic distribution of each species, and inferred each species environmental niche to the key environmental variables temperature and bathymetry. GAM model results are summarized in Table 3.

2.4.1 Geographic Range

Figure 2.6 shows the geographic distributions of both species over the period 1960-2000. *C. finmarchicus* has a range covering a large part of the North Atlantic, with known population centres in the Irminger Sea, Labrador Sea, Iceland Basin, Norwegian Trench and the Faroe Shetland Channel (Heath et al., 2004). *C. helgolandicus* has a range stretching from the Leventine Sea in the eastern Mediterranean Sea (Weikert et al., 2001) to the North Sea (Bonnet et al., 2005). *C. finmarchicus* is largely located within the Atlantic Polar Biome north of the Oceanic Polar Front, whereas *C. helgolandicus* occurs in the Oceanic Polar Front (Helaouët and Beaugrand, 2007). *C. helgolandicus* predominantly lives in waters with significantly lower oxygen, silicates and nutrients (Longhurst (2010), CPR).

The large scale geographic distribution of *C. finmarchicus* and *C. helgolandicus* were reasonably successfully reproduced (Figure 2.7) using the predictions from the GAM model

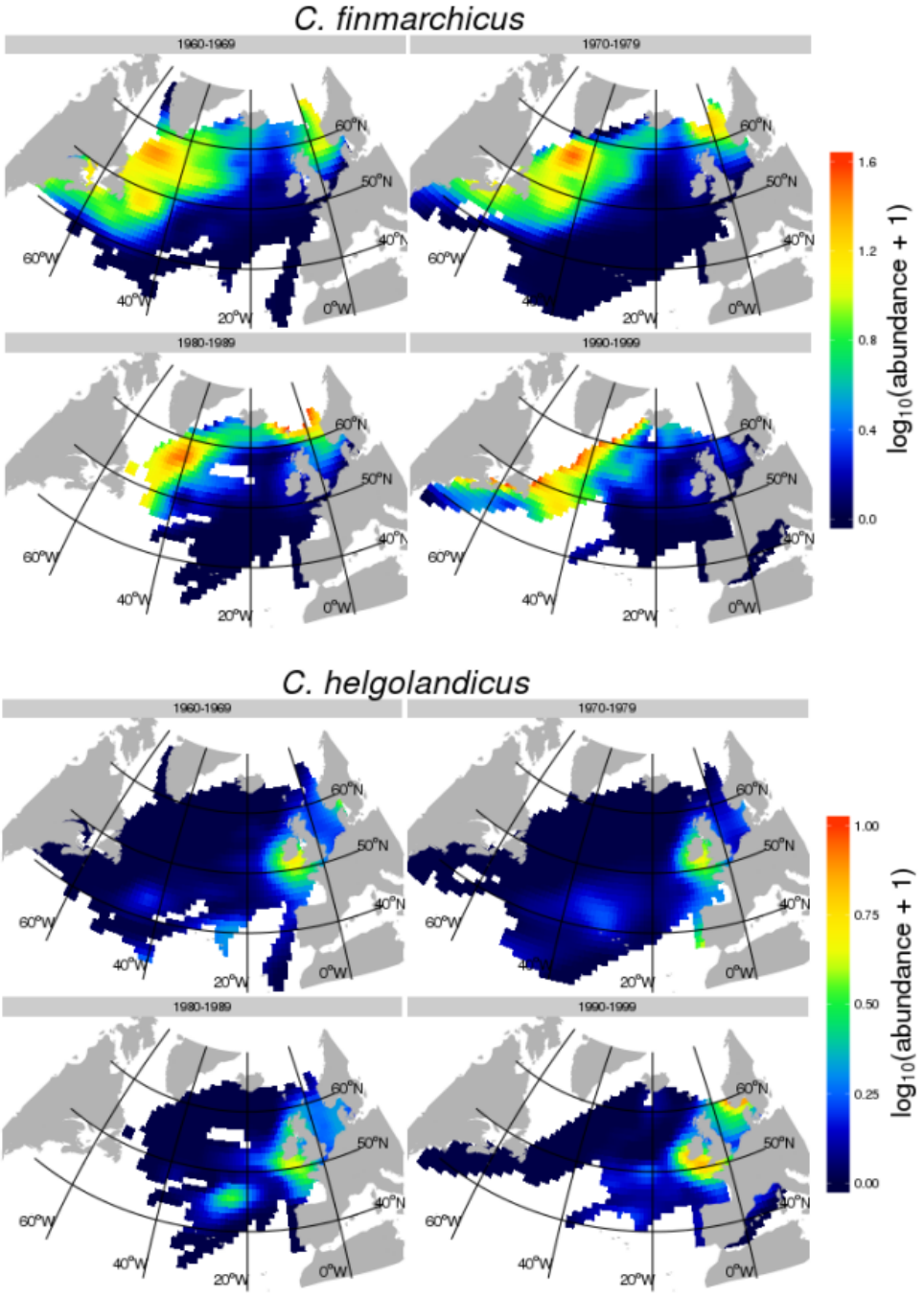


FIGURE 2.6: Decadal changes in *C. finmarchicus* and *C. helgolandicus* total stages C5 and adult abundances, from CPR data. Data was interpolated using Loess smooths, with a span of 0.05. We exclude any 1°E by 1°N grid cells where there are less than 5 total monthly observations in the cell and its direct neighbours during the respective decade.

relating abundance with temperature, bathymetry and salinity (te(MON,SAL,TEMP,BATH)) in Table 3). The R^2 value for the *C. finmarchicus* model, 0.5, is higher than for *C. helgolandicus*, 0.4, indicating greater predictive ability. However, spatial bias in the CPR data means that this should not necessarily be interpreted as meaning that these variables are stronger predictors of *C. finmarchicus* abundance than *C. helgolandicus*. Our temperature only model was much stronger for *C. finmarchicus* than for *C. helgolandicus*. However, the inclusion of bathymetry results in a significant improvement in the ability of the model to predict the geographic distribution of *C. helgolandicus*. *C. helgolandicus* is largely a continental shelf species, so the greater importance of bathymetry for *C. helgolandicus* than *C. finmarchicus* implied by our models is in line with expectations.

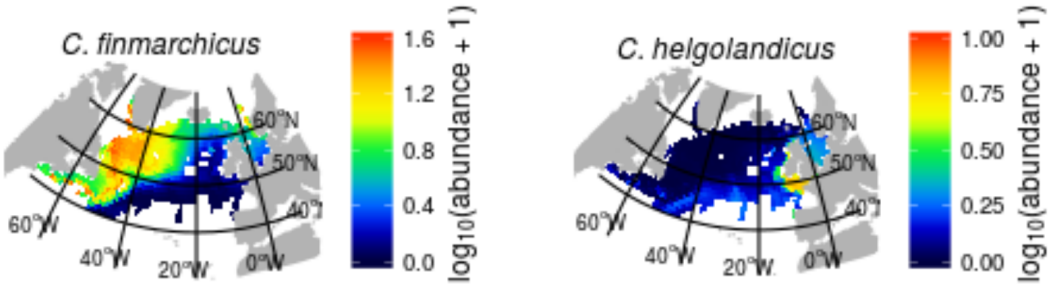


FIGURE 2.7: Average annual abundances of *C. finmarchicus* and *C. helgolandicus* stages CV and CVI during the period 1960-69 as predicted by a GAM model

Average annual abundances of C. finmarchicus and C. helgolandicus stages CV and CVI during the period 196069 as predicted by a GAM model, which related abun- dance to annual temperature, monthly salinity, bathymetry and month. Colour scale represents predicted average annual abundance of CV and CVI stages.

2.4.2 Environmental niches in relation to temperature and bathymetry

The southern extent of *C. finmarchicus* is thought to be the 11 °C isotherm (Planque and Fromentin, 1996), which also coincides closely with the northern extent of *C. helgolandicus*. *C. finmarchicus* has a known temperature range of 0-16 °C (Mauchline, 1991), whereas *C. helgolandicus* ranges from 5-28 °C (Bonnet et al., 2005).

We derived the relationship between *C. finmarchicus* and *C. helgolandicus* abundance and temperature and bathymetry using our GAM models, as shown in Figure 2.8. The annual temperature optimum is approximately 4 °C for *C. finmarchicus* and 14 °C for *C. helgolandicus* (in agreement with Helaouët and Beaugrand (2007)). These temperature preferences are demonstrated by co-occurring populations, where a vertical separation exists and *C. finmarchicus* predominantly exists in deeper, cooler waters than *C. helgolandicus* (Jønasdøttir and Koski, 2011; Williams, 1985). The derived thermal niche also indicates that the temperature tolerance range for *C. finmarchicus* is greater than for *C. helgolandicus*, which accords with Helaouët and Beaugrand (2007).

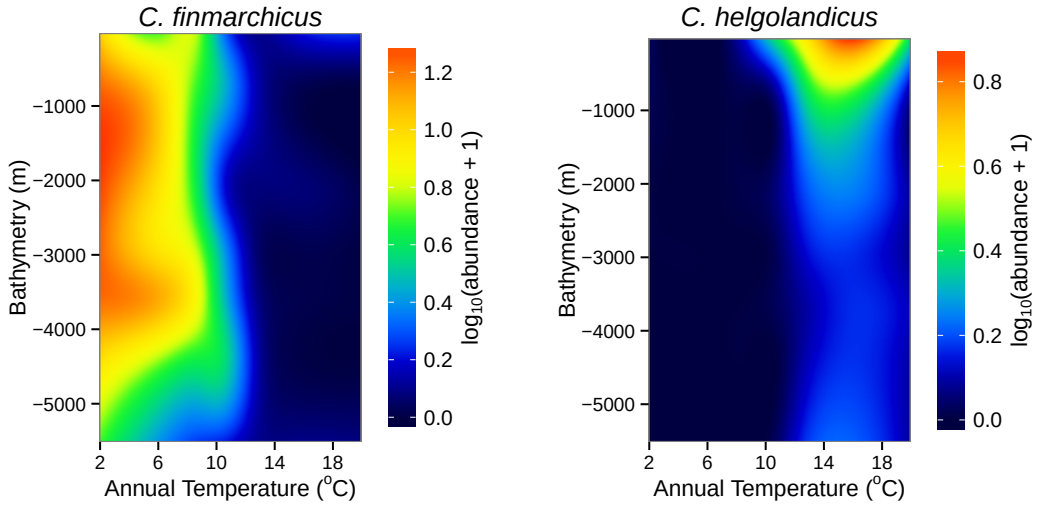


FIGURE 2.8: Relationship of annual average abundance to temperature and bathymetry for *C. finmarchicus* and *C. helgolandicus*. Relationship is derived using a GAM model relating abundance with temperature, bathymetry, and month.

C. finmarchicus is predominantly an oceanic species and this is reflected by the wide range of its bathymetry niche. In contrast, *C. helgolandicus* has a geographic range that is largely restricted to the Continental Shelf, and its bathymetry niche indicates that it is largely restricted to waters shallower than 1,000 m. The population map for *C. helgolandicus* also indicates a very abrupt decline in population numbers at the continental shelf to the south west of the British Isles. The reasons for this restriction are not fully know. Studies in the Mediterranean Sea (e.g. Andersen et al. (2001)) indicate that *C. helgolandicus* is capable of living at depths of up to 4000 m. However, we hypothesized in our section on diapause that this restriction may be explained by an inability of *C. helgolandicus* to undergo a significant period of diapause during winter.

2.5 Seasonality and interspecies interactions

2.5.1 Seasonal cycles

Broad scale geographic differences exist in the patterns of seasonality for each species. *C. finmarchicus* shows a clear seasonal cycle, with a single peak in spring occurring throughout its geographic range (Planque and Fromentin, 1996). In contrast, *C. helgolandicus* mostly has a seasonal peak that varies significantly with latitude, with peak seasonal abundance occurring in spring in the Mediterranean, whereas peak abundance occurs in autumn in the North Sea and North East Atlantic (Bonnet et al., 2005; Planque and Fromentin, 1996).

The main region where both species overlap, the North Sea, sees very clear differences in seasonality, which is shown in the Stonehaven time series (Bonnet et al., 2005). This time series, starting in 1997, shows that *C. helgolandicus* has a seasonal peak in autumn, with an earlier smaller peak in spring also evident in this time series. In contrast, *C. finmarchicus* has a seasonal peak significantly earlier in the year during spring.

Here we consider the trend in the region around Stonehaven since 1960 by analyzing CPR records. Figure 2.9 shows the seasonal pattern in abundance in the region around Stonehaven over 4 decades from 1960 to 2000, derived from CPR data using a GAM model that relates monthly abundance of each species purely with month. Our derived time series reflects the decline in the abundance of *C. finmarchicus*, and the increase in *C. helgolandicus* over the period 1960-2000 (Reid et al., 2003b), and as in the Stonehaven time series it indicates that abundance peaks significantly later in the year for *C. helgolandicus* than for *C. finmarchicus* throughout the time period.

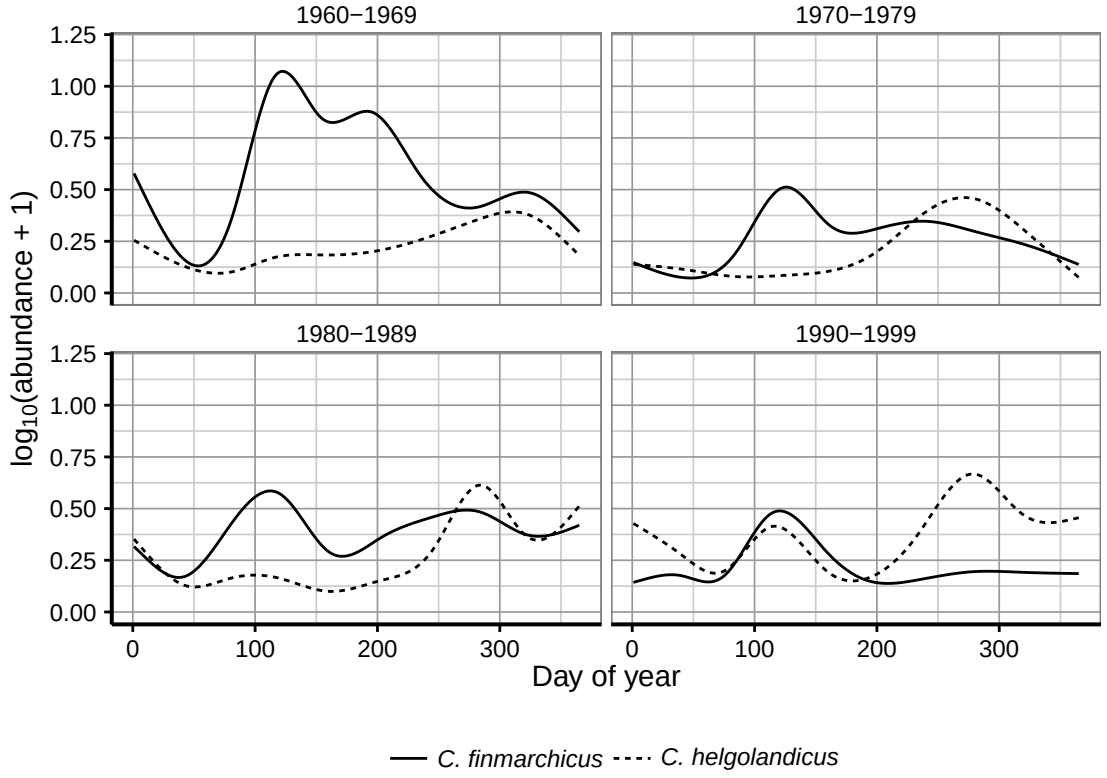


FIGURE 2.9: Seasonal Cycles in the North Sea for *C. finmarchicus* and *C. helgolandicus*. Derived from CPR abundance data using a GAM model relating monthly abundance with month

This mismatch in seasonality between the species has led some researchers to conclude that *C. finmarchicus* is more important as prey in the diets of many fish species in the North Sea (Jønasdøttir and Koski, 2011; van Deurs et al., 2009). The causes of this

mismatch between seasonal cycles are unclear. Different development responses to temperature probably play a role, with our review of development rate indicating *C. helgolandicus* developing more slowly at the temperatures experienced in this region. The stark difference between seasonal peak timing however appears to suggest that different transportation routes into the North Sea may play a role. *C. finmarchicus* is known to require annual transportation into the North Sea to maintain a summer population (Heath et al., 1999), however to date the role of transportation in North Sea populations of *C. helgolandicus* have not been studied. A greater understanding of the influences of seasonality on each species is therefore necessary to aid predictions of ecosystem impacts of *C. finmarchicus* being replaced by *C. helgolandicus*.

2.5.2 Interspecies competition

It remains unclear if there is significant interspecies competition where the two species coexist. Meyer et al. (2002) is the only existing study comparing the feeding behaviour of *C. finmarchicus* and *C. helgolandicus*. No significant differences between the two species in terms of feeding behaviour were found. This implies that some level of competition for resources should occur between the two species where they physically coexist. However, studies of the vertical structuring of co-occurring *C. finmarchicus* and *C. helgolandicus* populations indicate that there is often a lack of vertical overlap for the two species, thus possibly limiting the potential for interspecies competition. Jønasdøttir and Koski (2011) found that in the Dogger Bank, North Sea, *C. helgolandicus* stayed predominantly in the warm surface waters, with *C. finmarchicus* staying in the cooler, deep waters. This difference however appears to be dependent on the existence of a thermocline.

Williams and Conway (1985) studied difference in vertical distribution in the Celtic Sea. They found that after the development of the thermocline, there were distinct difference in the vertical distribution of the two species, but that prior to this there

was no significant difference in their vertical distributions. There is also a temporal mismatch in the seasonal population peaks (Bonnet et al., 2005) and EPR (Jønasdøttir et al., 2005) of co-occurring *C. finmarchicus* and *C. helgolandicus*. This may further limit the importance of interspecies competition.

2.6 Conclusions

We have reviewed the ecological and biological differences between *C. finmarchicus* and *C. helgolandicus* and our key conclusions are as follows:

- *C. finmarchicus* has an annual temperature optimum of approximately 5 °C, while *C. helgolandicus* has an optimum of 14 °C.
- *C. finmarchicus* develops faster than *C. helgolandicus* at temperatures below 12 °C. We have produced a new development model which indicates that *C. helgolandicus* develops faster than *C. finmarchicus* above 13 °C.
- Reviewed evidence indicates that both species grow to the same body size under identical environmental conditions, with large geographic differences in body size apparently being determined by in situ temperature
- Comparative evidence shows that, if they exist, interspecies differences in egg production do not follow a clear pattern
- There is no evidence that *C. helgolandicus* undergoes a period of diapause, and we suggest that due to higher diapause temperatures any period of diapause will be short in duration.
- Broad scale differences in lipid levels in each species can be explained without invoking interspecies differences, and are consistent with the lower lipid levels of *C. helgolandicus* resulting from temperature driven differences in body size.
- Both species undertake diel vertical migration, and existing evidence implies no interspecies differences in behaviour.
- Significant differences in seasonal cycle exist, with *C. helgolandicus* abundance peaking significantly later in the year in the North Sea, where the species co-occur.

Ongoing climate change is likely to result in the continued replacement of *C. finmarchicus* by *C. helgolandicus* in many ecosystems, in particular the North Sea. Our review sheds some light on the prospects of these changes, and uncertainties in our knowledge of the impacts of these changes. The ecosystem impacts of these changes rest in part on the ability of *C. helgolandicus* to "replace" *C. finmarchicus*. Interspecies differences, in particular in body size and lipid content, appear to be lower than has been assumed in some literature (Frederiksen et al., 2013). Current mismatch between seasonality in each species results in *C. finmarchicus* playing a much more important role in the diets of some fish species (van Deurs et al., 2009), and a fuller understanding of the potential future evolution of *C. helgolandicus* seasonality is necessary to get a more complete picture of the extent to which *C. helgolandicus* can replace *C. finmarchicus* in ecosystems.

The strong similarities between each species lead to the possibility of hybridization between *C. finmarchicus* and *C. helgolandicus* where they co-exist. Recent research has shown that *C. finmarchicus* and *C. glacialis* can inter-breed (Berchenko and Stupnikova, 2014; Parent et al., 2012), the first known instance in any zooplankton species. Hybrids often outnumbered the population of *C. finmarchicus* or *C. glacialis* in the Labrador Sea and Scotian Shelf (Parent et al., 2012). Whether hybridization occurs, and has the effect of masking inter-species differences, between *C. finmarchicus* and *C. helgolandicus* remains an open question. Other recent work has shown that there is more overlap in body size of *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* than previously thought (Parent et al., 2011). This confirms the need to look at traits where species co-exist if we want to identify differences between the species. Identification of the extent of overlap of key traits where *Calanus* species co-exist will be a good indicator of the potential ecosystem changes that may result from future regime shifts.

A key research question is whether geographic genetic differences have significant quantitative influences on populations. We parameterized our growth model using

development times of western North Atlantic *C. finmarchicus* and ingestion rates from eastern North Atlantic *C. finmarchicus*. Similarly, quantitative inferences based on traits measured for *C. helgolandicus* in the North Sea may not accurately reflect those found in the Mediterranean.

An important question for future research is the potential expansion of *C. helgolandicus* into oceanic environments. Its population is currently largely restricted to continental shelf regions, a phenomenon we hypothesize is largely determined by higher temperatures resulting in a shorter potential diapause period. A more complete understanding of the mechanisms explaining *C. helgolandicus*s current restriction to continental shelf is necessary to predict whether it will continue to be restricted to continental shelf regions, which may have significant impacts on ecosystems.

Part III

Statistical Modelling

Chapter 3

Niche and distribution analysis of *Calanus finmarchicus* and *C. helgolandicus* using Continuous Plankton Recorder observations

3.1 Introduction

Zooplankton populations play a critical role in transferring energy from primary producers, such as phytoplankton, to higher trophic levels such as fish. Changes in zooplankton communites will thus have a significant impact on marine ecosystems, and and important challenge of zooplankton ecology is therefore the tracking of long term changes in zooplankton communities. These changes may take many forms; the most important are changes in the phenology (Edwards and Richardson, 2004) and range (Sorte et al., 2010) of individual species, and of changes in zooplankton communities (Beaugrand et al., 2002).

The biogeography of many zooplankton species in the North Atlantic has changed significantly in recent decades (Beaugrand et al., 2009), with evidence indicating this is a result of climate change (Richardson, 2008; Hays et al., 2005). In simple terms, zooplankton species are moving north, and this is expected to continue (Reygondeau and Beaugrand, 2011). These changes in zooplankton communities are likely to have significant impacts on marine ecosystems (Frederiksen et al., 2013; Edwards and Richardson, 2004; Kristiansen et al., 2011; Burthe et al., 2012).

Tracking long term changes in zooplankton populations is carried out using a variety of time series (Mackas and Beaugrand, 2010). Time series can track abundance at a specified location over a long time period. For example, almost weekly records of zooplankton and phytoplankton abundance have been made at the L4 station in the English Channel since 1988 (Harris, 2010). Time series can also have shorter time duration, and are often related to specific multi-institution research programmes. The TASC programme led to a significant increase in sampling of *C. finmarchicus* in 1997, with multiple sites having time series long enough to estimate the annual cycle of populations across all copepodite and adult stages (Heath et al., 2000a). A final type, and what we consider here, are large scale spatial data sets. The most important is the Continuous Plankton Recorder (CPR), which provides consistent observations of zooplankton communities across the North Atlantic since 1931 (Reid et al., 2003a).

Time series can be used to answer many key questions, such as whether population abundance or phenology is changing over the long term and how abundance varies seasonally (Mackas and Beaugrand, 2010). However, these data sets must be interpreted carefully, and numerical interpretations in changes of abundance can be the source of controversy (Boyce et al., 2010; McQuatters-Gollop et al., 2011). Spatial and temporal bias can possibly lead to erroneous conclusions about long term changes.

The CPR was launched in 1931 by Sir Alister Hardy (Reid et al., 2003a). It is the largest monitoring program of plankton communities in the North Atlantic, in both geographic

and temporal scale (Richardson et al., 2006). Importantly, the methodology for collecting and analyzing zooplankton has largely been unchanged over 8 decades, and therefore long term changes in zooplankton communities can be tracked with reasonable reliability (Batten et al., 2003).

Distinguishing between *C. finmarchicus* and *C. helgolandicus* poses technical challenges, and it was not until 1958 that CPR distinguished between them. Similarly, the species are morphologically indistinguishable, except at the C5 and adult stages. Consequently, CPR has only recorded total combined abundance for the C5 and adult stages (Reid et al., 2003a).

Most of what we know about the biogeography of both species comes from analysis of historical CPR data. Its large geographic coverage allows us to estimate the spatial distribution of both species (Planque and Fromentin, 1996). Similarly, it has allowed range shifts of both species to be estimated (Hinder et al., 2013), and for statistical estimates to be made of potential future range shifts (Beaugrand et al., 2012).

The extensive nature of the CPR data set also means that we can make statistical comparisons between a species' abundance and key environmental variables such as temperature. As a result, we can estimate a species' ecological niche (Helaouët and Beaugrand, 2007).

Here we perform analysis of historic CPR data to estimate the ecological niches of *C. finmarchicus* and *C. helgolandicus*. We analyse CPR data to shed light on the changes in geographic distribution of species. In addition, we consider how *Calanus* community composition is changing in regions where *C. finmarchicus* and *C. helgolandicus* overlap.

The geographic distribution and ecological niche of species are typically estimated using statistical models, which relate recorded abundance with environmental data (Elith and Leathwick, 2009). Here we use the class of model called General Additive Models (GAMs) (Wood, 2006). GAMs have now been used extensively to model the distribution

of a variety of marine species (Daskalov, 1999; Zarauz et al., 2007; Tittensor et al., 2010; Cardinale and Arrhenius, 2011; Murase et al., 2009; Denis, 2002). In addition, previous studies have used GAM models to analyse the distribution of *C. finmarchicus* (Heath et al., 1999; Chust et al., 2013).

3.2 Methods

3.2.1 Zooplankton abundance data

We use data from the CPR survey as our measure of abundance for *C. finmarchicus* and *C. helgolandicus*. The history of the CPR and guides to how to use its data has been provided by a number of recent publications (Richardson et al., 2006; Batten et al., 2003; Reid et al., 2003a). Here I will outline a brief history and summary of the CPR.

Sir Alister Hardy started the Continuous Plankton Recorder survey in 1931 (Hardy, 1939). The Survey is made up of data collected by devices attached to ships which traverse commercial shipping lanes. The CPR device consists of two main parts, and has stayed largely unchanged since the survey began in 1931. It is towed behind vessels, and is designed to have a towing depth of 10 m at the operating speed of the vessel (Batten et al., 2003).

Water enters the CPR through a 1.27 cm^2 opening, and is then filtered by a 270 μm silk mesh. The samples are then processed. Samples are obtained continuously along the routes of ships, and are then randomly assigned to analysts, a process which began in 1957. This occurs to avoid the spatial bias that may result from differences in the methods of individual analysts.

Abundance estimates are then made in a semi-quantitative manner. A total of 12 abundance categories are used (Rae, 1952), with samples being assigned to each category. These categories are detailed in Table 3.1. For example, if 13 individuals were counted,

the sample would be placed into category 5, which in turn would be given a mean of 17, which is then given a zooplankton traverse mean of 850. Abundances are only estimated for a subsample of the silk, and therefore the abundance estimate is multiplied by 50 to give an estimate for the abundance of the zooplankton traverse.

TABLE 3.1: Zooplankton abundance categories used by Continuous Plankton Recorder analysts to convert raw CPR samples to create records of CPR abundance in abundance bins.

Number counted	Category	Accepted value	Abundance per sample for zooplankton traverse
1	1	1	50
2	2	2	100
3	3	3	150
4-11	4	6	300
12-25	5	17	850
26-50	6	35	1750
51-125	7	75	3750
126-250	8	160	8000
251-500	9	310	15,500
501-1000	10	640	32,000
1001-2000	11	1300	65,000
2001-4000	12	2690	134,500

C5 and adult abundance of *C. finmarchicus* and *C. helgolandicus* has been recorded since 1958. Here we use combined abundance of stages C5 and adult. Our data covers the period 1958-2002. In total there are 170,049 observations in this period. Figure 3.1 illustrates the distribution of samples by abundance class.

Inferences of long term trends and spatial patterns using CPR must be interpreted in the context of considerable spatial and temporal biases and of the uncertainties related to inferring actual *Calanus* distributions from CPR data. Bias and data gaps exist for a number of reasons. Devices are exclusively placed on merchant shipping vessels. As a result, data is restricted to commercial shipping routes, and large regions of the North Atlantic have minimal CPR samples. This dependence on merchant vessels has a number of other consequences. Routes can be dropped for commercial reasons, and

devices often have to be reassigned to another vessel or shipping company, which can result in a temporal gap in some routes.

The long term nature of the CPR means that annual nautical miles towed and spatial coverage is very sensitive to changes in funding. This is very pronounced during the 1980s when the CPR's long term existence came into question due to reduced funding, with annual observations in 1990 being approximately half that at their peak around 1970 (Figure 3.1).

A further potential source of bias comes from changes in the merchant shipping fleet. Long term improvements in engine efficiency and changes in shipping size have resulted in an increase in mean tow speed of vessels. However, Batten et al. (2003) provides clear evidence that this will not result in long term changes being biased.

CPR devices are designed to record abundances at a fixed depth of approximately 10 m. However, *Calanus* populations are not evenly distributed throughout the water column. An immediate result is that CPR is a risible measure of abundance during winter for those species which diapause at depths (Hirche, 1996). Deriving abundance for non-diapausing populations faces similar challenges. Vertical distribution of species is influenced by a range of factors including the existence of a seasonal thermocline (Andersen et al., 2004; Heath et al., 2004), bathymetry and water clarity (Dupont and Aksnes, 2012). As a result, it is possible to make spurious inferences about geographic variations in abundance.

This causes problems for interspecies comparisons. Vertical distributions may be strongly influenced by temperature preferences of individual species. This is of particular relevance to *C. finmarchicus* and *C. helgolandicus*. Where the 2 species coexist mean depth of *C. finmarchicus* is typically greater than for *C. helgolandicus*. As a result CPR may significantly underestimate the relative abundance of *C. finmarchicus* where both species co-occur. Jønasdøttir and Koski (2011) analysed vertical samples of *C. finmarchicus* and

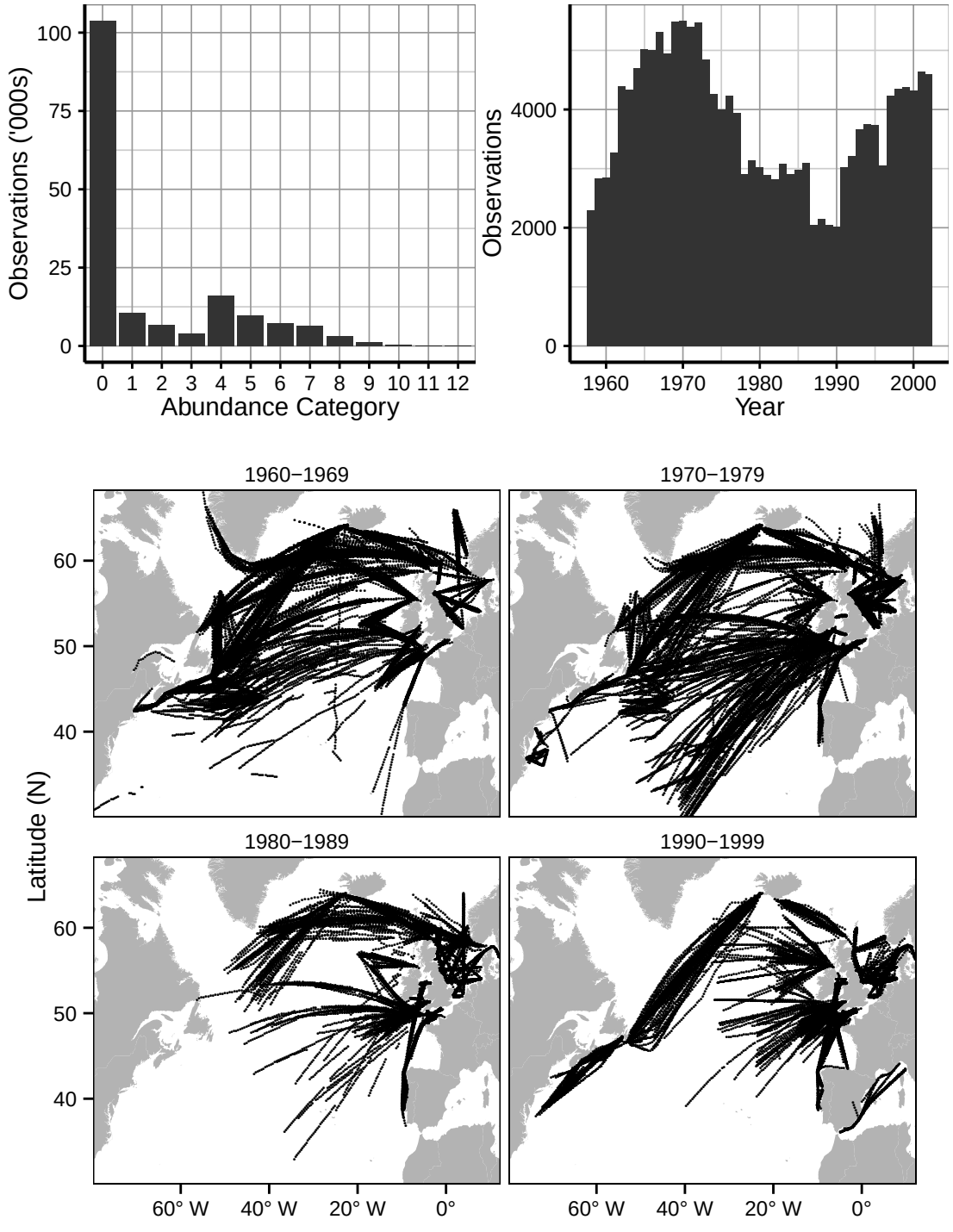


FIGURE 3.1: Geographic and temporal distribution of CPR data. The top left panel shows the distribution of abundance records by abundance class for *C. finmarchicus*. The top right shows the number of annual observations by CPR devices. The bottom panel shows the geographic distribution of CPR records by decade. Each dot represents a location that was sampled that decade.

C. helgolandicus and concluded that *C. finmarchicus* cannot be reliably sampled in the North Sea in summer.

3.2.2 Environmental data

Environmental data used in the analysis is listed in Table 3.2.

Sea surface temperature (SST) has a fundamental influence on the distribution of zooplankton, with some researchers concluding that different responses of physiological processes to temperature is the key determinant of the different geographic distributions of *C. finmarchicus* and *C. helgolandicus* (e.g. Møller et al. (2012)). We therefore considered the effect of both annual and monthly temperature, SST assumed to act as a proxy for the temperature experienced by animals throughout their life cycle. Temperature is taken from the Hadley Centre's Sea Surface Temperature data set (HadISST) (Rayner et al., 2003).

Salinity can have an influence on hatching success of eggs of calanoid copepod species (Holste and Peck, 2006; Holste et al., 2009; Peck and Holste, 2006). It can also influence nauplii survival in some calanoid copepod species (Chinnery and Williams, 2003). Similarly, population growth of calanoid copepods has been shown to be influenced by salinity (Milione and Zeng, 2008). The influence of annual and monthly salinity was therefore considered. Data for salinity was acquired, along with data for phosphates, nitrates, oxygen, silicates and nitrates, from the World Ocean Atlas 2009 (Antonov et al., 2010).

Some research suggests that bathymetry influences *Calanus* populations (Beaugrand et al., 2001; Dupont and Aksnes, 2012). In addition, *C. helgolandicus* has a population that is more or less exclusively restricted to continental shelf regions. We used bathymetry data from the "General Bathymetric Chart of the Oceans" (GEBCO).

3.3 Data processing

With the exception of bathymetry, our raw environmental data is gridded at a resolution of 1°E by 1°N. We therefore resolved all of our data at this resolution. GEBCO bathymetry data is at a resolution of 1 minute by 1 minute. We resolve this to our new resolution by calculating the mean bathymetry in each 1°E by 1°N cell.

CPR data is not gridded. Each individual record gives longitude, latitude, and time. The finest temporal resolution of our environmental data is monthly. Therefore we first separate our biological data into months and years. It is then resolved to the grid resolution by calculating the mean abundance observed for each species in every grid cell each month. After this resolution the number of observations is reduced from 170,149 to 87,518.

TABLE 3.2: Environmental data used for analysis of the environmental influences on *Calanus*

Data	Units	Type	N	Source
Calanus abundance	Number of individuals	1958-2002	N	SAHFOS
Sea surface temperature	°C	1958-2002	N	SAHFOS
Bathymetry	m	1958-2002	N	SAHFOS
Salinity	Unitless	Monthly mean (climatology)	N	World Ocean Atlas (2009)
Nitrate	μmol l^{-1}	Monthly mean (climatology)	N	World Ocean Atlas (2009)
Dissolved oxygen	ml l^{-1}	Monthly mean (climatology)	N	World Ocean Atlas (2009)
Silicate	μmol l^{-1}	Monthly mean (climatology)	N	World Ocean Atlas (2009)
Nitrate	μmol l^{-1}	Monthly mean (climatology)	N	World Ocean Atlas (2009)

3.3.1 Statistical analysis

We analysed the ecological niches of each species using the statistical modelling method of General Additive Modelling (GAM) (Wood, 2006; Hastie and Tibshirani, 1990). First, we transformed our abundance values to $\log_{10}(\text{abundance} + 1)$. We then carried out a suite of GAM models to test the influence of our environmental variables on *Calanus* abundance.

Our tests consider two questions, how much of the variation in abundance can be explained by particular variables, and the interactions between variables; and how many environmental variables are required for a model to provide a reasonable description of the geographic distribution of either species.

First, we related abundance to individual variables. Then, we performed GAMs which incorporated the potential interactions between environmental variables. To account for interactions between environmental variables we used tensor product smooths.

Statistical analysis was performed using the R statistical software and the package "mgcv" (Wood, 2001b).

3.4 Results

3.4.1 Baseline geographic distribution of *C. finmarchicus* and *C. helgolandicus*

We begin our analysis by considering the geographic distribution of *C. finmarchicus* and *C. helgolandicus* as revealed by the raw CPR data. Average abundance was estimated and mapped for the periods 1960-1969, 1970-1979, 1980-1989 and 1990-1999 (Figure 3.2).

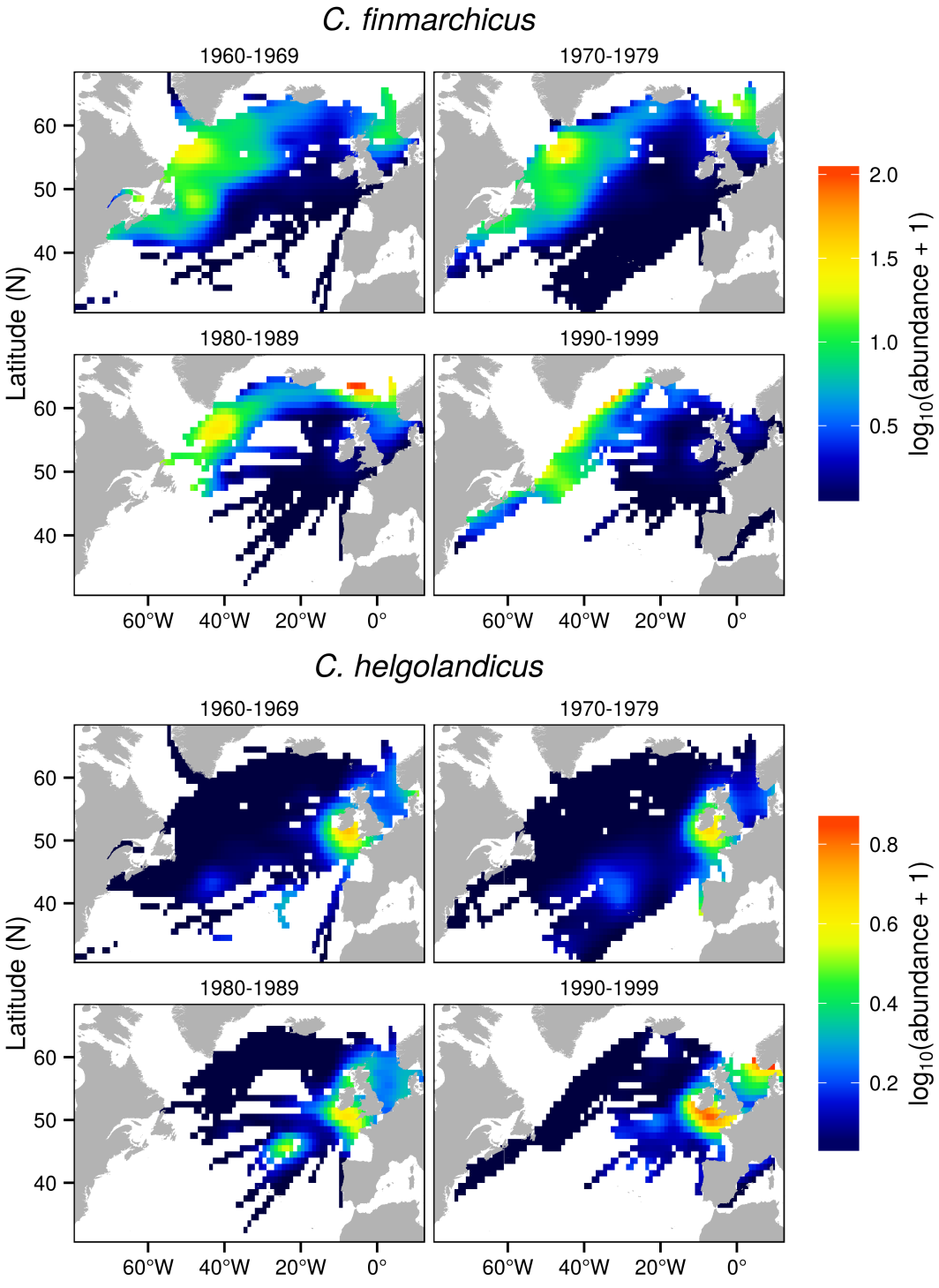


FIGURE 3.2: The geographic distribution of *C. finmarchicus* and *C. helgolandicus* by decade. The distribution of each species was estimated by first calculating the average abundance in each 1°E by 1°N cell, and secondly by using a loess smooth to to estimate the geographic distribution of each species. Cells with no data in the respective decade are excluded from each map.

First, the data was resolved to 1°E by 1°N resolution and by decade. The average abundance in each cell was then calculated for each decade. Finally, we performed a LOESS smooth on this averaged data to estimate the geographic distribution of decadal abundance. Reconstructions of the geographic distribution of Calanus typically extend into regions where there is minimal CPR coverage (e.g. Bonnet et al. (2005)), which can potentially lead to erroneous inferences about abundance. We therefore restrict our map to regions with actual CPR data in the relevant decade.

3.4.2 Temperature and seasonality

The influence of temperature was considered first by relating abundance in a location to monthly and annual temperature.

GAM models relating abundance to temperature ($\sim$te(Temperature, Month)) indicate that mean annual temperature (R^2 = 36.6%) is a better predictor of *C. finmarchicus* abundance than monthly temperature (R^2 = 34.9%). GAM models relating abundance to temperature ($\sim$te(Temperature, Month)) indicate that mean annual temperature (R^2 = 17.8%) is a better predictor of *C. helgolandicus* abundance than monthly temperature (R^2 = 14.5%).

The seasonal thermal profile of the population of both *C. finmarchicus* and *C. helgolandicus* were estimated using a GAM model relating abundance to monthly temperature and seasonality (Figure 3.3). This indicates that there is marginal overlap in the temperature profile for each species each month. *C. helgolandicus* apparently requires temperatures of approximately 10°C for significant population numbers to develop.

We estimated the broad influence of temperature on seasonality by considering the relationship between day of peak abundance and annual average temperature. This was modelled using a GAM relating abundance to temperature and day of year. For both species increasing temperature generally results in abundance peaking earlier in

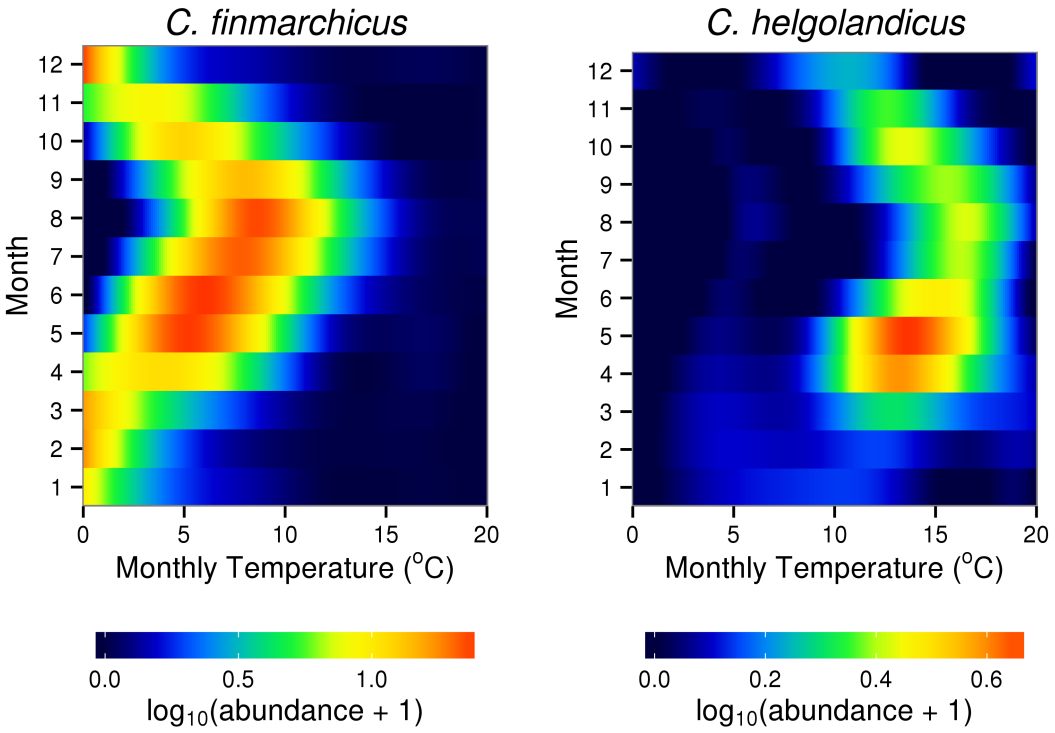


FIGURE 3.3: Average abundance of *C. finmarchicus* and *C. helgolandicus* observed in regions of different annual average temperatures. The thermal profile was derived using a GAM model which related abundance to temperature and month, using tensor smooths.

the year (figure 3.5). Notably, our model predicts a later peak in *C. helgolandicus* abundance than in *C. finmarchicus* in temperature regimes where they coexist. This is a reflection of the North Sea, where *C. helgolandicus* has a significantly delayed seasonal peak in comparison to other regions (Bonnet et al., 2005).

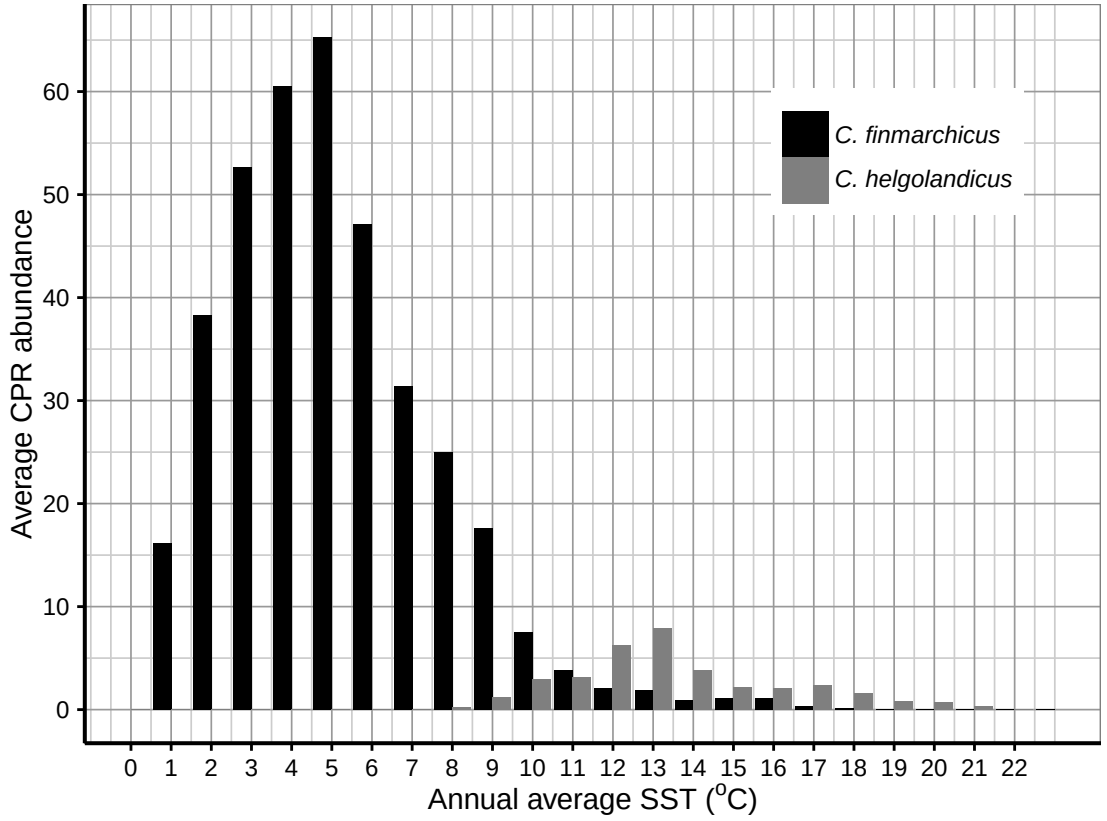


FIGURE 3.4: Mean CPR abundance of *C. finmarchicus* and *C. helgolandicus* observed in regions of different annual average temperatures.

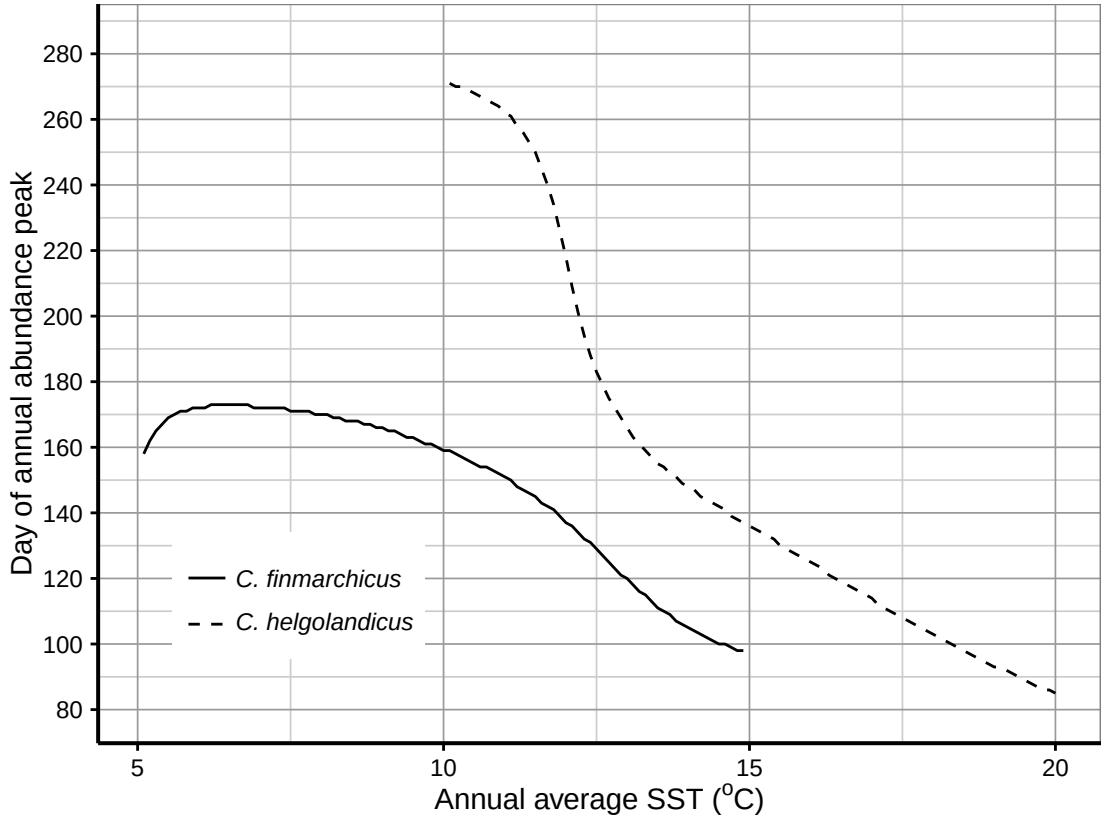


FIGURE 3.5: Temperature influence on seasonality. Day of peak abundance was modelled using a GAM model which related abundance to average annual SST.

3.4.3 The importance of bathymetry in determining the niche of *C. helgolandicus*

Visual inspection of the geographic distribution of *C. helgolandicus* makes it clear that temperature alone is not likely to be the overwhelming determinant of its geographic distribution. This can be illustrated by a simple GAM model of *C. helgolandicus*'s distribution under the assumption that temperature alone, along with seasonality, determines abundance (Figure 3.9).

Predictions from a GAM model are of questionable predictive power for bathymetries and temperatures not included in the data which drove the GAM model. Comparing temperature and bathymetry in regions covered by CPR shows a large part of potential temperature-bathymetry space that has bad quality or no CPR data (Figure 3.6). We therefore created an envelope around the region of temperature-bathymetry space with good data coverage, and estimated the temperature-bathymetry niche for this region only (Figure 3.7).

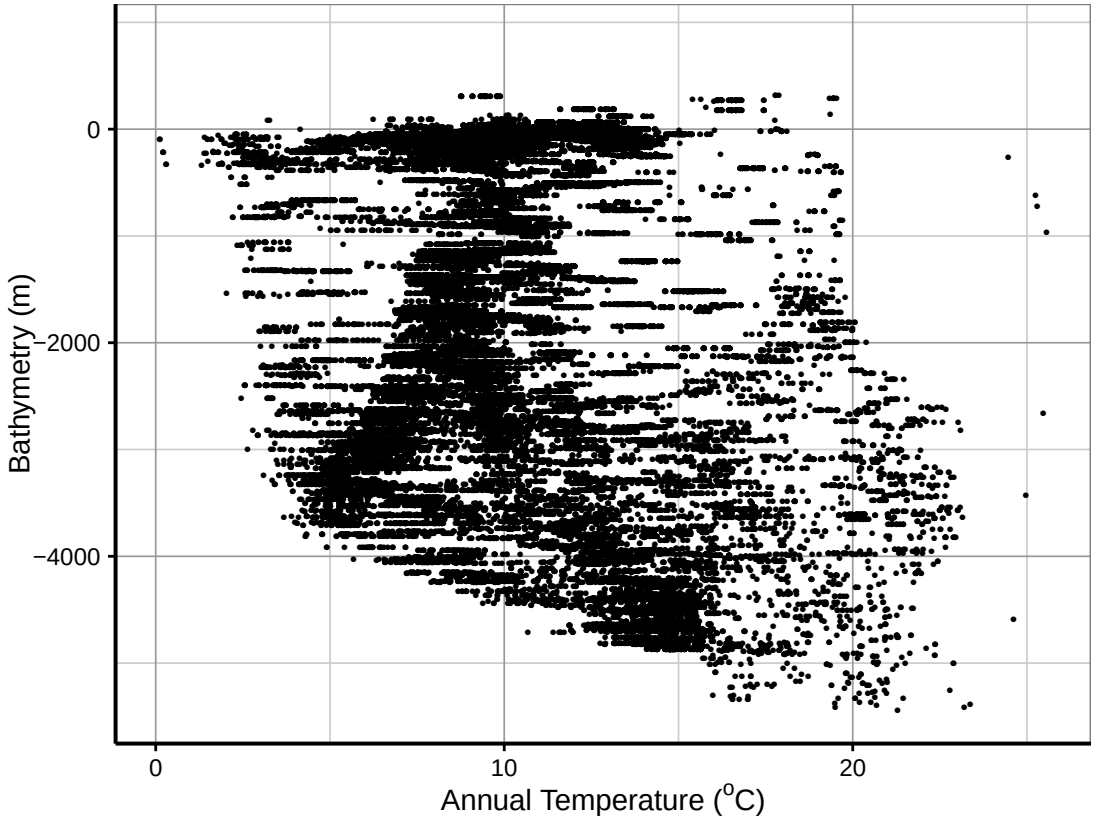


FIGURE 3.6: Scatter plot of CPR observations in relation to annual temperature and bathymetry at sample location.

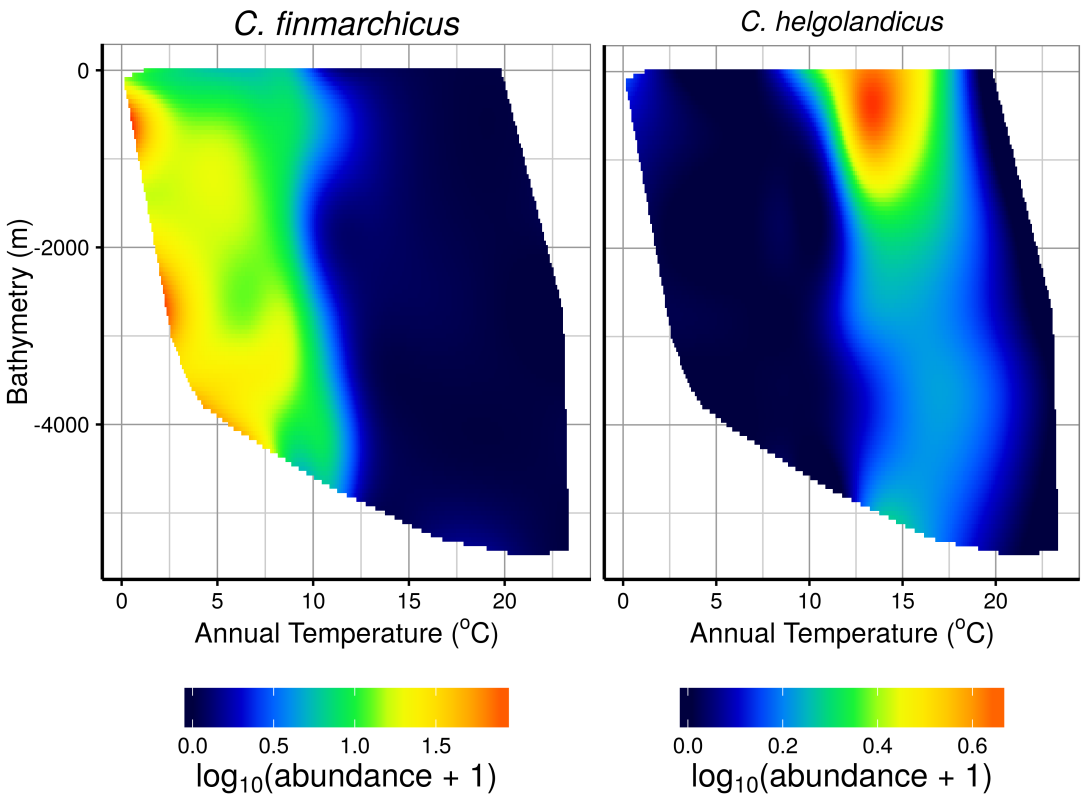


FIGURE 3.7: Temperature and bathymetry niches. The niches were estimated by using a GAM model which relates abundance with annual temperature, bathymetry and month, using tensor smooths.

3.4.4 Explanatory power of environmental variables

Single variable GAM models indicate that temperature is the best predictor of abundance for both species. Oxygen and salinity appear to have much more pronounced influences on the distribution of *C. finmarchicus* than for *C. helgolandicus*. Notably, bathymetry has a more pronounced influence for *C. helgolandicus*.

2 variable GAM models confirm the importance of bathymetry for *C. helgolandicus*. The best performing 2 variable model related *C. helgolandicus* abundance to annual temperature and bathymetry. In addition, they confirm the relative unimportance of phosphate, silicate and nitrate in influencing the distribution of either species. This is further confirmed by 3 and 4 variable GAM models, which imply that the addition of phosphate, silicate or nitrate to existing models adds little added explanatory value.

The models produced have varying abilities to reproduce the broad geographic distribution of both species. Our modelling indicates that the broad scale distribution of *C. finmarchicus* can be reproduced reasonably well (Figure 3.8) if we use a temperature only GAM model (with month used to incorporate seasonality). A GAM model with temperature alone is much less successful at reproducing the geographic distribution of *C. helgolandicus* (Figure 3.9). Consideration of the spatial maps produced with our suite of models indicates that only the inclusion of bathymetry results in a model which successfully reproduces the apparent restriction of *C. helgolandicus* to shelf regions.

3.4.5 Long term changes in *C. finmarchicus* and *C. helgolandicus* distributions and phenology

Figure 3.2 demonstrates that the geographic distributions of both species have changed in recent decades. In particular, there appears to have been a pronounced shift in the North Sea, with *C. helgolandicus* abundance increasing, while *C. finmarchicus* has declined. We will now consider the long term shifts in biogeography and phenology of

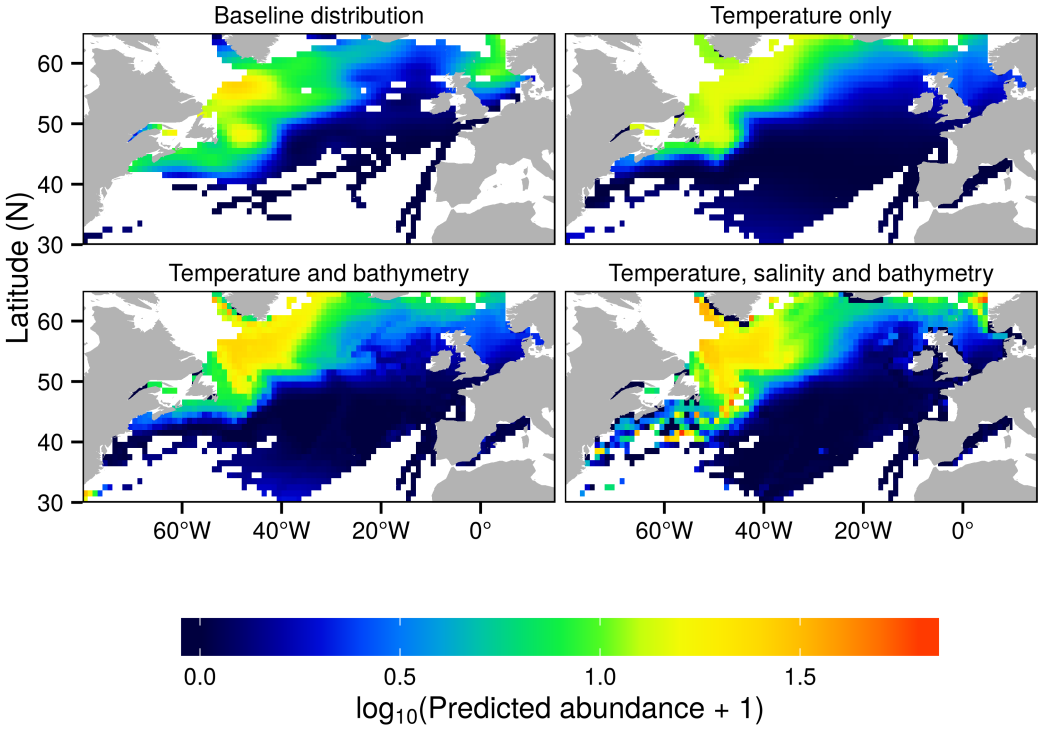


FIGURE 3.8: Ability of GAM models to reproduce the geographic distribution of *C. finmarchicus*. Each panel shows the predicted mean annual abundance from a GAM model which relates abundance to the variables listed. Seasonality was accounted for by including month in terms. Interactions were accounted for using tensor smooths.

both species in the regions surrounding the British Isles. This will indicate the extent of geographical shifts in or near regions where *C. helgolandicus* is replacing *C. finmarchicus*.

First, we considered long term abundance shifts of *C. helgolandicus* in the region to the south of the British Isles. This region was divided into 12 geographic subregions, which have sufficient data coverage to estimate long term changes in abundance. Average annual abundance was estimated, and the long term changes in annual abundance are shown in Figure 3.10. Comparison of time series in regions shows that there is a geographic pattern of abundance change. Regions off the Spanish coast have all seen long term declines in abundance. In contrast, there is no clear pattern in regions further

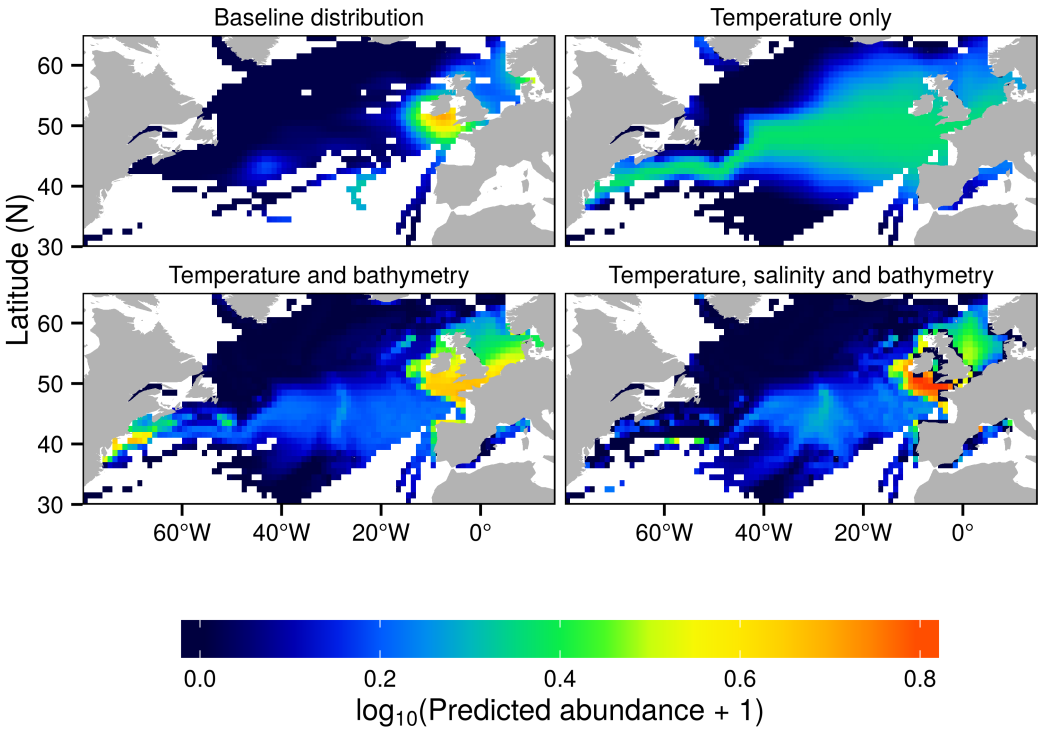


FIGURE 3.9: Ability of GAM models to reproduce the geographic distribution of *C. helgolandicus*. Each panel shows the predicted mean annual abundance from a GAM model which relates abundance to the variables listed. Seasonality was accounted for by including month in terms. Interactions were accounted for using tensor smooths.

north. However, patterns of annual abundance appear to be relatively stable south of Britain and Ireland.

We then performed a similar analysis in the North Sea, which was split into 12 subregions of approximately equal size (figure 3.11). The long term changes in the North Sea are consistent across all subregions. *C. helgolandicus* abundance has increased significantly in all regions (figure 3.12). In contrast, there is a long term decline in the abundance of *C. finmarchicus* in all but one subregion (figure 3.13).

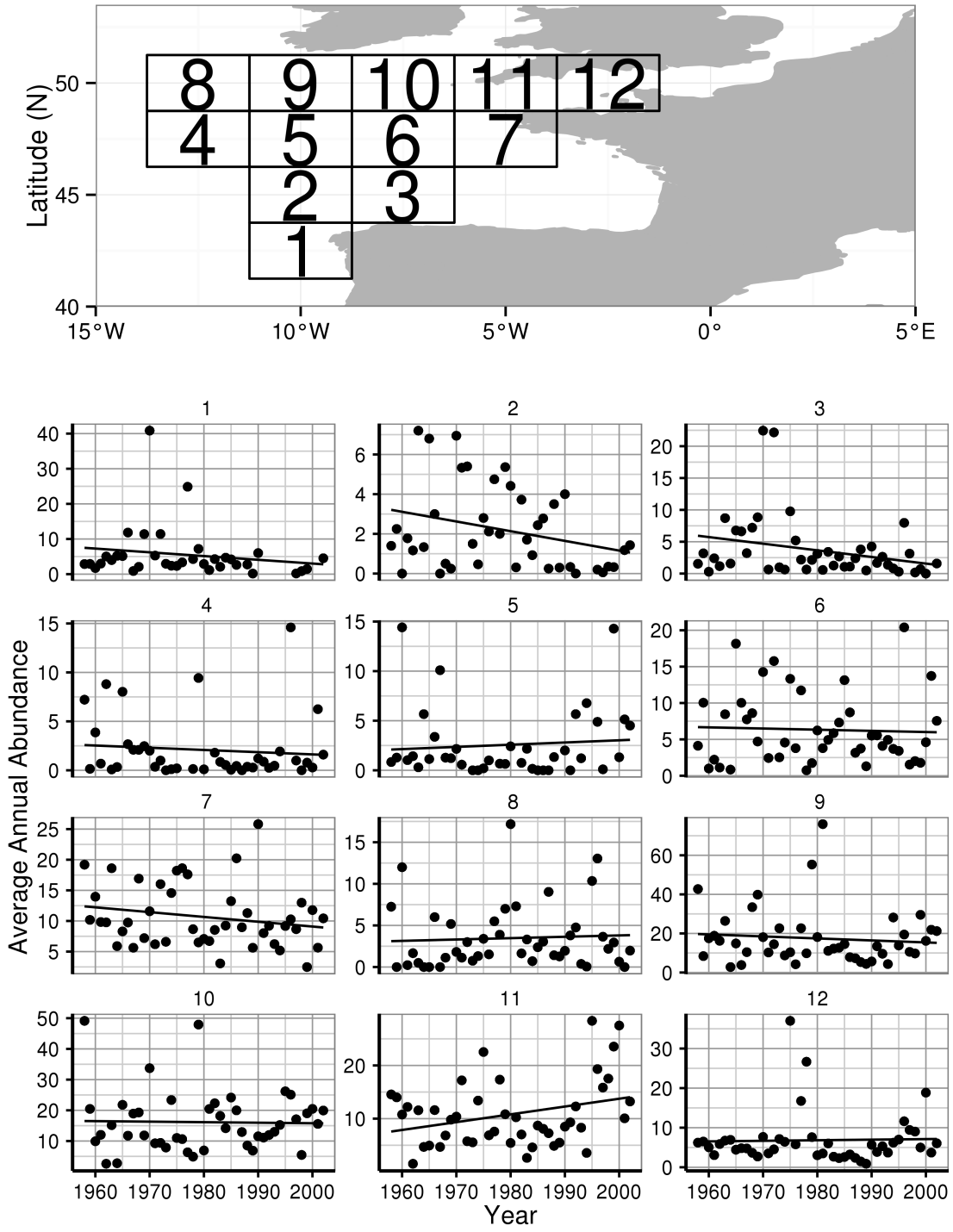


FIGURE 3.10: Estimated long term change in abundance of *C. helgolandicus* in regions to the south of the centre of its geographic distribution in the Celtic Sea region. Abundance is mean annual abundance estimated from CPR survey for each region shown. Lines represent a linear model of abundance against time. Numbered boxes show the geographic areas over which abundance was aggregated.

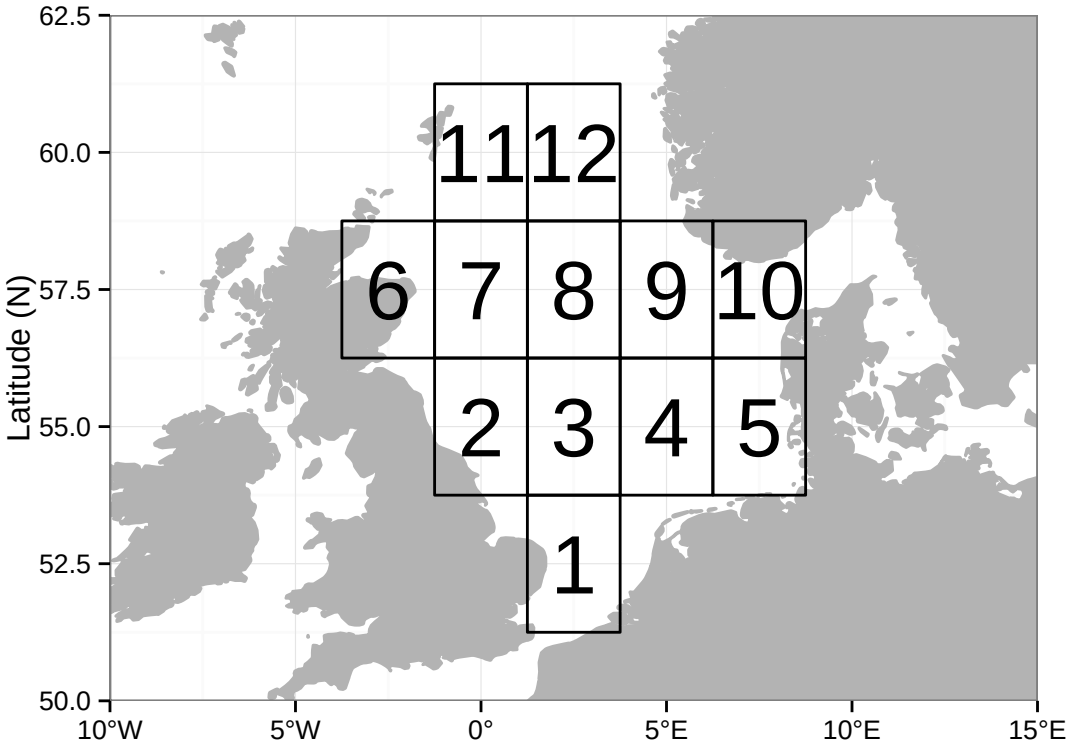


FIGURE 3.11: Regions considered for North Sea spatial shift analysis. Numbered boxes show the geographic areas over which abundance was aggregated.

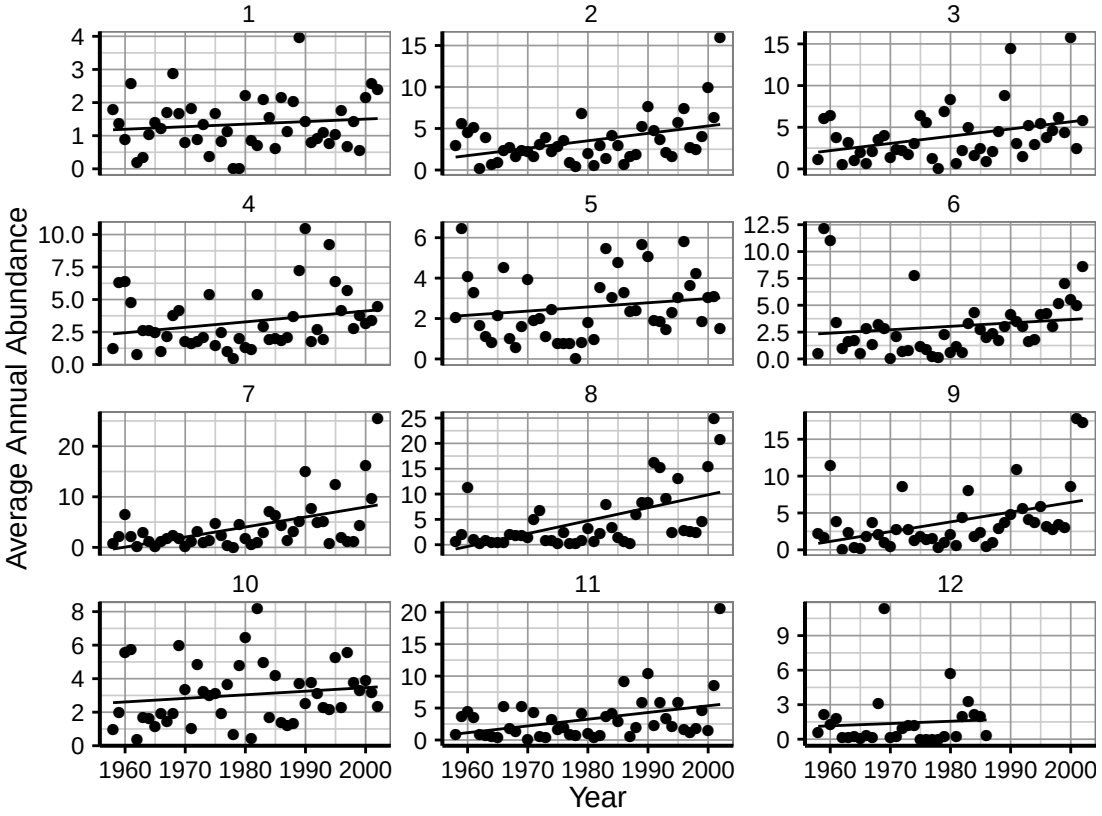


FIGURE 3.12: Reconstructed time series of historical *C. helgolandicus* abundance in the North Sea. Filled circles represented mean annual abundance in the respective aggregated area. Lines represent a linear model relating abundance to time.

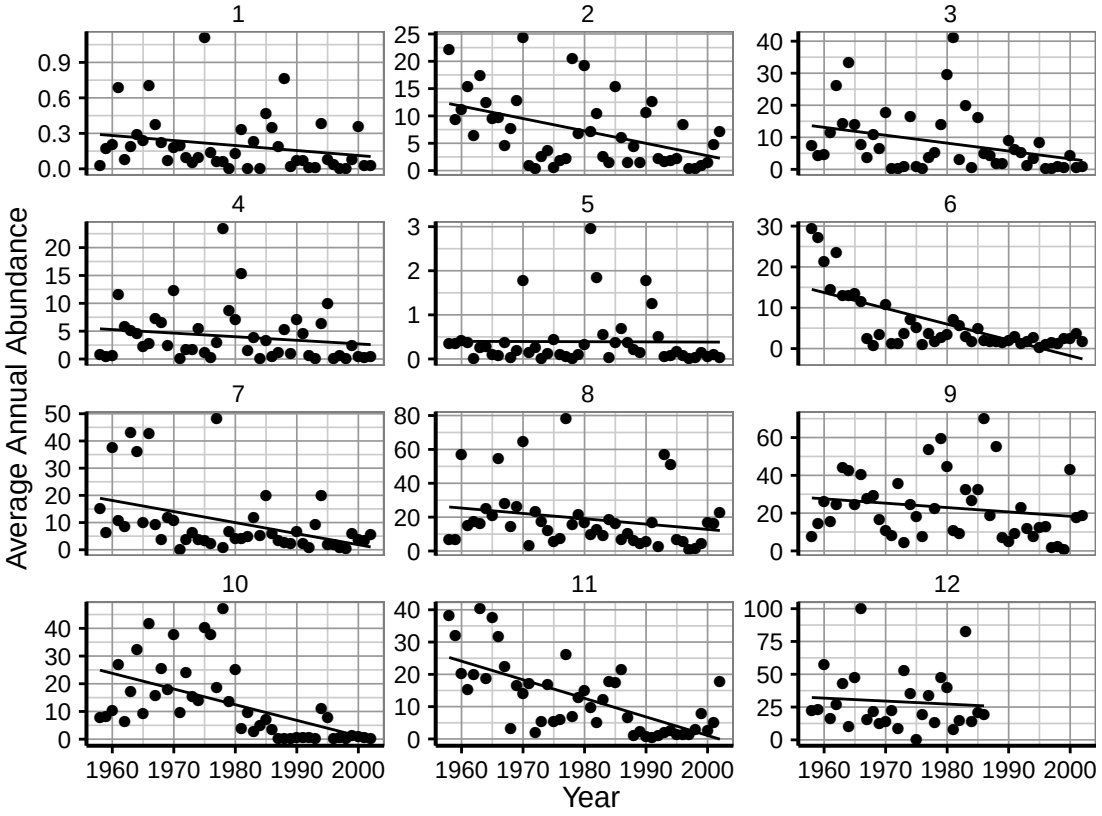


FIGURE 3.13: Reconstructed time series of historical *C. finmarchicus* abundance in the North Sea. Filled circles represented mean annual abundance in the respective aggregated area. Lines represent a linear model relating abundance to time.

These changes are further demonstrated by aggregating the abundance of both species across the North Sea (figure 3.14). The North Sea has seen a gradual transition from being dominated by *C. finmarchicus* to being dominated by *C. helgolandicus*. In addition to changes in *Calanus* community composition, there have been changes in abundance and phenology of aggregated *Calanus*. Total *Calanus* population has declined significantly between the 1960s and 1990s. In addition the seasonal cycle of total *Calanus* has become much less pronounced.Significantly, the spring peak in *C. finmarchicus* abundance in the 1960s was approximately an order of magnitude greater than the *C. helgolandicus* peak in autumn. In contrast, the peaks are numerically almost identical in the 1990s.

We analysed seasonality in *C. finmarchicus* and *C. helgolandicus* through GAM models relating abundance to time of year. Figure 3.15 shows seasonality in 4 regions around the British Isles. Other than in the North Sea, *C. helgolandicus* abundance peaks in spring or early summer. The North Sea abundance peak occurs approximately 150 d later in the year than in the other regions.

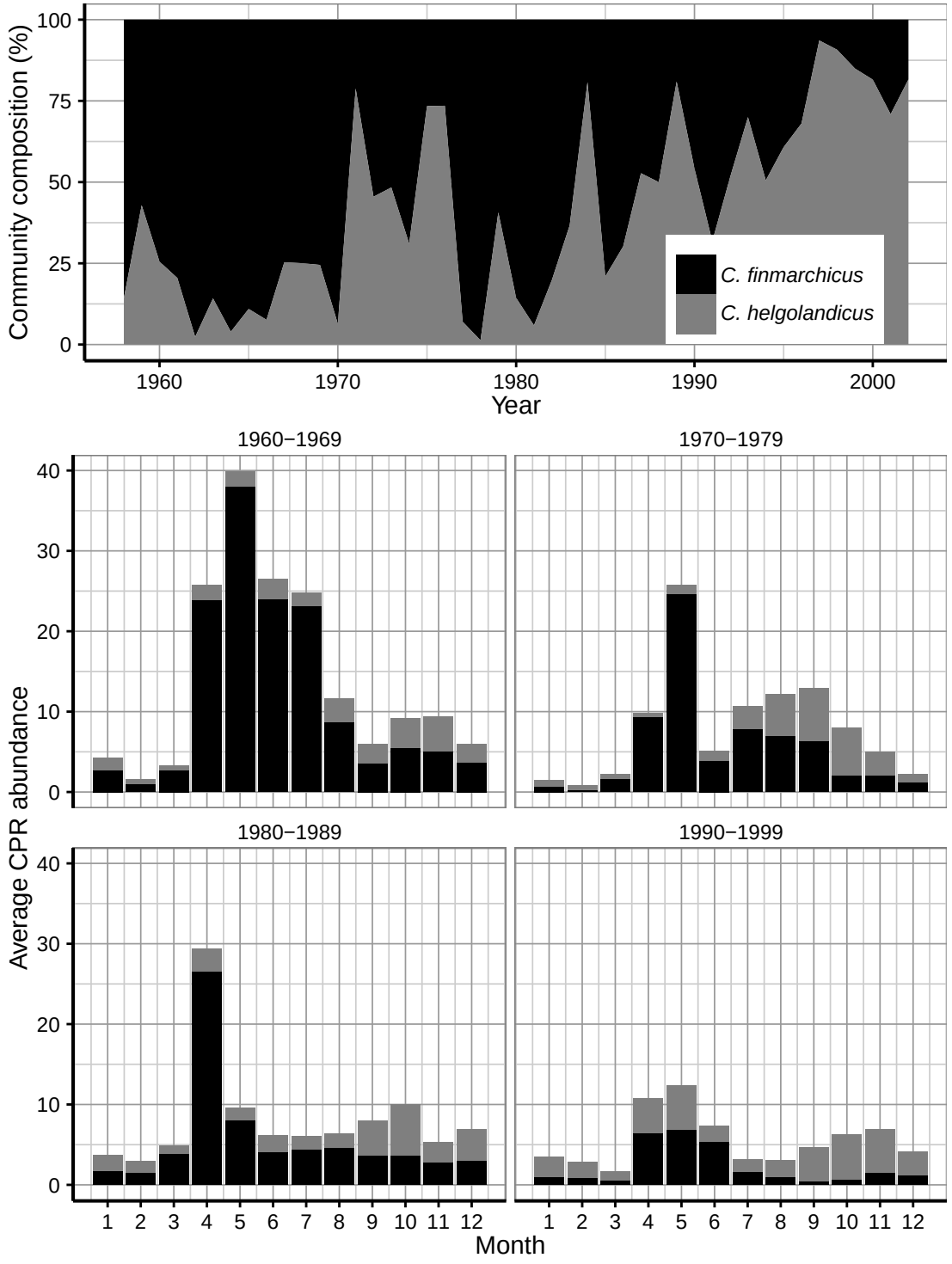


FIGURE 3.14: Changes in North Sea *Calanus* community composition between 1958 and 2002. Abundance shown is annual mean total C5 and adult CPR abundance for *C. finmarchicus* and *C. helgolandicus*

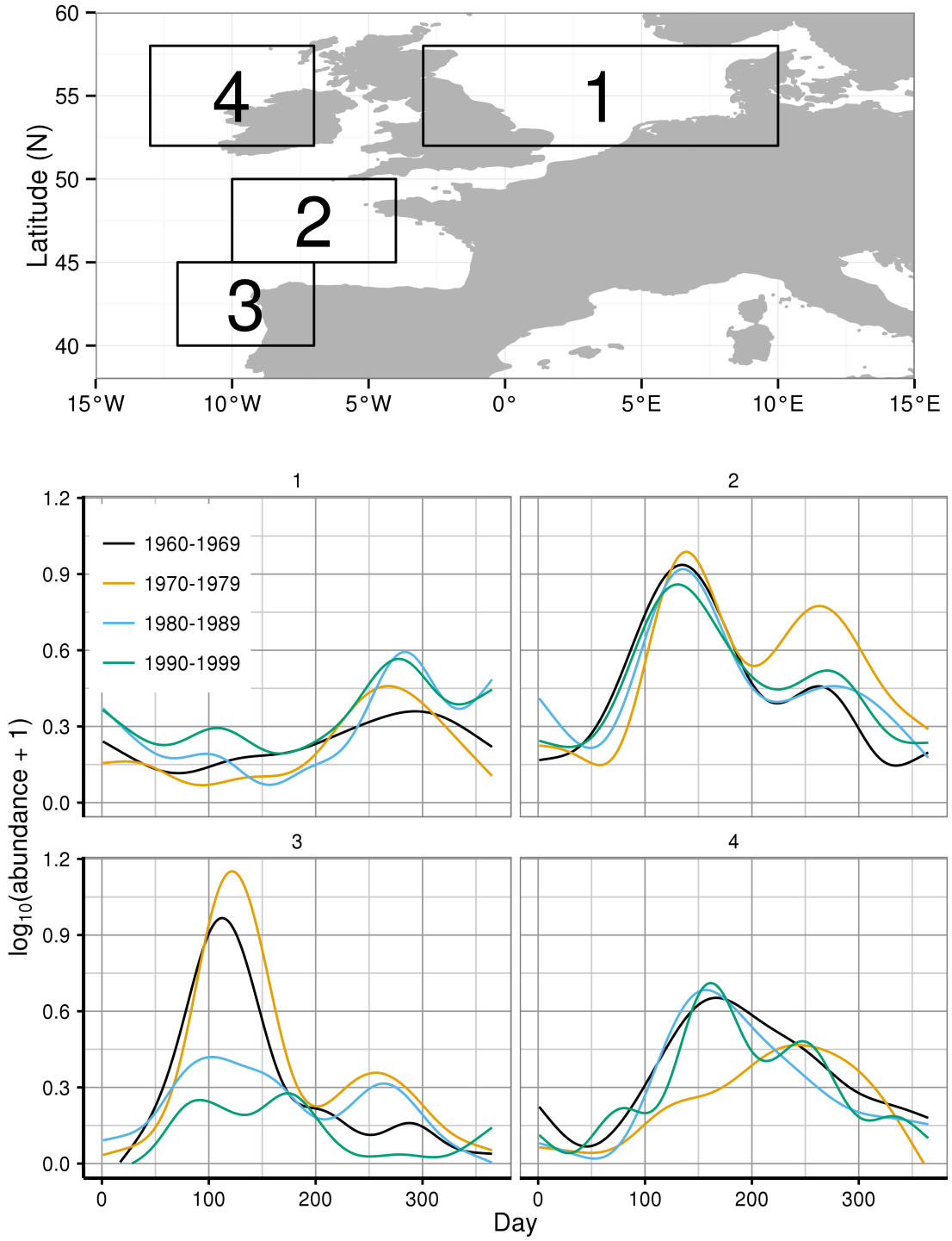


FIGURE 3.15: Seasonality of *C. helgolandicus*. Seasonal cycle was estimated using a GAM model relating abundance from CPR with day of year in the region and decade considered.

3.5 Discussion

Our statistical models indicate that differing responses to temperature are the key drivers of the different geographic distributions of each species.

The model which relates *C. helgolandicus* abundance to temperature and bathymetry is reasonably successful in the Eastern Atlantic. However, it notably predicts a large population of *C. helgolandicus* in the Western Atlantic (approximately 70°W and 40°N). Inclusion of salinity in our model results in a drastic reduction in the size of this population. In 1997, Fleminger and Hulsemann (1977) reported that there was a *C. helgolandicus* population between Cape Hatteras and the New York Bight. Our model provides weak evidence that such a population could be viable. However, no evidence appears to have been published since Fleminger and Hulsemann (1977) of a population of *C. helgolandicus* in the Western Atlantic. Similarly, there is little support from CPR records that the distribution of *C. helgolandicus* extends to the Western Atlantic.

Our analysis of *C. helgolandicus* abundance at different locations over recent decades indicates that its population has been largely stable at the apparent centre of its distribution (approximately 48 to 50°N). However, North and South of the centre of its distribution, *C. helgolandicus* has seen increases and decreases in its abundance. In contrast, Chust et al. (2013) performed a GAM analysis of CPR survey data and concluded that *C. helgolandicus* is expanding in every direction. This conclusion, however, appears to rest on GAM model predictions in regions where there is poor long term CPR coverage, and the model is unlikely to provide reliable predictions.

Some authors have proposed that *C. helgolandicus* will not be a full replacement of *C. finmarchicus* as prey for some species (e.g. Frederiksen et al. (2013)). Our analysis provides support for this hypothesis. *C. finmarchicus* production is much lower than *C. helgolandicus* production when measured in terms of CPR abundance. This is true, whether we are considering the aggregate of their populations throughout the North

Atlantic, or when comparing individual populations. Similarly, *C. finmarchicus* abundances seen in regions where *C. helgolandicus* may replace it are typically higher than those in existing *C. helgolandicus* populations. Body size of *C. helgolandicus* will be lower than that in the *C. finmarchicus* populations it is replacing. In addition, lipid content of *C. helgolandicus* individuals is lower than the *C. finmarchicus* they are replacing (see Section 2.2.5 on page 39), which may have an impact on species which are dependent on ingesting lipids from Calanus.

Seasonal mismatch between prey and predators can have a significant impact on populations (Edwards and Richardson, 2004; Burthe et al., 2012). This may be particularly important for ecosystems where *C. finmarchicus* is being replaced by *C. helgolandicus*. In the North Sea, *C. helgolandicus* peaks in abundance several months later than *C. finmarchicus*. Some species, including sandeels (van Deurs et al., 2009) feed on *Calanus* nauplii in spring and may be particularly sensitive to changes in *Calanus* phenology in the North Sea. Our reconstruction of changes in Calanus phenology in the North Sea indicate that total Calanus abundance has declined in recent decades, with a transition from *C. finmarchicus* to *C. helgolandicus* dominance (figure 3.14). Importantly, there has been a pronounced decline in the spring peak of total *Calanus*. A transition from *C. finmarchicus* to *C. helgolandicus* would also have resulted in a decline in mean size of *Calanus* in the North Sea. These changes in size and phenology in the Calanus community may potentially have impacted cod recruitment in the North Sea (Beaugrand et al., 2003). However, long term changes in the size composition of North Sea *Calanus* have yet to be rigorously quantified in the literature. Similarly, understanding long term changes in size is made complicated by seasonal variations in body size. *Calanus* body size varies significantly throughout the year (Jønasdøttir et al., 2005; Ceballos and Álvarez Marqués, 2006a; Swalethorp et al., 2011). Previously, CPR data has been used by an earlier study to estimate changing size composition of zooplankton communities (Pitois and Fox, 2006). However, these long term changes have not been well quantified. For example, Pitois and Fox (2006) assumed that *C. finmarchicus* had

weight 3 times greater for *C. helgolandicus*, an assumption that does not fit with published data showing both species are approximately the same size where they coexist (Wilson et al., 2015). Temperature appears to be the key driver of body size over a large geographic scale. Therefore, it may be possible to reconstruct changes in body size composition of *Calanus* communities using CPR data and known responses of body size to temperature.

Understanding the future evolution of the North Sea *Calanus* community is an issue of great importance. However, our analysis raises a number of questions. The *C. helgolandicus* community in the North Sea may potentially switch to a more typical phenology for the species, with a strong spring than autumn bloom. This would lessen the potential ecosystem impacts of a long term switch from *C. finmarchicus* to *C. helgolandicus*. However, current phenology of *C. helgolandicus* in the North Sea is difficult to explain fully. Temperatures throughout the North Sea are below 9 C prior to the occurrence of the spring bloom in *C. helgolandicus*. Bonnet et al. (2009) were incapable of developing *C. helgolandicus* beyond copepodite stages C1 at 9°C under controlled laboratory conditions. Similarly, Møller et al. (2012) found significantly reduced ingestion rates for *C. helgolandicus* at temperatures lower than 9°C. If this relationship between temperature and development holds in the North Sea, it would appear to be physically implausible for a spring bloom of *C. helgolandicus* to occur. The spring population in the North Sea may represent a population which has adapted to local environmental conditions. However, knowledge of local adaptations of physiological responses to temperature is currently lacking (Melle et al., 2014). Similarly, we cannot rule out the North Sea *C. helgolandicus* population representing hybrids between *C. helgolandicus* and *C. finmarchicus*. This phenomenon has recently been reported in *C. finmarchicus* and *C. glacialis*, where it may be much more widespread than thought (Parent et al., 2012; Berchenko and Stupnikova, 2014; Parent et al., 2011).

In agreement with existing findings (Beaugrand and Helaouët, 2008), we conclude

that *C. finmarchicus* has a much broader ecological niche than *C. helgolandicus*. Importantly, *C. finmarchicus* has a niche which is strongly influenced by bathymetry. The temperature-bathymetry niche (figure 3.7) reveals that *C. helgolandicus* is almost exclusively restricted to continental shelf regions. Our analysis indicates this pattern holds in the North East Atlantic throughout the history of the CPR. Evidence from surveys of diapausing populations in the Mediterranean indicate that *C. helgolandicus* populations diapause at depth. However, it is unclear if *C. helgolandicus* is able to persist in these deeper Mediterranean waters or if they are sink populations.

This apparent inability of *C. helgolandicus* to persist in oceanic waters may have significant ecosystem impacts. Increasing oceanic temperatures is likely to result in a northwards shift of *C. finmarchicus* populations to the north of Britain. Niche modelling by Reygondeau and Beaugrand (2011) indicated that *C. finmarchicus* populations may reduce significantly in number in East Atlantic regions south of 65°N. Modelling and the recent history of *Calanus* abundance in the North Sea, indicates that this reduction in *C. finmarchicus* may be partly offset by increasing *C. helgolandicus* abundance there (Maar et al., 2013). However, this may not hold in off-shelf regions, where *C. helgolandicus* currently appears incapable of persisting.

3.6 Conclusions

The key conclusions of this chapter are as follows:

- The geographic distribution of *C. finmarchicus* can be credibly reproduced using the predictions of a GAM relating abundance with temperature and salinity.
- The geographic distribution of C. finmarchicus can only be successfully reproduced if we include bathymetry as a model variable, highlighting the importance of bathymetry in influencing *C. helgolandicus*'s distribution.
- The temperature niches of both species are largely non-overlapping, with overlap where annual surface temperature is approximately 10 °C.
- The bathymetry niche of *C. helgolandicus* confirms that it is almost an exclusively shelf based species.
- Reconstructions of long trends in *C. helgolandicus* abundance shows that it has declined significantly at the southern edge of its distribution. This contradicts the previous finding of Chust et al. (2013), which used a GAM model to show that *C. helgolandicus* was expanding in all directions.
- Reconstructions of long term trends in abundance showed that *C. finmarchicus* has declined throughout the North Sea in the last decade, whereas *C. helgolandicus* has increased.
- Seasonality of the aggregate Calanus community is shown to have changed significantly in the North Sea. In the 1960s there was a pronounced spring bloom, which was largely *C. finmarchicus*. However, by the 1990s the seasonal cycle had flattened out significantly, with two approximately equal sized spring and autumn blooms.

TABLE 3.3: GAM models relating abundance with individual variables

Variable	*C. finmarchicus* R^2	*C. helgolandicus* R^2
Monthly Temperature	0.099	0.092
Annual Temperature	0.243	0.116
Month	0.085	0.013
Monthly Salinity	0.112	0.008
Monthly Silicate	0.003	0.016
Monthly Nitrate	0.003	0.031
Monthly Phosphate	0.016	0.050
Monthly Oxygen	0.149	0.030
Bathymetry	0.037	0.106
Annual Salinity	0.112	0.009
Annual Silicate	0.039	0.030
Annual Nitrate	0.017	0.047
Annual Phosphate	0.082	0.067
Annual Oxygen	0.206	0.051

TABLE 3.4: GAM models relating *C. finmarchicus* abundance with two variables

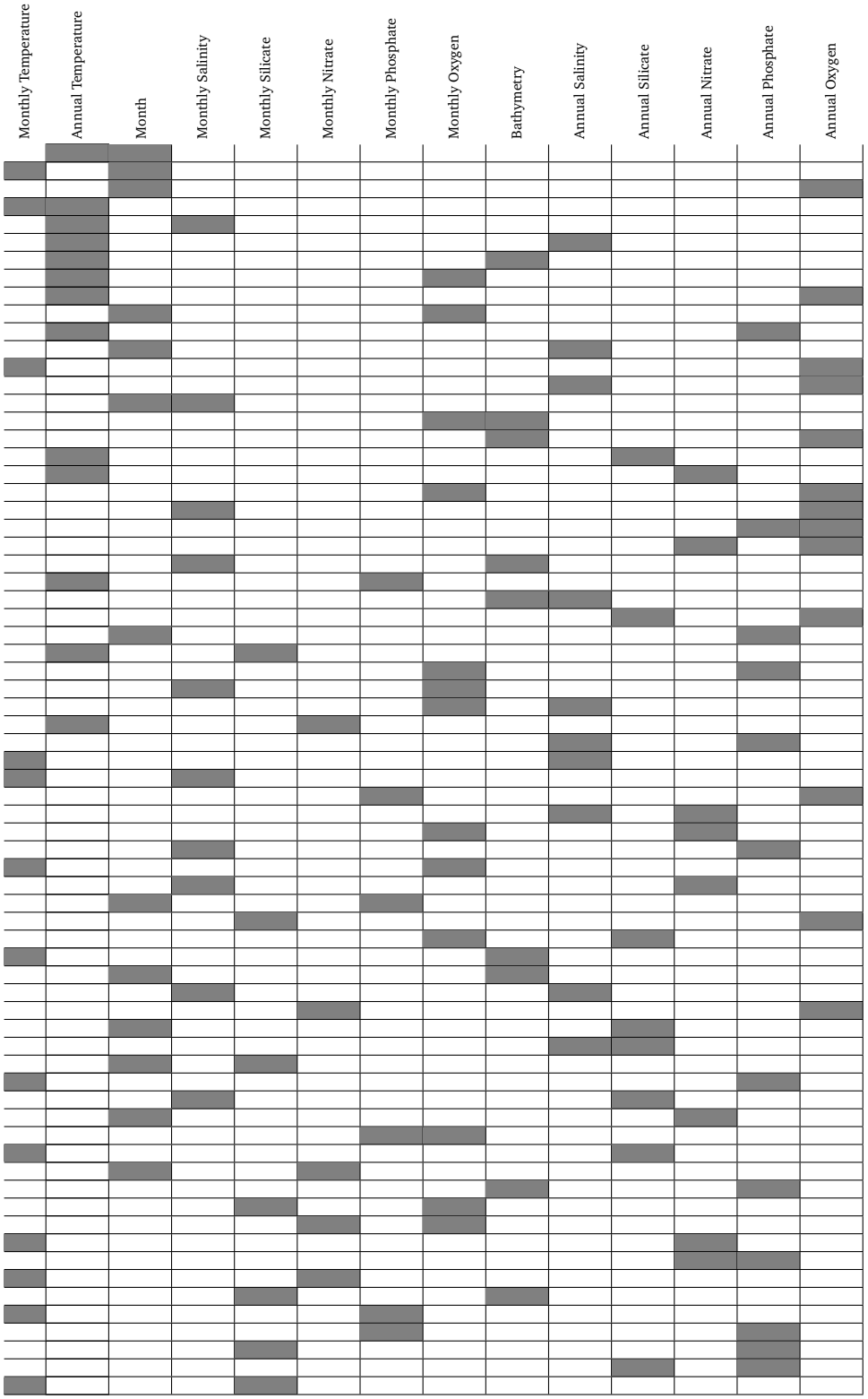


TABLE 3.5: GAM models relating *C. helgolandicus* abundance with two variables

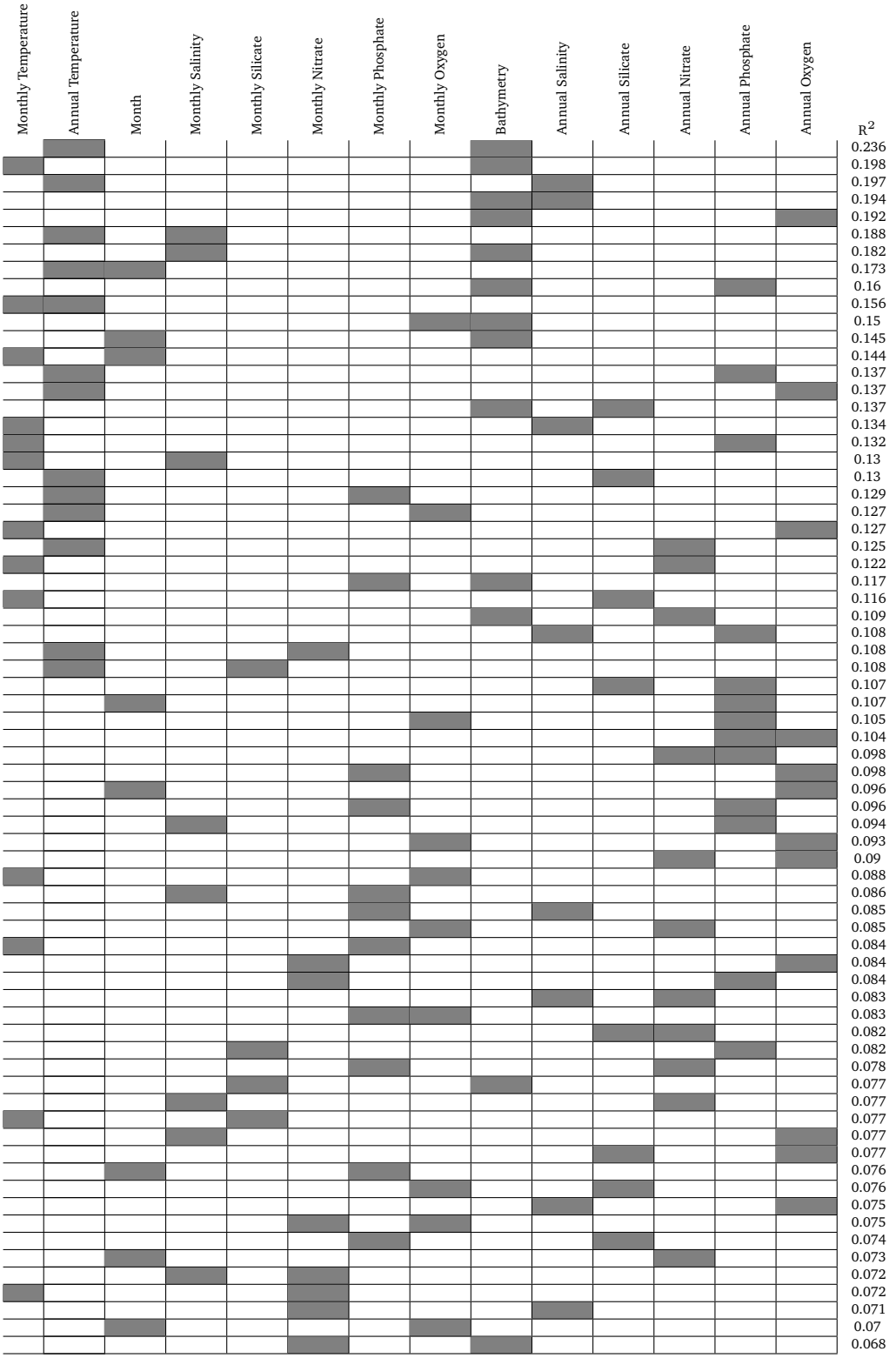


TABLE 3.6: GAM models relating *C. finmarchicus* abundance with three environmental variables

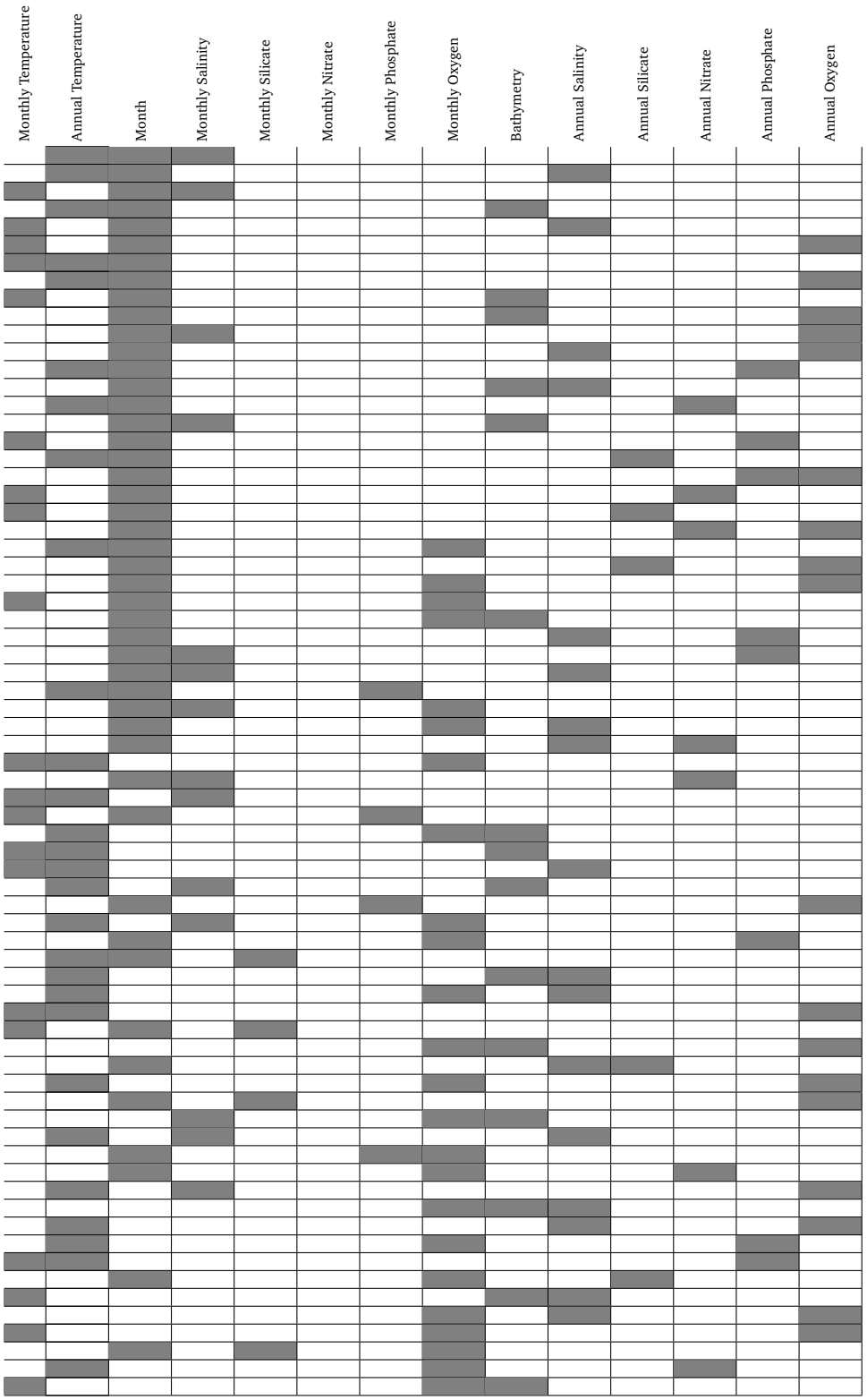


TABLE 3.7: GAM models relating *C. helgolandicus* abundance with three environmental variables

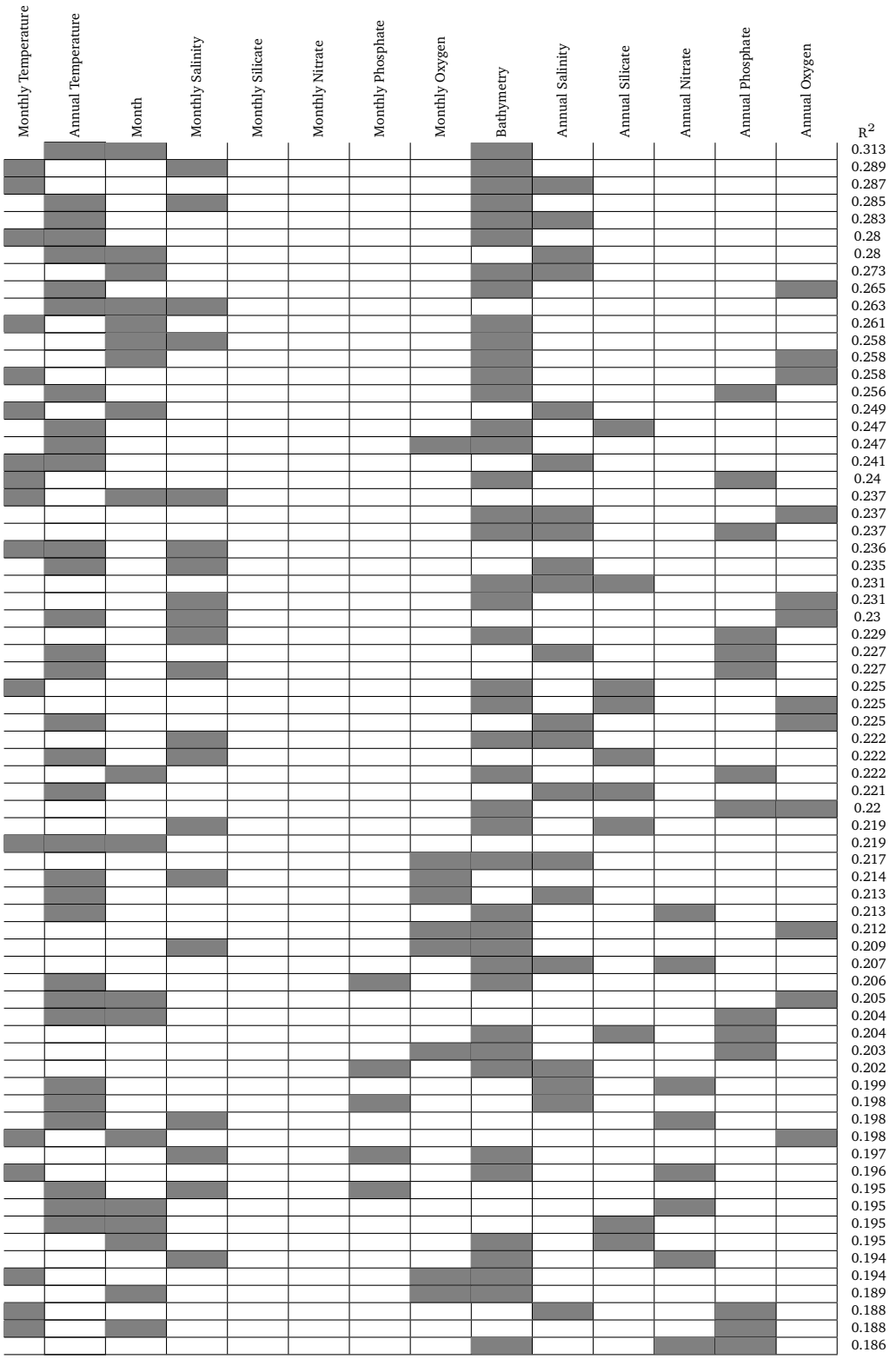


TABLE 3.8: GAM models relating *C. finmarchicus* abundance with four environmental variables

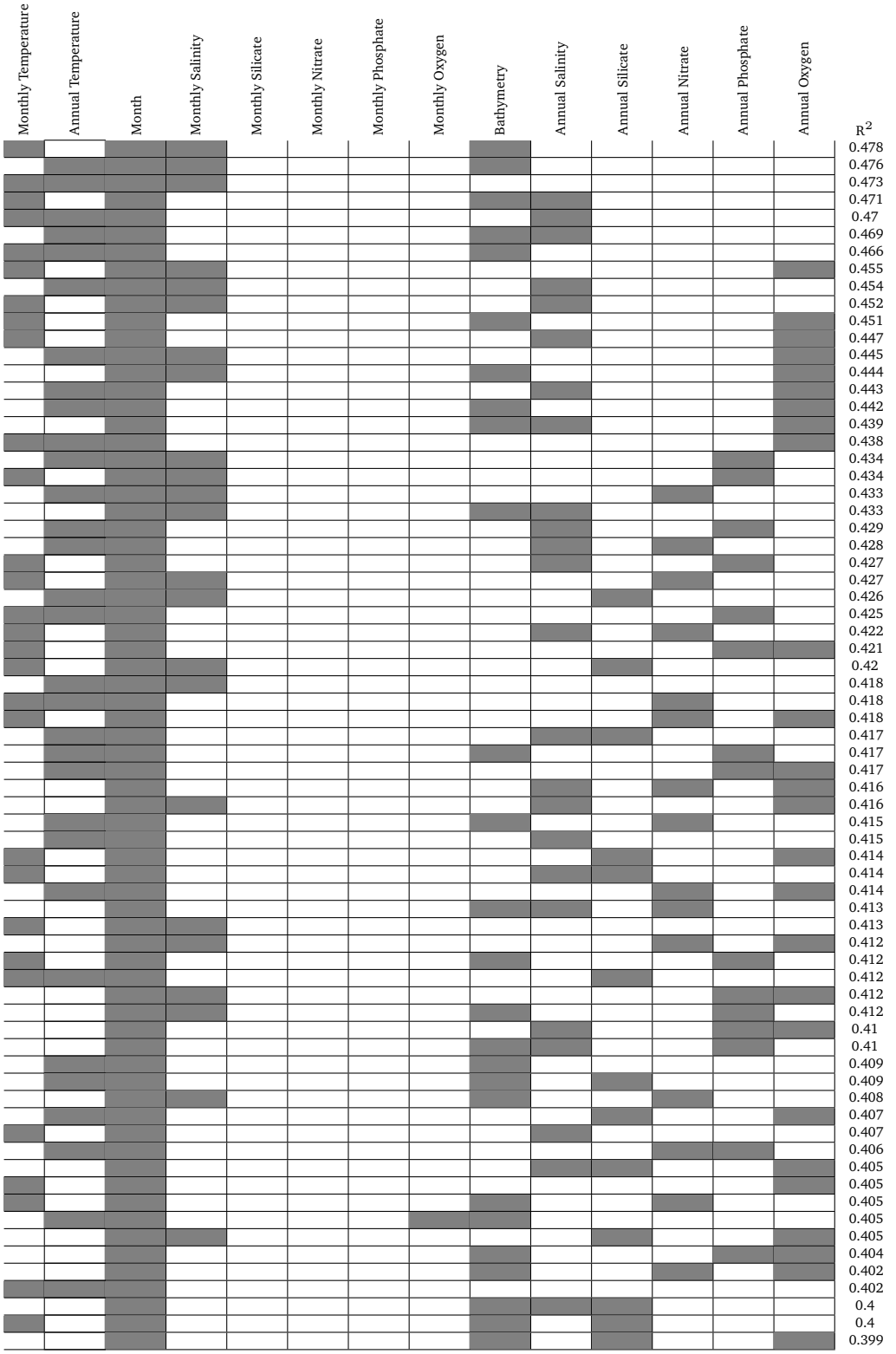
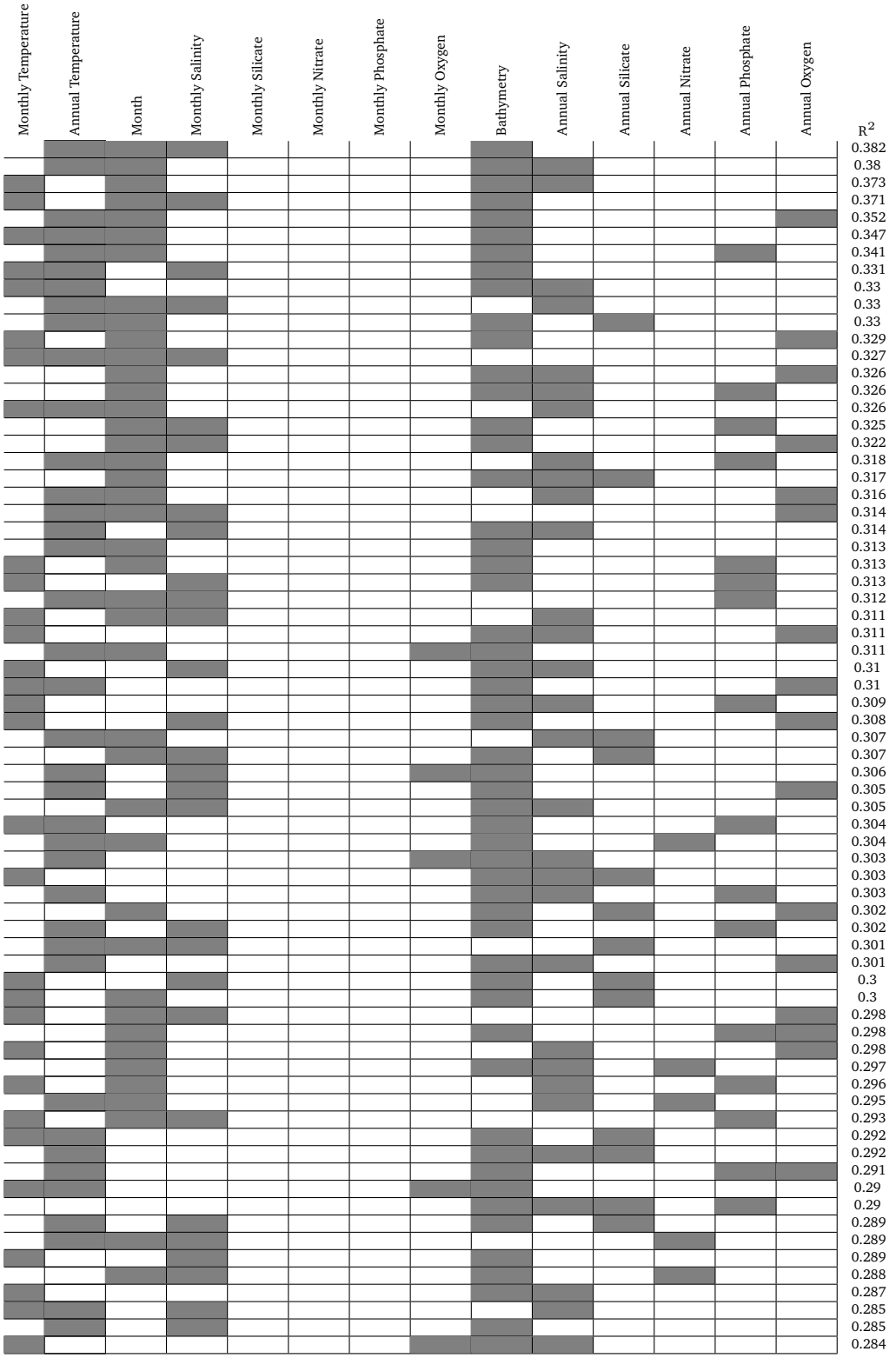


TABLE 3.9: GAM models relating *C. helgolandicus* abundance with four environmental variables



Part IV

Population Modelling

Chapter 4

Modelling Methodology

4.1 Modelling *Calanus*: a unified approach

The typical modelling approach for *Calanus* species is to view them in isolation. Model equations are formulated with reference to the known biology of species, and the model is then parameterized and tested against known data. Here we take a new approach.

Modelling the populations of *C. finmarchicus* and *C. helgolandicus* requires the mathematical representation of a number of key processes: development, fecundity, mortality, transportation and diapause behaviour. These processes are normally assumed to follow the form described by a laboratory study or they are parameterized. For example, the equations used for development time in *C. finmarchicus* models are regularly derived unchanged from (Campbell et al., 2001). On the other hand, mortality is poorly understood (Gentleman et al., 2012; Ohman, 2012), and modellers are forced to put in place undeniably ad hoc model elements.

Some of these processes, such as transportation, can be described identically for both species. In the case of development we use the model described in chapter two. However, with other model elements there is a large amount of freedom. This can be viewed

as both a freedom and a restriction. It is also likely to result in the sacrifice of clarity in the name of precision. If we want to understand why *C. finmarchicus* exists in the Norwegian Sea, while *C. helgolandicus* does not, then 2 separate models with an assortment of interspecies differences in assumptions and parameters is likely to confuse as much as clarify.

Similarly, independent model formulation and parametrization is likely to result in models which are biologically and ecologically incoherent. Chapter two's review of the biology and ecology of both species shows that there is a surprising level of unity across both species. In fact, interspecies differences are almost minimal. Models of both species should align with this.

We therefore approach the modelling and parametrization of our models with a simple philosophy. No interspecies differences are assumed, except where necessary or highlighted by our review in chapter two. This enables the creation of models which are more biologically and ecological coherent. Further, it results in 2 models which are easier to interpret.

Models cannot be easily erected from thin air, and fortunately there is a rich history of modelling the populations of *C. finmarchicus* (Table 4.1). The unified model presented here is based principally on Speirs et al. (2006), which itself was an extension of the earlier work of Speirs et al. (2005) and Gurney et al. (2001). Their modelling framework was enhanced and extended so that both species can be modelled in a unified way.

Some elements of the model of Speirs et al. (2006) are not suited to modelling both species in a unified manner. Starvation mortality was modelled purely with reference to food in Speirs et al. (2006). However, there is a significant difference in the response of ingestion rate to temperature for both species (Møller et al., 2012). In this case, we reformulate starvation mortality so that it relates to growth, and this enables this to be modelled in a unified manner. Similarly, we now incorporate body size as a model

element. As discussed below, this enables egg production rate and diapause duration to be modelled in a unified manner.

Our model covers the same geographic region as Speirs et al. (2006). Its latitudinal extent is 30-80°N and its longitudinal extent is 80°W-90°E. This domain covers all ecologically relevant regions for *C. finmarchicus* and *C. helgolandicus* (Bonnet et al., 2005). Further, the domain is resolved cells which measure 0.25°N by 0.5°E. Following from Speirs et al. (2006), we use 1997 as our model year.

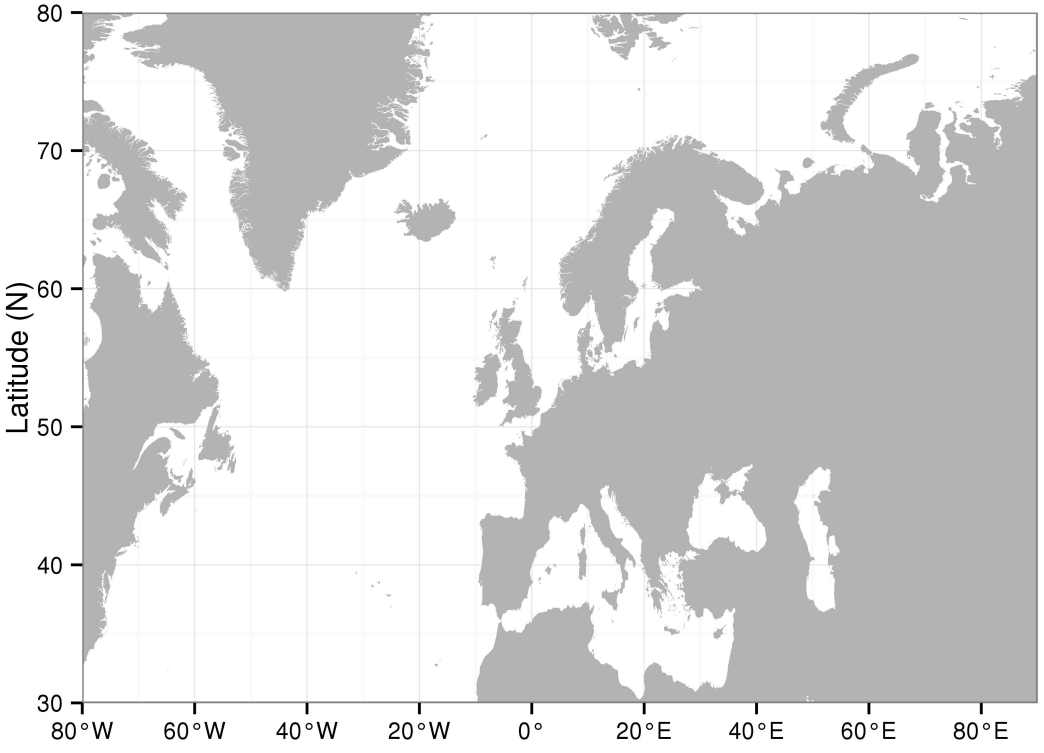


FIGURE 4.1: Spatial domain of the population model. Latitudinal extent is from 30 to 80°N. Longitudinal extent is from 80°W to 90°E. The model is resolved spatially to cells of dimension 0.25 °N and 0.5 °E.

TABLE 4.1: Previous process based models of *Calanus*. * indicates that the paper modelled *C. helgolandicus*.

Paper	Details	Region
Carlotti et al., 1993	Growth and development	NA
Miller and Tande, 1993	Stage duration	Malangen fjord
Aksnes and Blindheim, 1996	Influence of circulation	NA
Carlotti and Radach, 1996	Population Model	North Sea
Bryant et al., 1997	Population Model	North Sea
Carlotti and Hirche, 1997	Growth and egg production	NA
Heath et al., 1997	Population Model	Fair Isle Current
Bryant et al., 1998	Transport and persistence	South of Greenland
Carlotti and Wolf, 1998	Lagrangian ensemble model	Norwegian Sea
Fiksen and Carlotti, 1998	Vertical migration	NA
Lynch et al., 1998	Population Model	Gulf of Maine
Miller et al., 1998a	Population Model	Georges Bank
Gallego et al., 1999	Spring migration	North Sea
Heath et al., 1999	Invasion of North Sea	North Sea
Ingvarsdøttir et al., 1999	Diapause duration	NA
Harms, 2000	Invasion of shelf regions	NE Atlantic
Visser and Jønasdøttir, 1999	Buoyancy	NA
Fiksen, 2000	Diapause Timing	NA
Hind et al., 2000	Diapause Model	East Atlantic
Gurney et al., 2001	Population model	NE Atlantic
Pedersen et al., 2001	Demography	Norwegian Coast
Campbell and Dower, 2003	Buoyancy	NA
Tittensor et al., 2003	Population model	Labrador Sea
Speirs et al., 2004	Population Model	Norwegian Sea
Speirs et al., 2005	Population Model	North-East Atlantic
Johnson et al., 2006	Transport of diapausers	Gulf of Maine
Saumweber and Durbin, 2006	Diapause duration	NA
Speirs et al., 2006	Population Model	North Atlantic
Neuheimer et al., 2009	Larvae	Georges Bank
Pershing et al., 2009	Population model	Gulf of Maine
Ji et al., 2012	Population Model	Arctic Ocean
Maps et al., 2010	Diapause	Gulf of St. Lawrence
Record et al., 2010	Genetic algorithms etc.	NA
Maps et al., 2011	Seasonal and diel migration	Gulf of St. Lawrence
Maps et al., 2012b	Diapause phenology	N.W. Atlantic Shelf
Utne et al., 2012	Fish consumption of *C. finmarchicus*	Norwegian Sea
Hjøllo et al., 2012	Secondary production	Norwegian Sea
Maar et al., 2013*	Population Model	North Sea
Maps et al., 2014	Diapause Duration	NA
Pepin et al., 2013	Dispersal	Newfoundland Shelf
Pierson et al., 2013	Diapause Duration	NA
Skaret et al., 2014	Population dynamics	Barents Sea
Rullyanto et al., 2015	Transport of diapausers	Faroe-Shetland Channel

4.2 Biological variables

A computationally tractable mathematical formulation of *Calanus* development is enabled by the fact that development is equiproportional (Campbell et al., 2001). Development from egg to adult can therefore be divided into a fixed number of stages, with each having identical stage duration under the same environmental conditions (Gurney et al., 2001). This allows us to update the entire population simultaneously, that is the system is updated at a time step equivalent to the duration of each stage. The entire population can therefore be modelled with high computational efficiency (Speirs et al., 2006). We assume that there are 57 pre-adult stages and these stages are shown for both species in Table 4.2.

TABLE 4.2: Stage classes for *C. finmarchicus* assumed by the model. The model resolves development into 57 stage classes. The mapping between model stage classes and biological development stages are shown. For example, stage C5 of *C. finmarchicus* starts at class 41 and ends at class 57.

Stage	E	N1	N2	N3	N4	N5	N6	C1	C2	C3	C4	C5
C. finmarchicus												
Surface												
last class	2	5	8	11	14	17	20	25	30	35	41	57
Diapause												
last class	-	-	-	-	-	-	-	-	-	-	-	100
C. helgolandicus												
Surface												
last class	1	4	6	11	15	19	27	31	36	42	47	57

In common with most species (Horne et al., 2015), body size of *Calanus* varies geographically, largely due to the influence of temperature. Typical female prosome lengths range from 2.4 to 3.0 mm (Melle et al., 2014) in *C. finmarchicus*, and from 2 to 2.6 mm in *C. helgolandicus* (Bonnet et al., 2005; Jønasdøttir et al., 2005).

Body size can influence population dynamics for several reasons. It influences fecundity, mortality and potential diapause duration. However, the role of size has largely been ignored in population models. This is understandable. The inclusion of size in a model will increase its computational intensity significantly. In addition, the trade-off

between improved model precision and increased computational intensity is not clear. Body size influences are poorly understood. For example, existing evidence about the influence of body size on fecundity show very approximate quantifications (see references in Table 4.3); and current knowledge can arguably be simplified as follows, "bigger females lay more eggs".

However, there are important reasons for including body size in a model of both *C. finmarchicus* and *C. helgolandicus*. First, body size appears to have a strong influence on potential diapause duration (Saumweber and Durbin, 2006). Smaller individuals have both higher weight specific respiration rates (Maps et al., 2014) and relatively lower lipid levels than larger individuals (Miller et al., 2000; Pepin and Head, 2009; Saumweber and Durbin, 2006). Consequently, smaller individuals likely have significantly shorter diapause durations.

Inclusion of body size also allows a unified approach to modelling fecundity. Laboratory studies of the influence of temperature on *C. helgolandicus* EPR are currently lacking. We therefore cannot follow the approach of Speirs et al. (2006) and base EPR of *C. helgolandicus* on laboratory work. However, if we assume egg production and growth to be equivalent (Mclaren and Leonard, 1995), we can achieve a more elegant solution. As discussed below, this approach enables a unified model of egg production in both species, and to produce per-capita EPR that match fit reasonably well with existing laboratory studies.

Our model assumes that body size as an adult is determined by temperature at birth. Temperature experienced at birth is a reasonable approximation for temperature experienced throughout an animal's development, given the relatively short development times of *Calanus*.

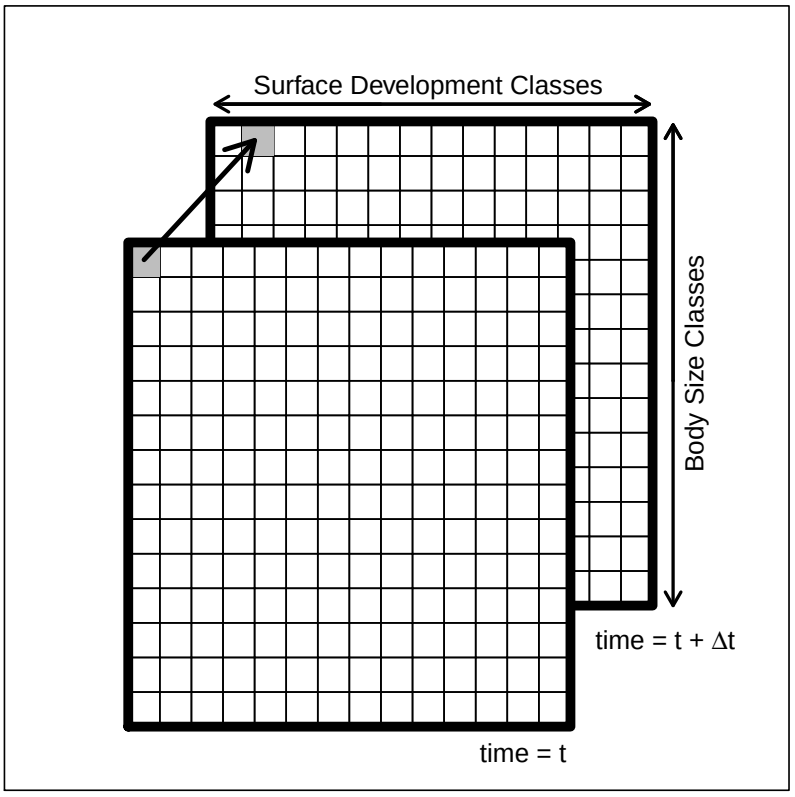


FIGURE 4.2: Illustration of model update process. Each development class has a development time Δt for a given location and time. System updates are therefore made at every Δt, with the population in each development stage moved to the next development stage, along with the application of mortality, fecundity etc. updates.

TABLE 4.3: Field studies reporting the relationship between fecundity and female body size in *Calanus*

Species	Metric	Reference
C. finmarchicus	Length	Jønasdøttir et al., 2008
C. finmarchicus	Length	Runge and Plourde, 1996
C. finmarchicus	Length	Gislason, 2005
C. finmarchicus	Length	Jønasdøttir et al., 2005
C. finmarchicus	Length	Melle et al., 2014
C. finmarchicus	Length and weight	Head et al., 2013a
C. helgolandicus	Length	Ceballos and Álvarez Marqués, 2006a
C. finmarchicus	Weight	Campbell and Head, 2000
C. finmarchicus	Length	Runge et al., 2006

Modelling Elements

I will now outline the modelling approach taken for each aspect of life cycle of *C. finmarchicus* and *C. helgolandicus*. In each case I will review and synthesize the published literature on the relevant life cycle aspect before formulating our modelling approach.

4.3 Body size

4.3.1 Influences on body size

Body size is principally influenced by temperature and food. A negative relationship between temperature and body size has been demonstrated by laboratory (Campbell et al., 2001; Bonnet et al., 2009) and field studies (Stenevik et al., 2007; Gislason, 2005; Head et al., 2013b). Female prosome length has also been observed to vary seasonally with temperature in both species (Grigg et al., 1989; Ceballos and Álvarez Marqués, 2006a). The relationship between annual sea surface temperature and observed female prosome length is similar to the relationship found in the laboratory study of Campbell et al. (2001) (Figure 4.3).

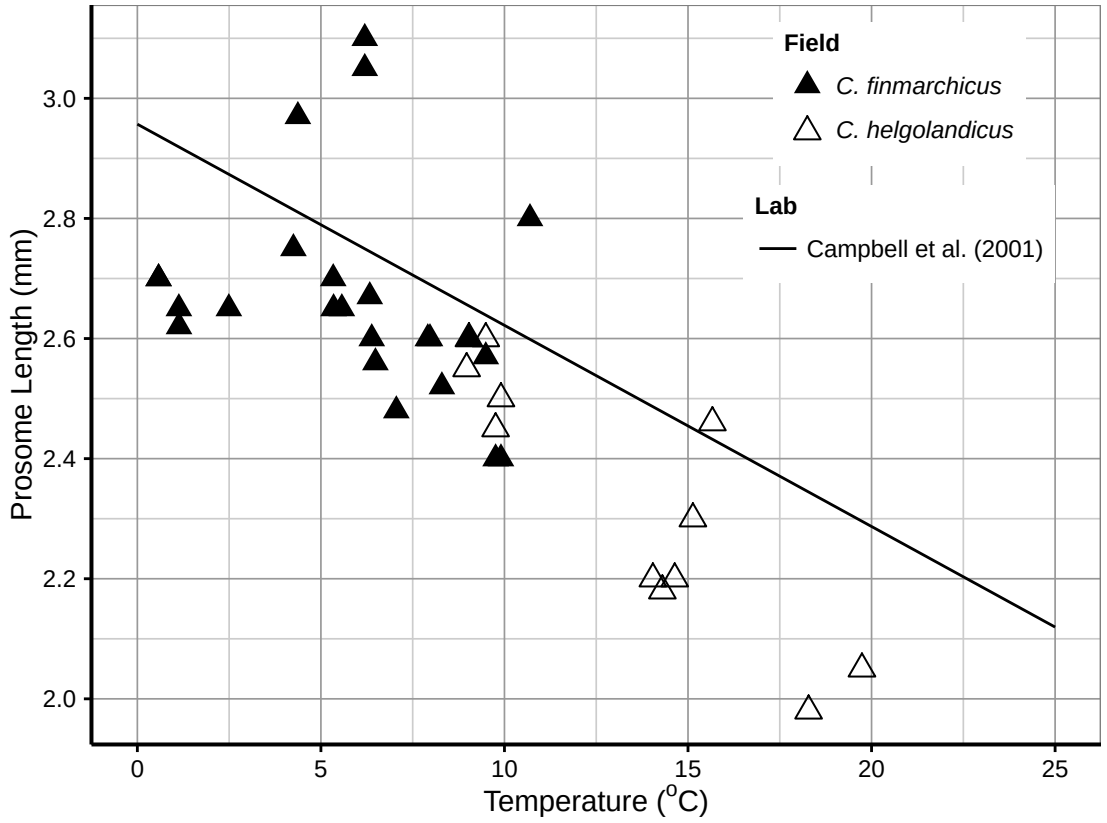


FIGURE 4.3: Comparison of the temperature-female prosome length relationship from the experimental study of Campbell et al. (2001) with field data. Temperature for field data is annual average SST. References for field data are given in figure 2.1.

Laboratory evidence shows that prosome length is influenced by food concentration. Hygum et al. (2000b) raised *C. finmarchicus* under both a high and low resource food regime. In the high resource regime females had average prosome length of 2.92 mm, while at a low resource food regime average prosome length was 2.78 mm. Importantly, the variation in prosome length resulting from the influence of food is lower than that observed due to variation in temperature. Females grown under food saturated conditions by Campbell et al. (2001) grew to 2.8 mm at 4°C, whereas individuals grew to 2.49 mm at 12°C.

4.3.2 Modelling body size

For computational reasons it is not plausible to explicitly model the influence of temperature and food on body size. In addition, biological knowledge is probably not strong enough to do so. We therefore assume, as a first approximation, that size as an adult is determined by temperature at birth.

This is a simplified approach; however there are reasonable grounds for taking it. Interstage changes in body size are likely to be constrained by the size of the exoskeleton in previous stages. Body size as an adult is therefore likely to be constrained by that at birth, which is largely determined by temperature (Campbell et al., 2001). In addition, temperature at birth is also good proxy for temperature throughout development. This approach is therefore likely to produce reasonable population level average prosome lengths.

Our starting point is the laboratory study of Campbell et al. (2001), which estimated the relationship between temperature and female prosome length as,

$$\mathrm{L} = mT + b \tag{4.1}$$

where L prosome length (μm), T is temperature (°C), $m = -39.1$ and $b = 3073$. Rey-Rassat et al. (2002b) recorded *C. helgolandicus* female prosome lengths of 2589 $\pm$93 μm, which is reasonably consistent with a prediction of 2487 μm using the model above. It is therefore reasonable to consider this to be a credible model of the influence of temperature on body size under food saturated conditions. However, varying food conditions are likely to result in lower body sizes in field conditions of identical temperatures. We therefore adjust modelled prosome length by a fixed temperature-independent factor, which was tuned after comparing predicted prosome length with field data.

A realistic representation of length-weight relationships is important, due to the influence of body weight on egg production. Length-weight relationship is of the form $w = aL^y$, where w is the carbon weight (μg), L is the prosome length (mm) and y is typically between 3 and 4. Published length-weight relationships are summarized in Figure 4.4 and Table 4.4.

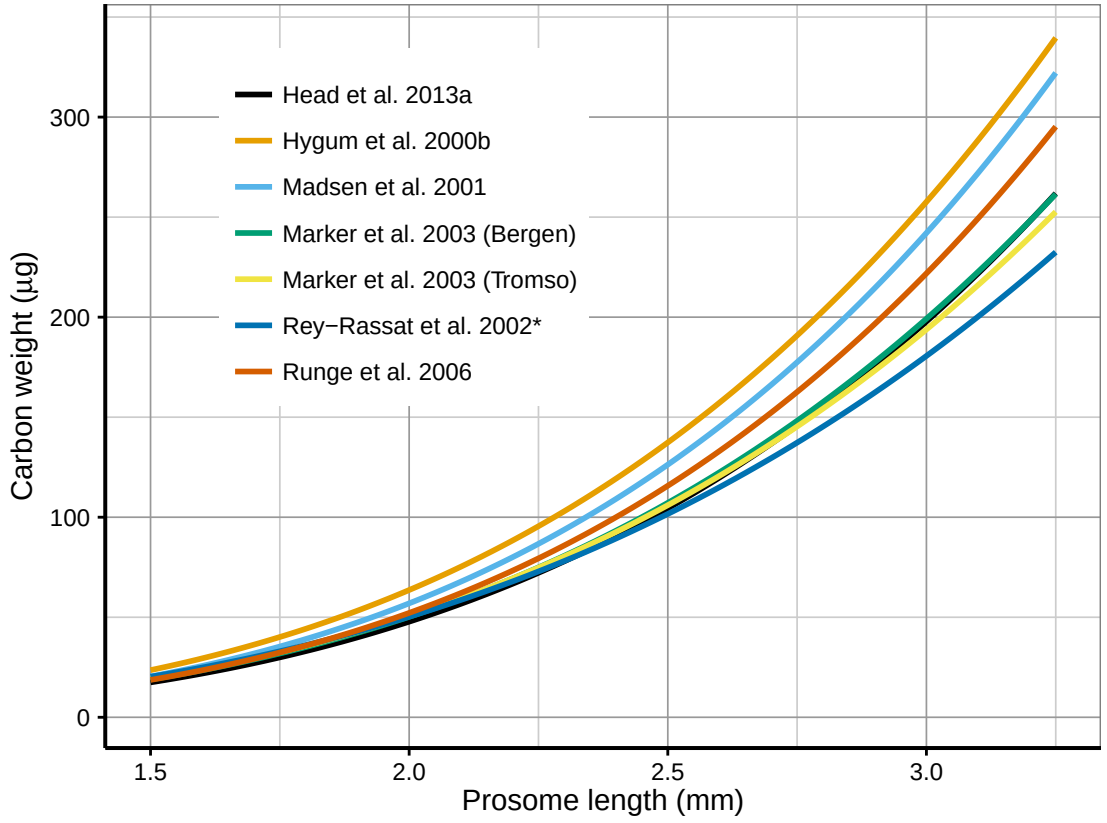


FIGURE 4.4: Published length-weight relationships for both species. Weight measurement is body carbon. Length is prosome length. * indicates relationship is for *C. helgolandicus*.

These relationships are reasonably consistent across studies. Importantly, there is no evidence that the length-weight relationship is different in *C. helgolandicus*. The length-weight relationship published by Runge et al. (2006) is close to the median of the published length-weight relationships, we therefore use it in our models of both species.

We follow Speirs et al. (2006) and use the body weights of each stage from Lynch et al. (2001) as our body weights for each pre-adult stage. However, these numbers are

TABLE 4.4: Summary of published length-weight relationships for *C. finmarchicus* and *C. helgolandicus*. Relationships are of the form $w = aL^y$, where w is carbon weight (μ g) and L is prosome length (mm). * indicates that a relationship is for *C. helgolandicus*.

Carbon weight	Reference
$7.4L^{3.5}$	Hygum et al. 2000b
$4.75L^{3.4}$	Marker et al. 2003 (Bergen)
$5.1L^{3.31}$	Marker et al. 2003 (Tromso)
$4.39L^{3.57}$	Runge et al. 2006
$4.2L^{3.53}$	Head et al. 2013a
$4.8L^{3.5687}$	Madsen et al. 2001
$5.65L^{3.15}$	Rey-Rassat et al. 2002c*

adjusted for the previously mentioned temperature effect on size.

4.4 Environmental drivers of the model

Only satellite estimates of sea surface colour can provide the required spatial coverage necessary for estimates of food in our model. We therefore used SeaWIFS satellite estimates of chlorophyll to derive food fields. Food concentration was estimated using the same methodology as Speirs et al. (2006). No observations are available for 1997, therefore a climatological 8 d average from 1998-2000 was used. There is a poor relationship between time series derived from SeaWIFS and field estimates of chlorophyll (Speirs et al., 2005; Clarke et al., 2006). A statistical methodology was therefore developed by Clarke et al. (2006), where thin plate regression splines modelled local estimates of chlorophyll concentration in relation to satellite SeaWIFS estimates, bathymetry and time of year.

We use the data set produced using this methodology. Field estimates of chlorophyll concentration in the top 5 m were used by Speirs et al. (2006), and we follow their assumption that these are reflective of the average chlorophyll concentration throughout

the vertical distribution of *Calanus*. Phytoplankton abundance was related to chlorophyll concentration under the assumption that 1 mg m^{-3} of Chl a is equivalent to 40 mg C m^{-3}.

The statistical fit of chlorophyll estimated by Speirs et al. (2006) extended into regions which are covered by sea ice. They therefore set food levels to zero when sea ice is present. This mask was derived from 1997 satellite percentage ice cover from the Defence Meteorological Satellite Program's (DMSP) spacial sensor microwave/imager (SSM/I) (Comiso, 1997).

Temperature and velocity fields come from the Nucleus for European Modelling of the Ocean (NEMO) Ocean General Circulation Model (OCGM) (version 3.2) (Madec, 2012). The forcings and model implementation are described in Yool et al. (2011). NEMO is resolved at 64 vertical levels, and it resolves the primitive equations on a C-type Arawkawa grid. Ocean surface forcing comes from the DFS4.1 fields produced by the European DRAKKAR collaboration (Dra, 2007).

Computation of the NEMO model was performed using the free Java tool Ichthyop version 3.2 (Lett et al., 2008). This tool, developed by Philippe Verley, is principally used to study the factors that affect ichthyoplankton dynamics. This software has now been used in a wide variety of marine settings (Andrello et al., 2013; Brochier et al., 2008; Lett et al., 2010; Nicolle et al., 2009).

At the start of each time step 100 seeds were placed at the centre of each model cell. Particle trajectories over a 7 d period were then calculated, and transition matrices were calculated to show the proportion of particles which move to each nearby cell (figure 4.6).

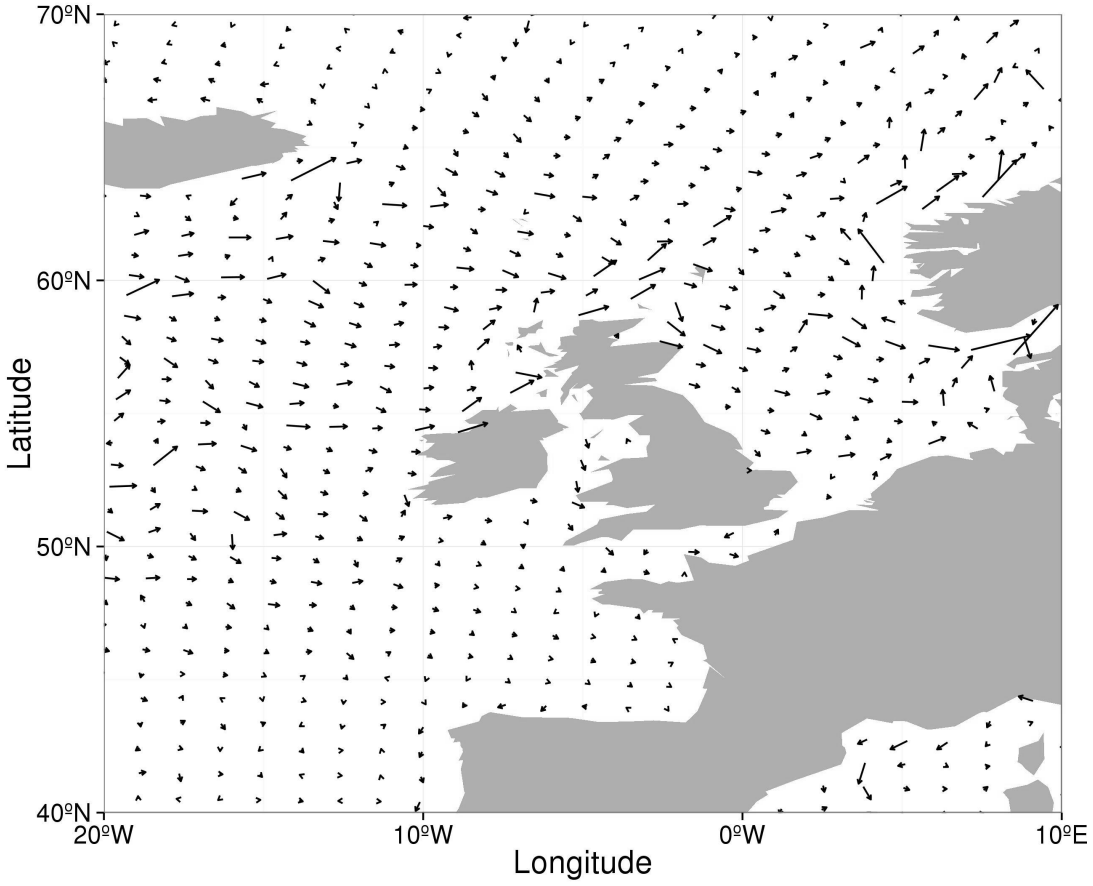


FIGURE 4.5: Illustration of flow fields from NEMO model on day 5, 1997. Direction of arrow shows the mean direction of flow and length shows the mean velocity.

4.5 Development

Development time is modelled assuming the equations shown in section 2.2.2.4 hold. We follow Speirs et al. (2006) and update the state of the surface developer population of cell $\mathbf{x}$ at a set of times $\{\mu^C_{\mathbf{x}}\}$, which are related to each other by the following requirement:

$$\Delta q = \int_{\mathbf{x},i-1}^{\mathbf{x},i} g^C_{\mathbf{x}}(\tau) d\tau \tag{4.2}$$

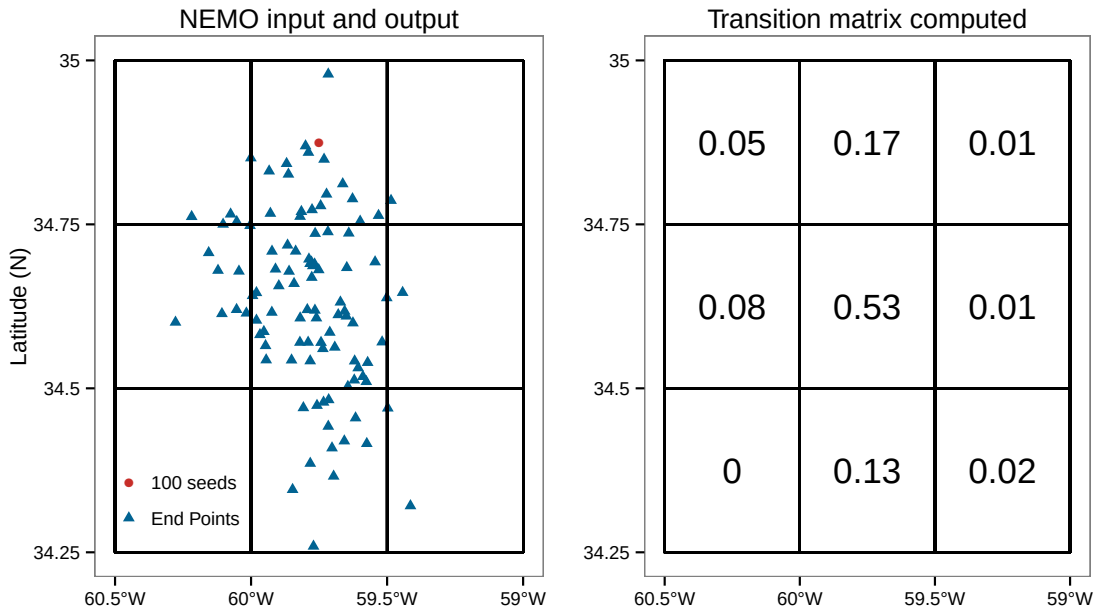


FIGURE 4.6: Illustration of calculation method for the transportation transition matrix for the cell centred on 59.75°W and 34.875°N during week 1, 1997. 100 seeds are placed in the centre of the cell at the start of the time period. The probability of moving to neighbouring cells is then calculated.

where Δq is the development time (d) for a model stage, and development rate, $g^C_{\mathbf{x}}(t)$, is given by,

$$g^C_{\mathbf{x}}(t) = 1/\mathrm{DT}\left(1 - \exp\left[-\frac{F_{\mathbf{x}}(t)}{F_G}\right]\right) \tag{4.3}$$

where DT is development time from egg to adult under food saturated conditions, $F_{\mathbf{x}}(t)$ is food concentration in cell $\mathbf{x}$ at time t and F_G is the half saturation coefficient of growth.

4.6 Fecundity

Fecundity is most suitably modelled purely with reference to in situ environmental conditions. *C. finmarchicus* and *C. helgolandicus* are income breeders (Conover, 1988),

that is their egg production results mostly from recent feeding. It can be argued that *C. finmarchicus* is not a pure income breeder. Post-diapause females can fuel egg production using lipid reserves (Richardson et al., 1999). However, it is unclear if these individuals are using residual post-diapause lipid reserves or if lipid reserves are specifically retained for post-diapause egg production. Similarly, feeding history (Rey-Rassat et al., 2002b; Hirche et al., 1997; Ceballos and Álvarez Marqués, 2006b), age (Diel and Tande, 1992; Hirche et al., 1997), and reproductive maturity (Plourde and Runge, 1993; Niehoff et al., 1999) influence EPR. However, quantitative understanding of these influences is not advanced enough to warrant the computational expense of their incorporation.

EPR of both species must be related to temperature and food concentration. Their influences on *C. helgolandicus* EPR have not been sufficiently studied for a model to be formulated based on existing data. However, using the functional form given by Hirche et al. (1997) for *C. finmarchicus*, while putting in place an ad hoc model for *C. helgolandicus*, would be unsatisfying. We therefore formulated a new model which equates growth and EPR. This model is found to accord well with the results of Hirche et al. (1997), and it allows us to model the EPR of both species in a unified manner, with interspecies differences emerging purely from differences in reported ingestion rates (Møller et al., 2012).

4.6.1 Influences on fecundity

Laboratory studies confirm that temperature has a pronounced effect on EPR in *C. finmarchicus*. Hirche et al. (1997) found that EPR increased by more than a factor of 3 when temperature was increased from 0-8°C. A positive influence of temperature on EPR is found across all zooplankton species where it has been studied (Table 4.5). This is generally viewed as following a Q_{10} relationship. This factor typically varies between 2 and 3 in zooplankton species.

TABLE 4.5: Published Q_{10} of EPR for zooplankton species from laboratory studies.

Species	Temperatures (°C)	Q_{10}	Reference
C. finmarchicus	-2-8	5	Hirche et al. (1997)
C. finmarchicus	5-10	2.2-3.7	Rey et al. (1999)
C. pacificus	8-15	2	Runge (1984)
A. biflosa	4-24	1.8	Koski and Kuosa (1999)
Acartia clausi husonica	2.3-19.6	2.9	Sekiguchi et al. (1980)
Acartia clausi	5-20	2.3	Castro-Longoria (2003)
Acartia discaudata	5-20	3.3	Castro-Longoria (2003)
Acartia margalefi	5-20	11.1	Castro-Longoria (2003)
Acartia tonsi	5-20	4.3	Castro-Longoria (2003)
Acartia tonsi	5.2-22.9	16.6	Holste and Peck (2006)
Centropages hamatus	2-25	3.6	Halsband-Lenk et al. (2002)
Centropages typicus	2-25	3.2	Halsband-Lenk et al. (2002)
Eurytemora affinis	10-20	3.2	Ban (1994)
Pseudocalanus newmani	3-20	2.9	Lee et al. (2003)
Temora Longicornis	2-22	2.5	Halsband-Lenk et al. (2002)
Temora Longicornis	2-10	5.8	Maps et al. (2005)

The temperature influence shown by laboratory studies is not as clear in field studies. Statistical modelling using field estimates of EPR indicate that there is a positive relationship between EPR and temperature; however, this influence is not found to be strong (Melle et al., 2014; Bonnet et al., 2005). This weak relationship with temperature is expected, and results from the confounding influences of temperature on EPR.

EPR of a given individual may follow a Q_{10} relationship with temperature; that of a population will not. Increases in temperature will result in significant decreases in body size (Campbell et al., 2001). In turn this decrease in body size will result in lowered EPR (Jønasdøttir et al., 2005). However, in situ temperature itself is often a poor measure of the temperature at which an individual was raised. Many early season females are individuals that became female after diapausing as C5. Their development temperatures were therefore those experienced during the previous year.

Multiregion studies of EPR in *C. finmarchicus* (Melle et al., 2014) and *C. helgolandicus* (Bonnet et al., 2005) indicate that EPR saturates at high food concentrations, with what

appears to an Ivlev type functional response. This is further confirmed by the laboratory work of Hirche et al. (1997).

A final influence on EPR is body size, with larger individuals known to lay more eggs. This is confirmed by field studies for *C. finmarchicus* (Table 4.3). In particular, the data collated by Melle et al. (2014) indicates that prosome length variations alone could result in differences in EPR of more than a factor of 3 when we consider the smallest *C. helgolandicus* and large *C. finmarchicus* females.

4.6.2 Modelling fecundity

A period of egg production can be viewed as being similar to a period of growth, with the difference that ingested food is converted to eggs instead of structural mass. This has led some to suggest that egg production and growth are equivalent (Mclaren and Leonard, 1995), an idea that has some support in evidence (Sekiguchi et al., 1980). Metabolic costs are likely to be independent of whether an individual is developing or producing eggs. Likewise, processes governing ingestion are largely governed by body size, not by whether an individual is fecund or developing. EPR is therefore probably determined by the efficiency at which individuals can convert ingested food into eggs. Similarly, evidence indicates that EPR is strongly related to ingestion rate (Båmstedt et al., 1999).

We therefore developed a model of egg production using the assumption that egg production and growth are equivalent. This approach is similar to that in some existing studies, which have assumed that growth and egg production are equivalent (e.g. Maps et al. (2012a)).

Our egg production model is as follows. Food saturated egg carbon production rate is assumed to follow the relationship given earlier for growth of carbon (equation 2.1 on page 31),

$$\dot{g}_C = C^{0.75}(f_2 * AE * \mu - Q_{10}^{T/10}\lambda) \tag{4.4}$$

where $\dot{g}_C$ is the carbon growth rate (μgC h^{-1}) and

$$f_2 = \frac{P_5}{[1 + exp(\frac{P_3}{T+273} - \frac{P_3}{P_1}) + exp(\frac{P_4}{P_2} - \frac{P_4}{T+273})]} \tag{4.5}$$

where $P_1 = 293, P_2 = 284, P_3 = 13,282, P_4 = 29,725andP_5 = 6.05$ for *C. finmarchicus*.

Per capita egg carbon production rate (μgC h^{-1}) is then converted into a per capita EPR (eggs^{-1}individual^{-1}d^{-1}). We do this using the relationship between egg size and temperature given by Campbell et al. (2001):

$$\text{Egg}_\text{C} = -0.00255T + 0.216$$

where T is temperature (°C), and Egg$_\text{C}$ is egg carbon (μg C).

Model predictions were then compared with the data in the laboratory study of Hirche et al. (1997), which measured EPR at -1.5, 0, 2, 5 and 8 °C. Carbon content of females was not fixed across all temperatures in Hirche et al. (1997), varying between 159 and 198 μg. We therefore assumed a carbon weight of 170 μg.

The comparison between our model predictions and the laboratory results of Hirche et al. (1997) are shown in Figure 4.7. Our model fits the *C. finmarchicus* experimental data remarkably well. It therefore appears very reasonable to use this model in a population model.

To date *C. helgolandicus* EPR has not been studied over multiple temperatures, therefore only a limited number of comparisons can be made between our model for *C. helgolandicus* and laboratory studies. The laboratory study of Huskin et al. (2000)

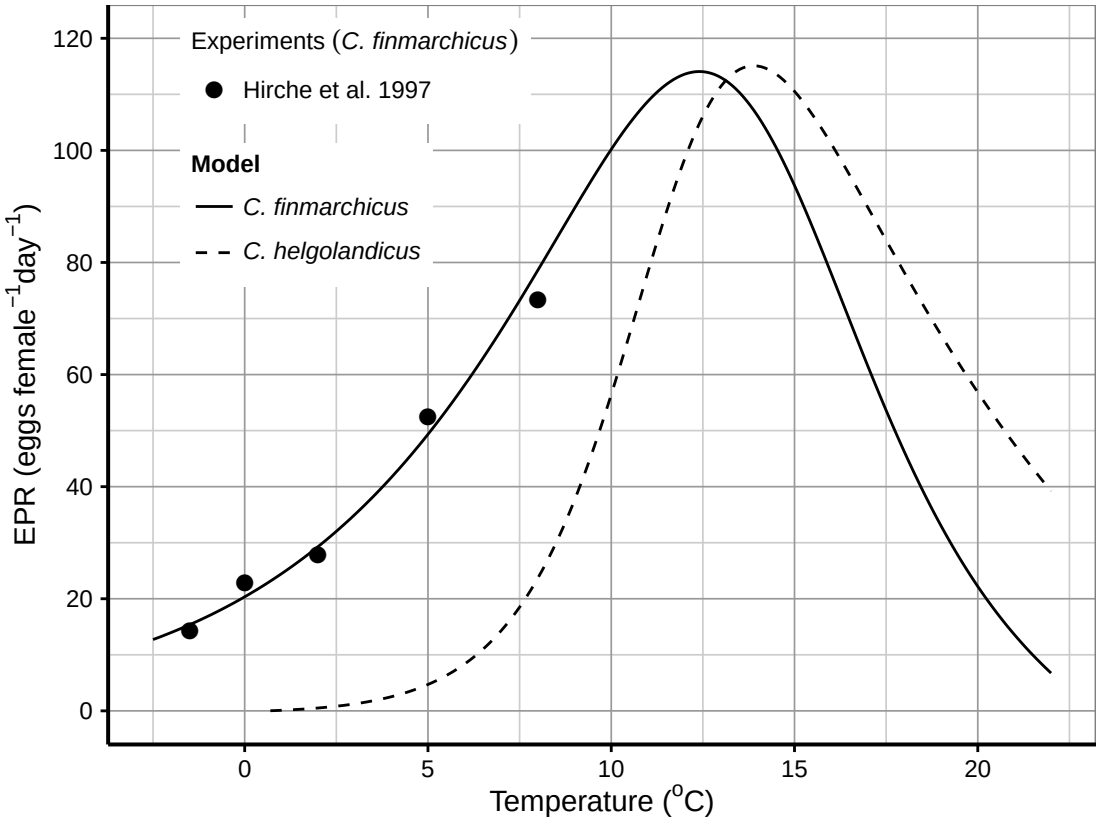


FIGURE 4.7: Comparison of predicted per capita EPR from egg production model with the experimental results of Hirche et al. (1997).

reported *C. helgolandicus* EPR between 8.86 and 22.27 eggs female^{-1}d^{-1}, and they assumed a female carbon weight of 71.1 μg C per female. Using this carbon weight, our model predicts EPR of 38 eggs female^{-1} d^{-1}. However, the carbon weight used in this study was not derived from their experimental data, so this overestimate may just be a result of their assumption about carbon weight.

Rey-Rassat et al. (2002b) reported *C. helgolandicus* EPR at food saturated conditions, fed on *P. micans*. This feeding regime should provide very similar conditions to those assumed in our model. Egg production experiments were carried out at 15 °C, with females of average carbon content of 84 μg C. Average EPR was 35.5 eggs female^{-1} d^{-1}, compared with our model prediction of 43. Therefore it appears reasonable to use our model for both species.

Our model predicts a dome-shaped response of EPR to temperature. Empirical evidence showing this is currently lacking. Temperatures above 12°C are generally viewed as being of limited ecological relevance, therefore studies focusing on the quantitative relationship between life cycle traits and temperatures have largely ignored these temperatures. However, evidence for other species suggests that a dome-shaped response is plausible and perhaps to be expected. Dome-shaped responses of EPR to temperature have been shown in 10 other calanoid copepod species (table 4.6). This suggests that a dome-shaped response of EPR to temperature may be universal across calanoid copepod species.

TABLE 4.6: Zooplankton species with recorded dome shaped responses of EPR to temperature

Species	Reference
Centropages typicus	Halsband-Lenk et al. (2002)
Centropages hamatus	Halsband-Lenk et al. (2002)
Temora longicornis	Halsband-Lenk et al. (2002)
Temora stylifera	Halsband-Lenk et al. (2002)
Acartia tonsa	Holste and Peck (2006)
Temora longicornis	Holste et al. (2009)
Pseudodiaptomus pelagicus	Rhyne et al. (2009)
Acartia tonsa	White and Roman (1992)
Acartia bifilosa	Koski and Kuosa (1999)
C. glacialis	Pasternak et al. (2013)

4.6.3 Influence of food on fecundity

Population models normally assume that EPR saturates at high food concentrations, with the functional response typically taking an Ivlev type response. EPR may be influenced by food quality as well as quantity. Huskin et al. (2000) measured *C. helgolandicus* EPR under a number of different dietary regimes, finding significant variation in efficiency of conversion of food into eggs. However, we have ignored food quality because we are restricted to chlorophyll levels.

The precise functional form of the relationship between EPR and food concentration is unclear. In fact, what we know about the relationship between *Calanus* EPR and food largely comes from one study (Hirche et al., 1997), which measured EPR over multiple food concentrations. As stated by Hirche et al. (1997), their study 'cannot be used to estimate critical and limiting food concentration' due to the food concentration being the initial food concentration of each experiment.

Hirche et al. (1997) provides evidence that EPR approximately follows a Holling type II response to food concentration. However, the ability to derive the precise quantitative form of this relationship from Hirche et al. (1997) is questionable. With this caveat stated, we follow Speirs et al. (2006) and assume that EPR saturates with food concentration using their equation derived from Hirche et al. (1997).

$$f_3 = \frac{F(t)}{F_h + F(t)} \tag{4.6}$$

where $F(t)$ is food concentration (mg C m^{-3}), F_h is the half saturation coefficient (mg C m^{-3}). F_h has been estimated for *C. finmarchicus* as 82.02 mg C m^{-3}.

4.6.4 Sex ratio

Adult sex ratio shows clear female bias in both *C. finmarchicus* (Hirst and Kiørboe, 2002; Kiørboe, 2006; Crain and Miller, 2000; Svensen and Tande, 1999; Nash and Geffen, 2004; Diel and Tande, 1992; Niehoff et al., 2011) and *C. helgolandicus* (Green et al., 1993; Pond et al., 1996; Nash and Geffen, 2004). The skewed nature of adult populations was observed by Marshall and Orr (1955) and was attributed largely to sex differences in mortality and longevity.

Similarly, it has been argued that skewed sex ratios result from different predatory impacts on each sex (Hirst et al., 2010). Surprisingly, there has been little laboratory

research on the sex ratio of newly molted adults. In fact, the recently published study of Burris and Dam (2015) on *Arcatia tonsa* is the first such study on a calanoid copepod, which found evidence of sex bias. However, existing evidence is not strong enough to explicitly model sex ratio based on environmental conditions. Modelling studies therefore usually assume that 50% of the adult population is female (e.g. Tittensor et al. (2003); Carlotti and Radach (1996); Maps et al. (2010, 2012b)). We therefore assume that 50% of adults are female.

4.7 Mortality

Mortality plays a critical role in controlling the population dynamics of *Calanus* species (Plourde et al., 2009a). It is also a key requirement of *Calanus* population models, without which population size will tend to infinity. Predation (Dalpadado, 2000; Gislason and Astthorsson, 2002; Prokopchuk and Sentyabov, 2006; Dommasnes et al., 2004; Utne et al., 2012), starvation (Lopez, 1996), temperature dependence (Hirst et al., 2007), and density dependence (Ohman and Hirche, 2001) are the principal elements of mortality, each of which may be stage dependent (Eiane and Ohman, 2004). All of these elements must be explicitly or implicitly incorporated in a model of mortality, and they are all poorly understood. In addition, cannibalism may have a significant effect on *Calanus* populations (Laabir et al., 1995; Bonnet et al., 2004).

The core problem of mortality in population models is that mortality must be represented over a large spatial scale. However, mortality varies geographically (Ohman et al., 2004) and with predation regime (Eiane et al., 2002). Predation, temperature and food conditions all vary spatially; however the inclusion of geographic variation of predation is not plausible. Therefore geographic variations in mortality can only be related to temperature and food.

Challenges are posed by estimating variation in seasonal mortality, in particular that during diapause (Melle et al., 2014). Estimates of diapause mortality require repeated population sampling, under very challenging conditions. Unsurprisingly, this high risk and costly research has not been undertaken to a great extent (Daase et al., 2014).

TABLE 4.7: Papers reporting field estimates of *Calanus* mortality rates

Reference	Details	Region
Bagøien et al., 2001	Diapause mortality	NA
Daase et al., 2014	Diapause mortality	NA
Eiane et al., 2002	Stage specific mortality	NA
Gentleman et al., 2012	Estimate methodology	NA
Gislason et al., 2007	Diapause mortality	NA
Hirst et al., 2007	*C. helgolandicus*	English Channel
Hirst and Kiørboe, 2002	Global patterns	NA
Ohman, 2012	Methodology	NA
Ohman and Hirche, 2001	Density dependence	NA
Ohman et al., 2004	Comparative study	North Atlantic
Plourde et al., 2009a	Early stages	Gulf of St. Lawrence
Eiane and Ohman, 2004	Stage specific	North Sea
Ohman et al., 2002	Check usefulness	NA
Plourde et al., 2009b	Seasonal and spatial	NW Atlantic
Skardhamar et al., 2011	Field and Modelling	Atlantic
Bonnet et al., 2004	Cannibalism	NA
Tande, 1988	Mortality	Laboratory

Unsurprisingly, given the limited number of studies of mortality in Calanus species (table 4.7), comparisons between mortality rates in each species are challenging. The only existing multistage studies of mortality in *C. finmarchicus* and *C. helgolandicus* are Eiane et al. (2002) and Hirst et al. (2007) respectively. Direct comparisons between mortality rates in these studies are not possible. Eiane et al. (2002) only considered mortality at temperatures below 8°C, while Hirst et al. (2007) largely considered mortality at temperatures above 8°C. Differences in predation and food regimes in these studies make the discernment of interspecies differences almost impossible.

We can therefore only make partially quantitative comparisons between each species. A key similarity between both species is that highest mortality rates are observed in egg and early nauplii stages. Peak egg mortality in *C. helgolandicus* (Hirst et al., 2007) was

found to be similar to that observed for *C. finmarchicus* (Ohman and Hirche, 2001). *C. helgolandicus*'s has slightly higher peak EPR, however this may be a result of the high temperatures it experienced in the relevant study.

Similarly, C5 and adults had comparable mortality rates in both species, with *C. helgolandicus* being slightly higher. These differences, again, could be explainable by differences in temperature, food and predation regime. We are therefore not able to say anything concrete about interspecies differences.

A review of global patterns in zooplankton mortality estimated that 67-75% of mortality results from predation (Hirst and Kiørboe, 2002).

4.7.1 Modelling mortality

The basis of our model of mortality is that of Speirs et al. (2006). However, we make one major change. Starvation mortality was based purely on food concentration. However, the stark differences in the response of both species' ingestion rate temperature means that there should be a temperature dependent element of starvation mortality. We therefore related starvation mortality with growth, that is low growth rates induce starvation mortality. Starvation mortality has been related to growth in previous *Calanus* models (Tittensor et al., 2003).

Relating starvation mortality to growth can only be done in an non-ad hoc manner. There is limited knowledge of mortality rates under low food conditions. Likewise, there has been little study of respiration rates of *Calanus* under low food conditions (Mayor et al., 2011). Some evidence suggests that respiration rates initially reduce, but then return to their original levels during starvation Mayzaud (1976). However, this cannot be rigorously related to mortality. We therefore assume a simple linear relationship between mortality and low growth rates.

Using u_n to denote the nth update time in $u^K_{\mathbf{x}}$, with $K \in [A, C, D]$ to denote the target population, we write:

$$\xi^K_{q,\mathbf{x},u_i} = \exp[-m^K_{q,\mathbf{x},u_i}(u_{i-1})] \tag{4.7}$$

where m is mortality rate, q is the development stage and **x** is the model cell. For surface developers total mortality was assumed to consist of a background rate that is an increasing function of temperature, together with density dependent and starvation terms.

If $T^S_{\mathbf{x}}(t)$, $W_{\mathbf{x},t}$ and $F_{\mathbf{x},t}$ are respectively the surface temperature, Calanus biomass, and food at cell **x** and time t, we have:

$$m^C_{i,\mathbf{x},t} = \gamma(T^S_{\mathbf{x}}(t))\mu^C_i(1 + \phi W_{\mathbf{x},t}) + \mu_S \tag{4.8}$$

$$m^A_{\mathbf{x},t} = \gamma(T^S_{\mathbf{x}}(t))\mu^A_i(1 + \phi W_{\mathbf{x},t}) + \mu_S \tag{4.9}$$

where γ and μ_S are temperature and starvation-dependent mortality respectively.

Temperature dependence is given by:

$$\gamma(T^S_{\mathbf{x}}(t)) = \gamma_0 + (1 - \gamma_0)(T/T_c)^z \tag{4.10}$$

The parameter γ_0 is the fraction of the mortality at some characteristic temperature T_c, that is experienced at 0°C, and z determines the non-linearity, and hence how fast the mortality increases for temperatures above T_c. The starvation mortality is zero when carbon growth rate, g_w (as defined in equation 2.1 on page 31) is above a lower threshold g_{m_thresh}, and varies linearly to a maximum $\mu^{\max}_F$ below that threshold.

$$\mu_S(F_{\mathbf{x}}(t), F_M) = \begin{cases} 0 & \text{if } g_w > g_{m_t hresh} \\ \frac{g_{m_t hresh} - g_w}{s_c} & \text{otherwise} \end{cases}$$

where s_c is scaling factor.

Total biomass density in cell **x** is given by the sum over all developer classes of the number of individuals in each class multiplied by the dry weight of each individual plus a similar sum over the adult population, divided by the surface area of the cell $\alpha_{\mathbf{x}}$.

$$W_{\mathbf{x},t} = \frac{1}{\alpha_{\mathbf{x}}} \left[\sum_{i-1}^{n} w_i^C C_{i,\mathbf{x},t} + w^A A_{\mathbf{x},t} \right] \tag{4.11}$$

4.8 Diapause

As discussed in chapter two, *C. finmarchicus* undergoes an extensive period of diapause. We suggested that *C. helgolandicus* populations are restricted to continental shelf regions due to an inability to diapause for long enough. This may not be a result of interspecies differences. Instead, it is likely a result of the relationship between body size and lipids and that between respiration rate and temperature. We will now provide a more in depth outline of these ideas before detailing a new model of diapause duration in *Calanus*.

Diapause occurs in many zooplankton species for a simple reason. Food supply is highly seasonal, and if individuals remain at the surface throughout winter they will starve. This is most pronounced at higher latitudes, where food concentrations can be close to zero throughout large parts of the year. Figure 4.8 illustrates seasonal food levels at OWS M (Niehoff et al., 1999), derived from SeaWIFS chlorophyll measurements (Clarke et al., 2006). A time period therefore exists, during which it is disadvantageous

for an individual to be at the surface, due to low food levels. This time period varies geographically, and it is much longer at higher latitudes (Lee et al., 2006).

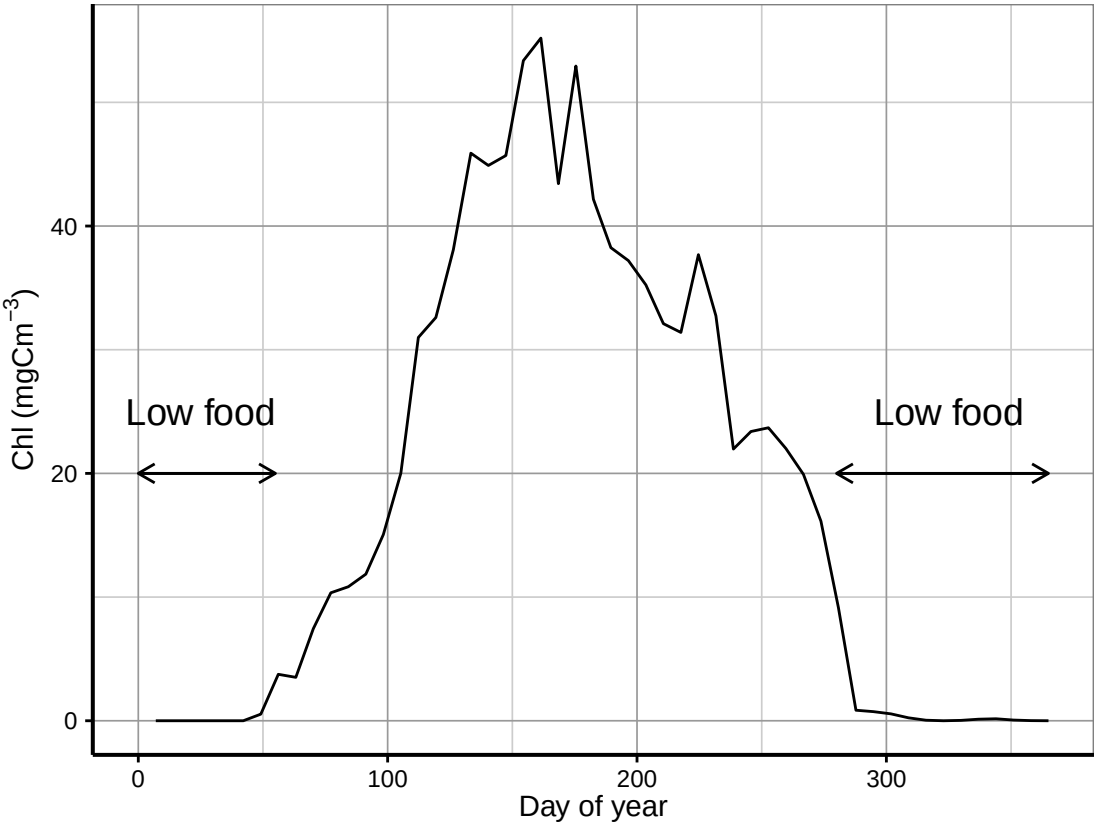


FIGURE 4.8: Illustration of seasonal cycle of food availability at OWS M in the Norwegian Sea. *C. finmarchicus* must diapause at depths in oceanic regions because of low food availability at the surface.

From a simple physical point of view, then, we expect that diapause is initiated at least when food levels are too low (Hind et al., 2000). However, modelling indicates that food concentration itself is not a completely satisfactory cue for diapause initiation (Speirs et al., 2006). This indicates that diapause initiation behaviour shows plasticity. At stage C5 individuals have to allocate resources between energy storage and somatic growth (Fiksen, 2000). However, *C. finmarchicus* often has multiple generations each year (Melle et al., 2014). Individuals, then, have a "choice" between diapausing and molting to become adult.

However, the environmental conditions for *C. finmarchicus* show high stochasticity. It is unclear therefore what environmental cue should be used by C5 individuals. Molting from C5 to adult is only adaptive when offspring do not see adverse environmental conditions. An optimal diapause strategy may therefore be for a fraction of individuals to diapause and for the remainder to stay at the surface, which was assumed by Speirs et al. (2006).

Diapause requires *C. finmarchicus* to maintain metabolism without ingesting food. *C. finmarchicus* therefore requires a long term source of energy, and this is provided by lipids (Irigoien, 2004). The energy density of lipids (approximately 39 kJg^{-1} (Michaud and Taggart, 2011)) is greater than that of any other biopolymer, including proteins and carbohydrates (Smil, 2011).

Lipids are composed primarily of wax esters (WE) and triacylglycerols (TAG). However, they can essentially be viewed as wax esters. 80-90% of lipids in diapausing individuals are wax esters. Similarly, percentage of lipids composed of TAG declines significantly with increasing lipid levels, and TAG levels appear to be largely fixed in diapausers (Miller et al., 1998b). In addition, TAG do not appear to be used as a long-term energy reserve.

Diapause typically occurs during the C5 stage; however C4 individuals have been observed among some diapausing populations (Heath et al., 2004). The predominance of C5 in diapausing populations has resulted in population models assuming that diapause occurs strictly at the C5 stage (Maps et al., 2012b; Speirs et al., 2006).

As discussed in chapter two, it remains unclear if *C. helgolandicus* undergoes a period of true diapause. Williams and Conway (1982) analysed gut contents of *C. helgolandicus* during winter in the Celtic Sea, and concluded that it was actively feeding.

4.8.1 Energetic requirements of diapause

From an energetic point of view, diapause has some key requirements. Individuals must have sufficient energy reserves to descend to diapause depth, maintain metabolism during diapause, ascend from diapause, and then molt to adult and form gonads (Jønasdøttir, 1999). In addition, females have been observed to use remaining lipids to fuel pre-bloom egg production (Richardson et al., 1999). However, it remains unclear if selection pressures will have favoured individuals who exit diapause with large lipid reserves remaining. Diapause duration is therefore limited by 2 key variables: diapause respiration rate and the lipid complement acquired prior to diapause (Saumweber and Durbin, 2006).

Respiration rates are influenced by both temperature and body size (Hernandez-Leon and Ikeda, 2005). Further, lipid levels may also be dependent on prosome length; i.e. if smaller individuals have relatively lower lipid levels they will also have shorter diapause duration.

Diapause in *C. finmarchicus* is a process that has been the focus on much discussion in the last 2 decades. A review of published literature makes it clear that modelling and proposing new ideas about diapause in *C. finmarchicus* is much less challenging than the arduous and difficult task of performing experiments on diapausing animals. Respiration rates of diapausing *C. finmarchicus* have been reported in only three studies (Saumweber and Durbin, 2006; Ingvarsdøttir et al., 1999; Hirche, 1983). However, they shed important light on respiration in diapausing animals. Whether these respiration rates fully reflect those at depths is uncertain. Individuals will no longer be in a state of neutral buoyancy (Visser and Jønasdøttir, 1999), and animals may no longer be in a true diapause condition.

A full understanding of diapause respiration in *Calanus* requires knowledge of the influence of temperature and body size on respiration rates, and an understanding of

absolute respiration rates. Published estimates of Q_{10} of the respiration rate of diapausing *Calanus* species have been summarized in the meta-analysis of Maps et al. (2014). Estimates of Q_{10} for *C. finmarchicus* are 2.55 (Hirche, 1983), 2.77 (Saumweber and Durbin, 2006) and 3.12 (Ingvarsdøttir et al., 1999). An increase in temperature of 10°C will therefore approximately see a tripling of respiration rate, and consequently diapause duration will be 3 times shorter.

TABLE 4.8: Published Q_{10} for respiration rates of diapausing *C. finmarchicus* and similar species, adapted from Maps et al. (2014)

Species	Q_{10}	Reference
C. finmarchicus	3.12	Ingvarsdøttir et al. 1999
C. finmarchicus	2.55	Hirche 1983
C. finmarchicus	2.77	Saumweber and Durbin 2006
Calanoides acutus	2.25	Auel et al. 2005
Calanus euxinus	1.79	Svetlichny et al. 2000
Calanus pacificus	2.25	Ohman et al. 1998
Eucalanus californicus	2.44	Ohman et al. 1998

Empirical studies of the relationship between body size and respiration rate in *C. finmarchicus* or *C. helgolandicus* are currently lacking. However, the meta-analysis of Maps et al. (2014) suggests that respiration rate has 3/4 power scaling with body size. Allometric scaling of respiration rate therefore appears to be an important, but not overwhelming influence on diapause duration. Given known length-weight relationships, individuals with prosome length 2.6 mm will have approximately 30% higher weight-specific respiration rates than those at 1.8 mm. This indicates allometric scaling will cause at most a 30% difference in diapause duration between the largest and smallest diapausing *C. finmarchicus* and *C. helgolandicus*.

Published diapause respiration rates for *C. finmarchicus* are shown in Figure 4.9. These respiration rates have been used as the basis for modelling studies of diapause duration (Ingvarsdøttir et al., 1999; Saumweber and Durbin, 2006). However, it should be noted that diapause duration calculations are particularly sensitive to respiration rate

assumed. A 20% difference in respiration rate will result in a 40 d change in diapause duration if the original diapause duration was 200 d.

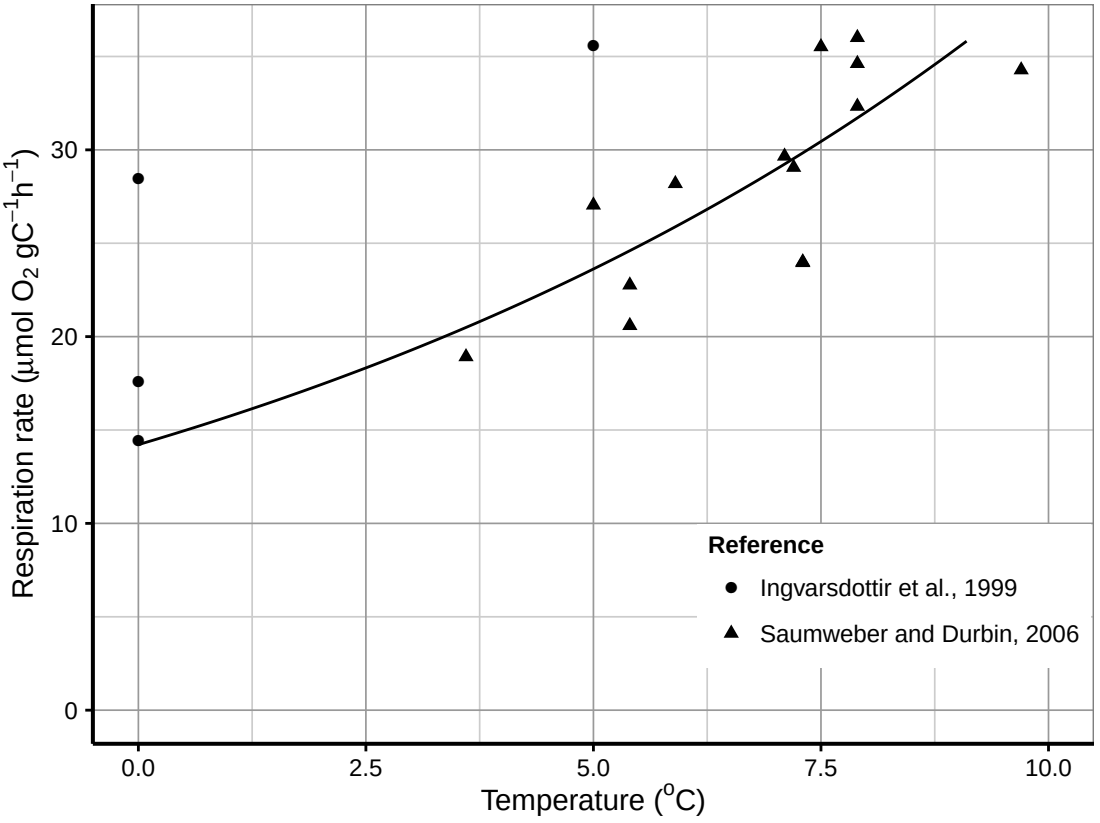


FIGURE 4.9: Respiration rates of diapausing *C. finmarchicus* (Saumweber and Durbin, 2006; Ingvarsdøttir et al., 1999). Bold line is the relationship between respiration rate and temperature estimated by Saumweber and Durbin (2006). $r = 10^{0.0441T+1.1528}$

4.8.2 The relationship between size and lipid levels

Length-weight relationships are typically represented using an equation of the form aL^y. The influence of prosome length on diapause duration will therefore be partly determined by the difference between the y parameter in the length-weight and length-lipid equations. A starting assumption is that the ratio between lipid levels and body weight is fixed across all body sizes. In other words, the y parameter is the same,

or only marginally different, for body weight and for lipid. The influence of prosome length on lipids would therefore have negligible influence on diapause duration.

Published data contradicts this view. In the case of body weight, the y parameter is typically close to 3, when either nitrogen (Mclaren and Leonard, 1995; Saumweber and Durbin, 2006; Marker et al., 2003; Head et al., 2013a; Runge et al., 2006) or carbon weight (Figure 4.4) is considered. In contrast, the y parameter for the length-lipid relationship is between 4 and 5 in all published studies (Miller et al., 2000; Saumweber and Durbin, 2006; Pepin and Head, 2009; Pepin et al., 2011).

The ratio between lipid weight and body weight therefore appears to increase with body size (Figure 4.10). This is further illustrated by Bergvik et al. (2012), which reported the relationship between prosome volume and total fatty acids. The relationship between prosome length and total fatty acids can be estimated using published prosome length-prosome volume relationship (Miller et al., 2000). In this case, the y parameter of our scaling equation is greater than 5.

All existing evidence therefore indicates that lipid levels scale much more steeply than body weight with length. The reasons for this remain unclear. Miller et al. (2000) suggested that this was due to body organs taking up relatively less space in larger individuals, i.e. larger individuals simply have more room to store lipid. Arguments from first principles indicate that this is a reasonable hypothesis; however direct evidence is currently lacking. Other influences could potentially explain a large part of this trend of bigger individuals having relatively more lipid. Individuals may be smaller due to higher temperatures and lower food concentrations. Lower food concentrations appear to result in relatively fewer lipids in individuals (Hygum et al., 2000b). However, field evidence indicates that lipid concentration in phytoplankton may be a more important determinant of *Calanus* lipid levels than absolute food levels (Gatten et al., 1980). Similarly, higher temperatures may result in lower lipid levels due to a greater need to use food to maintain metabolism compared with energy storage.

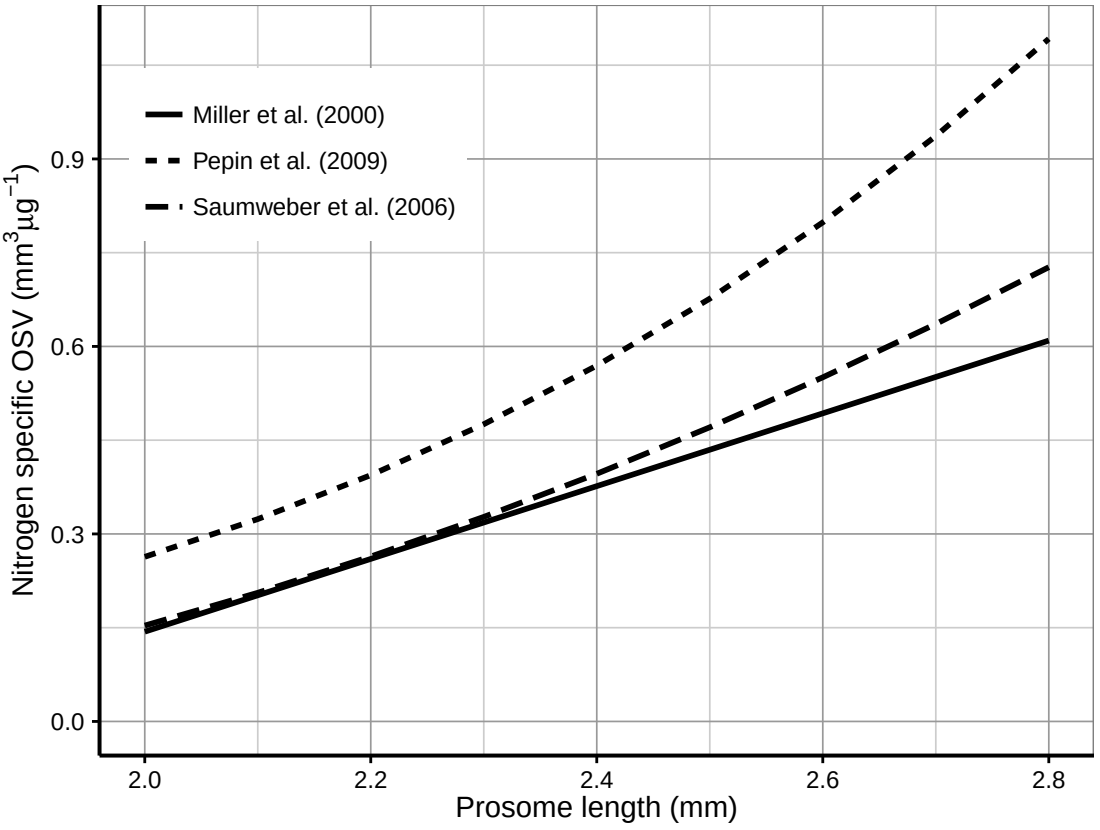


FIGURE 4.10: Published relationships between maximum oil sac volume (OSV) and nitrogen content. Nitrogen content is estimated using length-weight relationships (Runge et al., 2006). For Miller et al. (2000) and Saumweber and Durbin (2006) we use their maximum envelope, while for Pepin and Head (2009) we use their estimate of the 95th percentile of oil sac volume.

In addition, smaller individuals appear to have less full oil sacs. Tarrant et al. (2008) found that surface individuals had mean prosome length of 2.5 mm, while diapausers had mean prosome length 2.65 mm in Georges Bank. However, oil sac fullness was 0.5 for surface, but 0.75 for deep individuals.

If smaller individuals acquire fewer lipids, we would expect them to be less capable of acquiring sufficient lipids for diapause. And this further suggests that diapausers should, on average, have larger prosome lengths than those in shallow waters. This is confirmed by field evidence, with multiple studies showing that surface individuals have smaller prosome lengths than their diapausing counterparts (Tarrant et al., 2008; Miller et al., 1998b; Pepin and Head, 2009)

4.8.3 Modelling diapause duration

As outlined above, maximum potential diapause duration is determined by lipid levels and diapause respiration rates, which in turn are influenced by temperature and body size. We therefore formulated a new maximum diapause duration model which relates potential diapause duration to temperature and prosome length. A number of papers have modelled diapause in Calanus, summarised in Table 4.9. Our new model is principally influenced by the earlier work of Ingvarsdøttir et al. (1999) and Hind et al. (2000) and Saumweber and Durbin (2006).

TABLE 4.9: Papers that have modelled diapause in *Calanus*

Reference	Species
Fiksen and Carlotti, 1998	*C. finmarchicus*
Ingvarsdøttir et al., 1999	*C. finmarchicus*
Visser and Jønasdøttir, 1999	*C. finmarchicus*
Fiksen, 2000	*C. finmarchicus*
Hind et al., 2000	*C. finmarchicus*
Saumweber and Durbin, 2006	*C. finmarchicus*
Johnson et al., 2006	*C. finmarchicus*
Maps et al., 2010	*C. finmarchicus*
Maps et al., 2012b	*C. finmarchicus*
Pierson et al., 2013	*C. finmarchicus*
Maps et al., 2014	*C. finmarchicus*

Explicitly modelling lipid levels would result in our model being excessively computationally expensive. It would require an extra biological dimensions to be added to the model, which would be severely expensive both in terms of run time and memory use. We therefore had to produce a simplified representation of lipid levels. This simplification is to assume that lipid levels are determined by body size prior to diapause. We then assume that animals enter diapause with the maximum lipid complement implied by field studies of *C. finmarchicus* lipid levels.

Prosome length-lipid relationships have been published by a number of studies (Saumweber and Durbin, 2006; Pepin and Head, 2009; Miller et al., 2000; Bergvik et al., 2012).

Comparisons of these studies indicate that the length-oil sac volume relationship reported by Pepin and Head (2009) shows the highest lipid levels at each prosome length. We therefore assume that individuals enter diapause with the levels of lipid implied by the 95th percentile at each length class reported by Pepin and Head (2009).

Cross species analysis by Maps et al. (2014) indicates that 0.75 is an appropriate choice for allometric scaling of respiration rate. We choose a Q_{10} of 2.8, which is the approximate mean of published values (Hirche, 1983; Saumweber and Durbin, 2006; Ingvarsdøttir et al., 1999).

Individuals must exit diapause with a sufficient complement of lipids to be able to molt and form gonads. Quantification of these requirements is, to date, not particularly extensive. Here we assume that they are a simple multiple of nitrogen weight, specifically that diapause exit requirements are 3 times nitrogen weight. This is approximate; however, it accords reasonably well with the estimates produced by Rey-Rassat et al. (2002a).

There are therefore 2 wax ester complements: WE at the start of diapause and WE remaining after diapause, which is used for molting and gonad formation. The difference between the two is the WE available for diapause metabolism (Figure 4.12). Maximum diapause duration is therefore defined as the time it takes an individual to metabolize this WE complement.

We therefore define WE_d (μg C) to be the total wax esters available for diapause metabolism. The form of this can be approximated more or less identically, using the equation,

$$\text{WE}_d = aL^y \tag{4.12}$$

where $a = 3.66$ and $y = 4.6$, and L is prosome length.

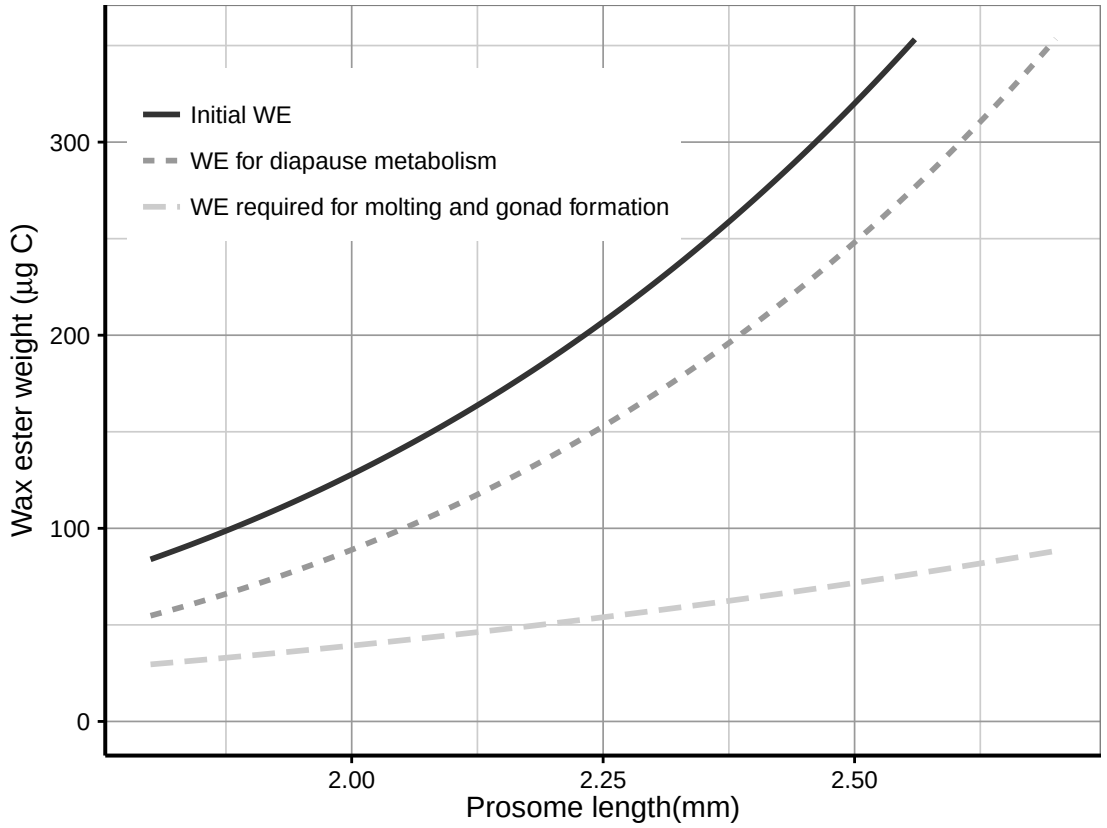


FIGURE 4.11: Wax ester requirements for diapause in model. We assume that maximum lipids at diapause entrance are related to prosome length using the empirical estimates of Pepin and Head (2009). We assume that wax esters required for molting and gonad formation are fixed multiple of structural body weight, with this multiple fitted, approximately, to the energy requirements of molting and gonad formation estimated by Rey-Rassat et al. (2002a)

Diapause metabolism is assumed to relate strictly to structural weight, that is nitrogen weight. Further, we assume that structural weight is fixed throughout diapause. This assumption means that respiration rates are constant throughout diapause under fixed temperatures, which results in a more elegant model formulation.

Respiration rate, r (μmol $O_2 gN^{-1} hr^{-1}$) is estimated using the data of Saumweber and Durbin (2006), and follows the equation:

$$r = \mu w^{0.75} Q_{10}^{T/10} \tag{4.13}$$

where μ is a constant, w is nitrogen weight (μg), and T is temperature in °C.

Nitrogen weight, w (μg), is related to prosome length, L (mm) using the following equation derived from Runge et al. (2006),

$$w = \alpha L^{\beta} \tag{4.14}$$

where $\alpha = 2.014$ and $\beta = 2.7$.

Using this equation, we can separate the weight specific respiration rate, $\mu w^{-0.25} Q_{10}^{T/10}$. This enables us to estimate μ using the weight-specific respiration data of Saumweber and Durbin (2006), with μ = 280.

Our initial respiration rate is in (μmol O_2g$N^{-1}h^{-1}$). We therefore convert the oxygen respiration rate into a carbon respiration rate, R (μg C$\mu N^{-1}d^{-1}$).

$$R = \frac{24 \cdot \text{RQ} \cdot 12.011 \cdot r}{10^6} \tag{4.15}$$

where RQ is the respiratory quotient.

This can be simplifed to the form

$$R = \xi w^{0.75} Q_{10}^{T/10} \tag{4.16}$$

where

$$\xi = \mu * 24 * RQ * 12.011 * 10^{-6} = 0.06$$

Therefore diapause duration is of the form

$$\begin{aligned} \text{Duration} &= \frac{aL^y}{\xi w^{0.75}\cdot Q_{10}^{T/10}} \\ &= \frac{aL^y}{\xi(\alpha L^\beta)^{0.75}\cdot Q_{10}^{T/10}} \\ &= \frac{a\cdot L^{y-0.75\beta}}{\xi\alpha^{0.75}Q_{10}^{T/10}} \end{aligned} \tag{4.17}$$

We then have the final equation which relates diapause duration with body size and temperature,

$$\text{Duration } = \gamma L^\lambda \cdot Q_{10}^{-T/10}$$

where $\gamma = 36.08$ and $\lambda = 2.58$.

The relationship between prosome length and diapause duration are shown in Figure 4.12. Median diapause duration has been estimated as 200 d in the Western Atlantic and 250 d in the Eastern Atlantic (Melle et al., 2014). Our model is broadly consistent with this. Prosome length of diapausers is approximately 2.4 mm, while diapause temperatures vary between 0 and 4°C (Heath et al., 2004). The model therefore predicts diapause durations that sit within the range shown by published studies.

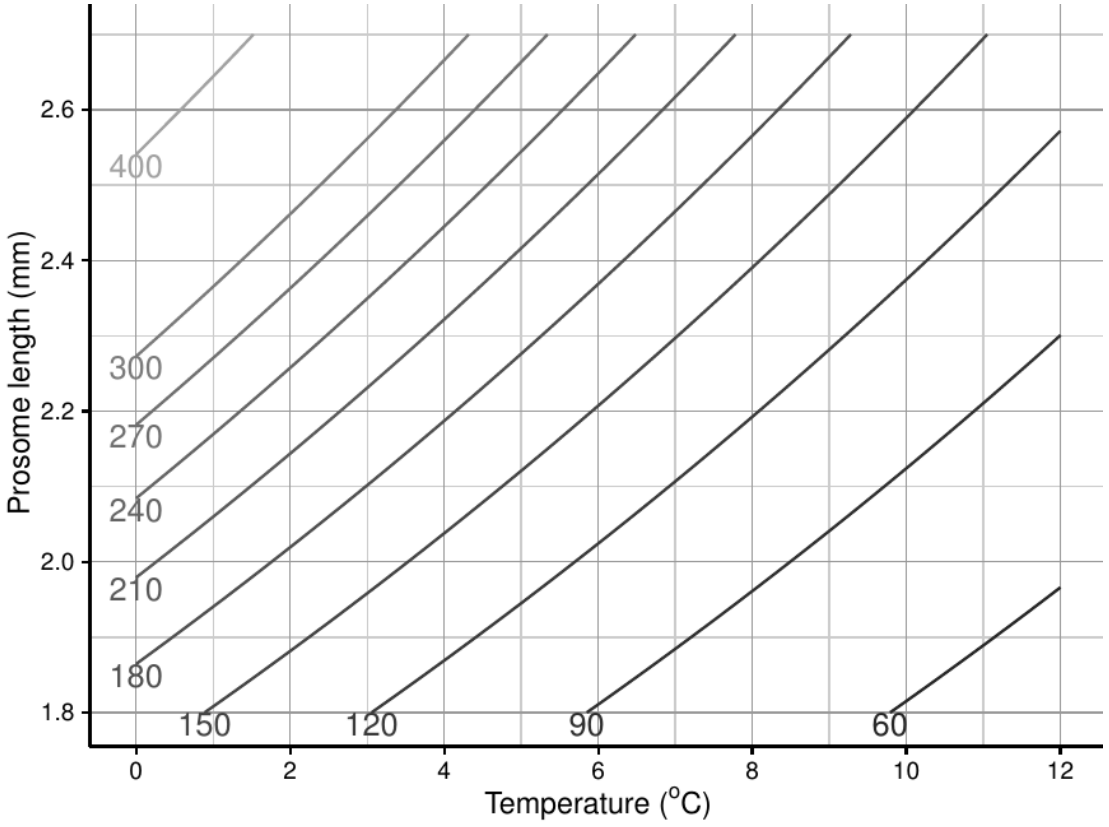


FIGURE 4.12: Modelled maximum diapause duration (d). Diapause duration is modelled assuming that pre-diapause energy reserves are determined by prosome length. Diapause duration is then defined as the time it takes an animal to deplete these reserves to the level required for post-diapause molting and gonad formation. Overwinter metabolism is determined by body size and temperature.

4.8.3.1 Diapause depth, initiation and exit

Speirs et al. (2006) assumed a fixed fraction diapause at the end of stage C5. Here, we maintain the concept of a fraction diapausing. However, we assume that this fraction is not fixed, but is dependent on growth rate. A fraction of the population which persists at the surface after most have commenced diapause has been observed on many occasions (e.g. Meise and O'Reilly (1996).)

Similar to Speirs et al. (2006), we derive *C. finmarchicus* diapause depths partly using the data set produced by Heath et al. (2004), which calculated median diapause depth of *C. finmarchicus* populations in a number of regions of the North Atlantic.

Comparison of median diapause depth with bathymetry indicates that there is an approximately linear relationship between the two at bathymetries of below 1500 m. However, this relationship breaks down at higher bathymetries, where median diapause depths begin to decrease. These higher bathymetry ($>$2000 m) samples however are almost entirely from the Labrador Sea samples. We therefore estimate diapause depths as follows. All points within 500 km of a data point from Heath et al. (2004) are estimated using GAM model which relates diapause depth to longitude, latitude and bathymetry. At the remaining points are assumed to diapause at 1000 m, if depth is greater than 1000 m.

4.9 Conclusions

The key conclusions of this chapter are as follows:

- Body size is determined largely by temperature. Evidence shows that both species have similar or identical relationships between body size and temperature. We therefore model prosome length under the assumption that it is determined by temperature at birth.
- Egg production rate was modelled under the assumption that egg production rate was equivalent to growth. Predicted egg production rates showed excellent correspondence to experiment results. We therefore model egg production rate for both species using the growth model outlined in chapter 2.
- We reviewed the drivers of diapause duration in *C. finmarchicus*, finding that lipid levels are strongly determined by prosome length. We therefore modelled diapause duration as a function of prosome length and temperature experienced during diapause.

Chapter 5

Parameterization and testing methodology

Our model results are presented in 3 key ways. First, we show our baseline parameterization. This is a parameterization which optimizes the spatial fit of the model to CPR data. Second, we perform a sensitivity analysis using our baseline model to consider the influence of choice of OGCM on model predictions. This demonstrates that biases in surface temperatures can have a significant influence on predictions of phenology and raises questions about the wisdom of excessive reliance on time series data to parameterize spatial models.

Finally, we present the results of a suite of runs for both species which demonstrate the importance of diapause assumptions used. Importantly, this demonstrates how improved knowledge of diapause is necessary if we are to reliably predict the future distribution of *C. helgolandicus*.

The predictions from this baseline model were then tested by comparing modelled abundance at spot locations with time series for 1997 (listed in Table 5.1).

5.1 The baseline parameterization

Parameterization of models is inherently subjective (Wood, 2001a). A model can be characterized by a number of metrics, including predicted annual production, phenology and spatial distribution. Further, these metrics can have a number of submetrics. Phenology can be characterized by the following metrics: timing of the start of seasonal increase, seasonal peak, middle of season, end of season, and duration of season (Ji et al., 2010). In addition, the data available is likely to both constrain and potentially bias any model parameterization.

The data available for parameterization and testing of our model is of 3 forms: time series of the annual cycle of abundance at spot locations, diapauser abundance surveys, and Continuous Plankton Recorder data. We will use all of this information to test our model. However, we will rely almost exclusively on CPR data to parameterize it, using time series data for testing and sensitivity analysis purposes. There are two reasons for this. First, the underlying goal of our modelling is to understand what drives the differences in the geographic distributions of both species. We are concerned principally with two large scale questions. Why do *C. finmarchicus* and *C. helgolandicus* have different distributions, and why is *C. helgolandicus* restricted to shelf regions? Second, model runs indicate that biases in surface temperatures in the NEMO model result in significant biases in model predictions at our time series locations, which are largely in the Eastern Atlantic.

If we want to produce optimal models for each species, then we should tune our models for each species separately. However, this is unsatisfying. We seek to understand what drives the relative distributions of each species, which will not be made easy by two models where each parameter is different for both species. We therefore sought a unified parameterization, where interspecies differences were minimized, while maintaining a strong fit of the model to CPR data. As a result, there was only one parameter

different between each species: z, the scaling of background mortality with temperature.

The Continuous Plankton Recorder is described in depth on page 62. CPR data was used for our baseline parameterization.

We optimized the fit of the model with CPR data by comparing predicted annual abundance in model locations with that from CPR. Predicted abundance of combined C5 and adult stages were used. In each case our model is run to a quasi-stable state and we then calculate the correlation coefficient between predicted annual surface abundance and the CPR. The quality of CPR data varies significantly in space (Figure 5.1). We therefore must first resolve our data into spatial bins and restrict our analysis to bins with reasonable coverage.

This was done by resolving our data into cells of dimension 2°E and 1°N. Further, we remove cells which do not have a CPR abundance record for each month of the year. Annual average abundance is therefore calculated by averaging the mean abundance of the monthly mean abundance in each cell. This results in a total of 333 cells for comparison.

Comparisons with CPR data are unlikely to provide population numbers to a reliable scale. We therefore fine tuned our model by altering density dependent mortality to give model predictions which had similar predicted total abundances to those in time series.

Each CPR represents approximately 3 m^3 of filtered seawater (Richardson et al., 2006). Therefore CPR must be divided by 3 to get estimates of abundance per m^3. This must then be multiplied by a further conversion factor to provide estimates of abundance (m^{-2}) over the top 100 m of the water column. We follow Speirs et al. (2006) and use 20 as this conversion factor.

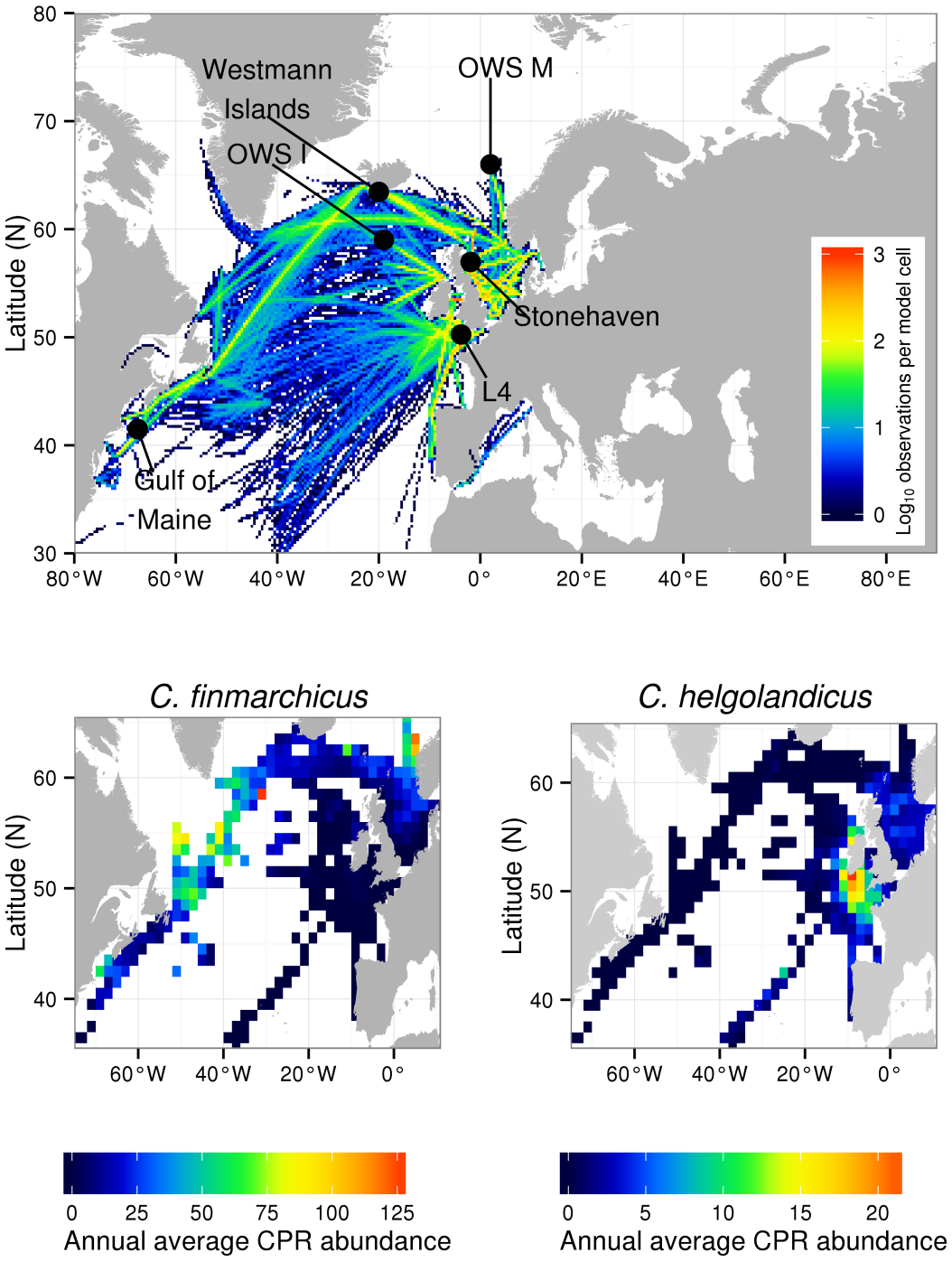


FIGURE 5.1: CPR data used for model parameterization. The top panel shows the spatial distribution of CPR (1958-2002). The bottom panels show annual average abundance for *C. finmarchicus* and *C. helgolandicus*. We resolved the data to a resolution of 2°E by 1°N, and ignored cells with less than 12 months of data. We then calculated annual average abundance in each cell.

5.2 Model initiation and convergence to quasi-steady state

We initiate the model by seeding model cells with eggs at the start of the year. In the case of *C. finmarchicus* eggs are seeded in each cell throughout the model domain. For *C. helgolandicus*, we restrict the seeding to regions east of 20 °W, in line with C. helgolandicus not existing in the western Atlantic.

The model is then run for a number of years until it reaches a quasi-steady state. This steady state is identified by analyzing whether predictions at time series locations have converged. Convergence to a steady state occurs by year 5 in the baseline model.

5.3 The sensitivities

5.3.1 Sensitivity to OCGM temperatures

Speirs et al. (2006) used the OCCAM OCGM to drive its model, whereas we used NEMO. Work by Sinha et al. (2010) showed that the emergent properties of an ecosystem model were significantly driven by the OCCAM or NEMO models. Phenology may be particularly influenced by model divergences from real temperatures. In particular, seasonal peaks in abundance may diverge if temperatures are significantly different from reality.

This causes a relatively unexplored problem for *Calanus* models. Models can be fine tuned to optimize the phenology in different spot locations. However, bias in the OCGM can lead to unrealistic tuning of the model to achieve matches in seasonal timing at spot locations. Seasonal peaks in modelled abundance may be time shifted compared with spot time series abundance. This may simply be a result of temperature biases in the OCGM chosen.

We therefore tested model sensitivity to choice of OCGM by running our model first using the NEMO temperature and flow fields. And second, we ran our model using the same set up, but with the temperatures from OCCAM used by Speirs et al. (2006). The sensitivity of the model to temperature both at the scale of spot locations and throughout its geographic domain is then tested. We then consider whether these sensitivities call into question the wisdom of tuning zooplankton models based on spot location phenology.

5.3.2 Sensitivity to diapause assumptions

A key question is why *C. helgolandicus* is essentially restricted to the continental shelf. In chapter two we proposed that this is caused by the inability of *C. helgolandicus* to diapause for a long enough period of time. In chapter 4, we modelled potential diapause duration of *Calanus* from first principles. The inability of *C. helgolandicus* to exist off the continental shelf is therefore proposed to be a result of the combination of short diapause durations and high mortality when individuals exit diapause. We therefore perform a sensitivity analysis to consider the influence of this on the distribution of *C. helgolandicus*.

5.4 Data sources

5.4.1 Time series data

C. finmarchicus and *C. helgolandicus* abundance data from a number of time series (detailed below) in N. Atlantic locations was used for model testing. Details for the time series are summarized in Table 5.1 and their environmental conditions are summarized in Figure 5.2.

TABLE 5.1: Locations of time series of *Calanus* abundance, against which the model is tested. See text for details of timing and method of time series sampling.

Site	Institute	Vessel	Position	Bottom depth (m)
Westmann Islands	MRI	RV "Fridrik Jesson"	63°27.25'N 20°00.00'W	100
			63°22.20'N 19°54.85'W	
OWS M	IMR, AWI, PML	MV "Polarfront"	66°00.00'N 02°00.00'E	2500
Murchison	MLA	Offshore platform	61°30.00'N 01°40.00'E	160
Stonehaven	MLA	RV "Shuna"	56°57.80'N 02°06.20'E	47
OWS India (TBC)	MLA	RV "Shuna"	56°57.80'N 02°06.20'E	47
Gulf of Maine (TBC)	MLA	RV "Shuna"	56°65-70 °N	65-70 °E
L4 (English Channel)	PML	TBC	50°15.00'N 04°13.00'W	55

5.4.1.1 The TASC time series

The EU TASC project was a multi-institutional research project that resulted in the production of a number of time series of *C. finmarchicus* for copepodite abundance at sites throughout the N. Atlantic in 1997, the "Year of Calanus" (Planque and Batten, 2000; Heath et al., 2000a). Data was collected at Ocean Weather Ship Mike (OWS M) (66°N, 2°E) from 24 February to 17 December 1997 using a 180 μm mesh opening and closing multinet (Heath et al., 2000a; Hirche et al., 2001). Concentrations of copepodite stages (m^{-3}) were converted to stage abundances (m^{-2}) at 0-100 and 100-1600 m. During autumn and winter, the population largely resided in the winter, and we assume that the deep populations at this time were diapausers. Egg production rate data was also collected at OWS M, which we use

Data was collected at 2 locations near the Westmann Islands (63°27.25'N, 20°00.00'W, depth 100 m, and 63°22.20'N, 19°54.85'W, depth 200 m) (Gislason et al., 2000). This site was visited 29 times in 1997, with *C. finmarchicus* being collected by vertically integrating hauls from 5 m above the seabed to the sea surface with a 200 μ m mesh, 56 cm Bongo net.

In addition, data was collected from Murchison (61°30.00' N, 01°40.00' E, depth 160 m) on 29 occasions in 1997. Data was collected using a 200 μm mesh with a 30 cm Bongo net from a depth of 150 m to the surface.

5.4.1.2 Ocean Weather Ship India

Similar to Speirs et al. (2006) we include data from Ocean Weather Ship India (OWS I) (59°N, 19°E), which was collected between 1971 and 1975 (Irigoien, 1999). This time series is used because we lack data for a truly oceanic for or close to 1997. Data was collected in this region at approximately weekly intervals from 1971 to 1975. Samples were attained using oblique hauls of a Longhurst-Hardy plankton recorder (280 μm

mesh). Stage resolved copepod samples were then collected from a depth of 500 m to the surface, with a resolution of 10 m. Data from the top 100 m was used.

5.4.1.3 Gulf of Maine

The US GLOBEC program was initiated in 1995 (Durbin et al., 2000). This program involves extensive zooplankton sampling in the Gulf of Maine and Georges Bank. *C. finmarchicus* densities (m^{-3})) is estimated during the first half of the year at varying depth levels using a 1 m^2 MOCNESS fitted with 0.15 mm mesh nets. Estimates of density (m^{-2}) over the top 100 m and from 100 m to the sea bottom by considering regions where bathymetry exceeded 200 m.

5.4.1.4 Stonehaven

Zooplankton abundance data has been collected off Stonehaven, Scotland (56°57.8' N, 2°6.2'W) since 1997. Three vessels (M. V. Shuna (1997-1999), M.V. Stella (1999-2003) and M. V. Temora (2003-)) have been used in this period. Temporal coverage in the Stonehaven time series is good; during the period 1997-2009 the site was sampled on average 48 weeks of the year, with the worst year seeing 45 weeks being sampled (Serpetti et al., 2012).

Routine monitoring collects a range of environmental data at the site; however data for *C. finmarchicus* and *C. helgolandicus* is only relevant to our model testing. Zooplankton sampling is performed using fine mesh nets. These nets collect an integrated sample of zooplankton throughout the water column. Integrated abundance data is provided for C5, female and male stages for both species. Total *Calanus* abundance is provided for stages C1 to C4.

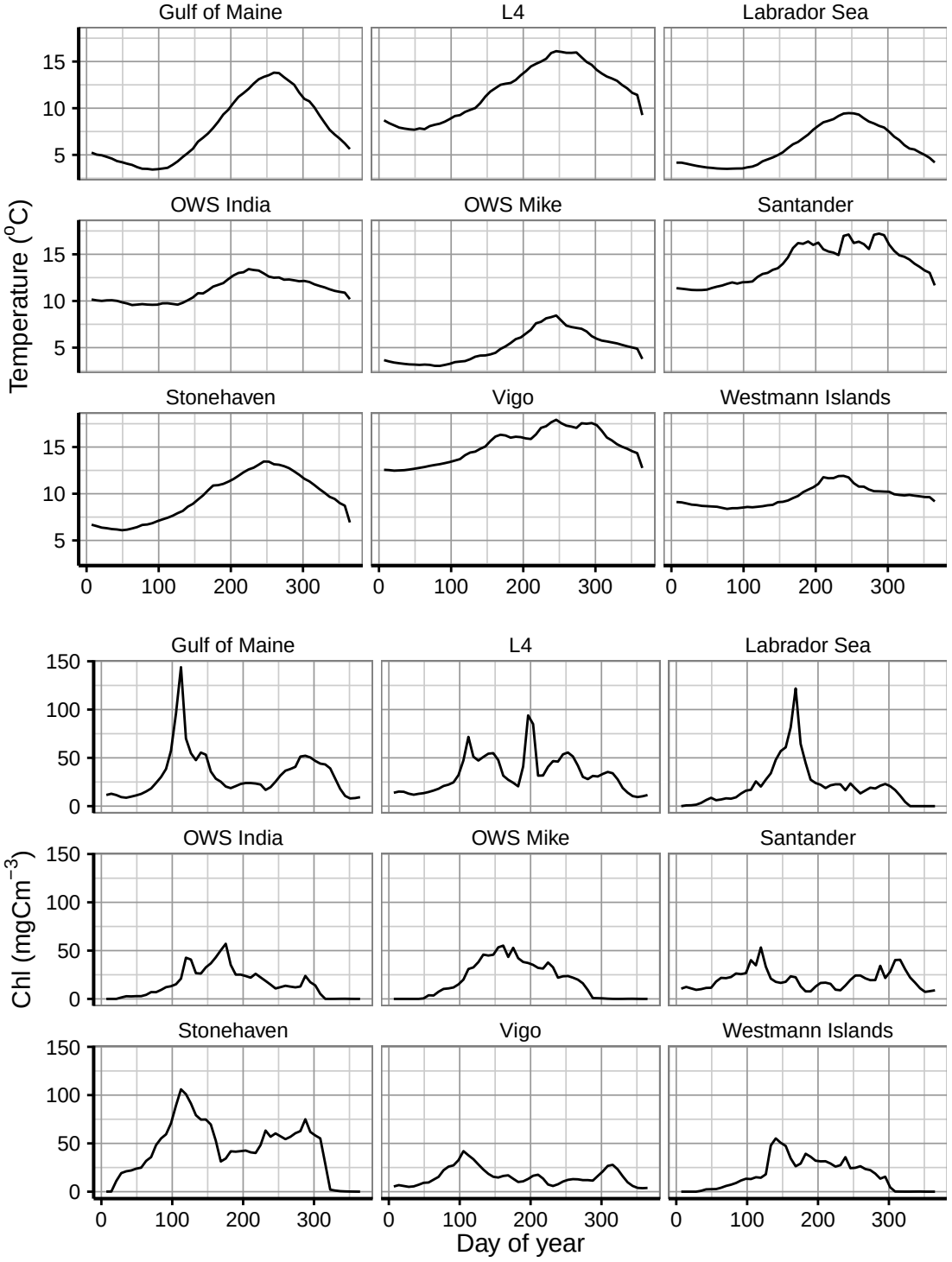


FIGURE 5.2: Food and temperature regimes at each time series location used for model testing. Temperatures shown are those from the NEMO model, and Chl is derived from SeaWifs satellite data.

5.4.1.5 L4

Station L4, in the English Channel (50°15'N, 4°13'W) is one of the longest longest standing zooplankton time series in European waters (Harris, 2010).Zooplankton monitoring began at this station in March 1988. Sea bed depth at the site is 51 m, while observations typically range between 40 and 45 times each year (Harris, 2010).

The L4 time series contains information on the abundance of male, female and total copepodites. Data on males is not available until 1996. And a full annual cycle of adult abundance is not available until 1997.

In addition to abundance data, L4 has a long term time series of EPR (Irigoien et al., 2000b). We therefore test our model of per capita EPR for *C. helgolandicus* against L4 EPR data.

5.4.2 Body size data

Insufficient data for prosome length is available for 1997. We therefore compiled *C. finmarchicus* prosome length data for multiple years to compare with model predictions. Researchers rarely consider prosome length as a phenomenon worth studying itself. In fact, it is almost exclusively reported as part of egg production rate studies, where egg production rate is reported to body size. Large scale patterns of Calanus body size have not been analyzed previously. Figure 5.3 shows the geographic locations of the sites where prosome length was measured in the compiled studies.

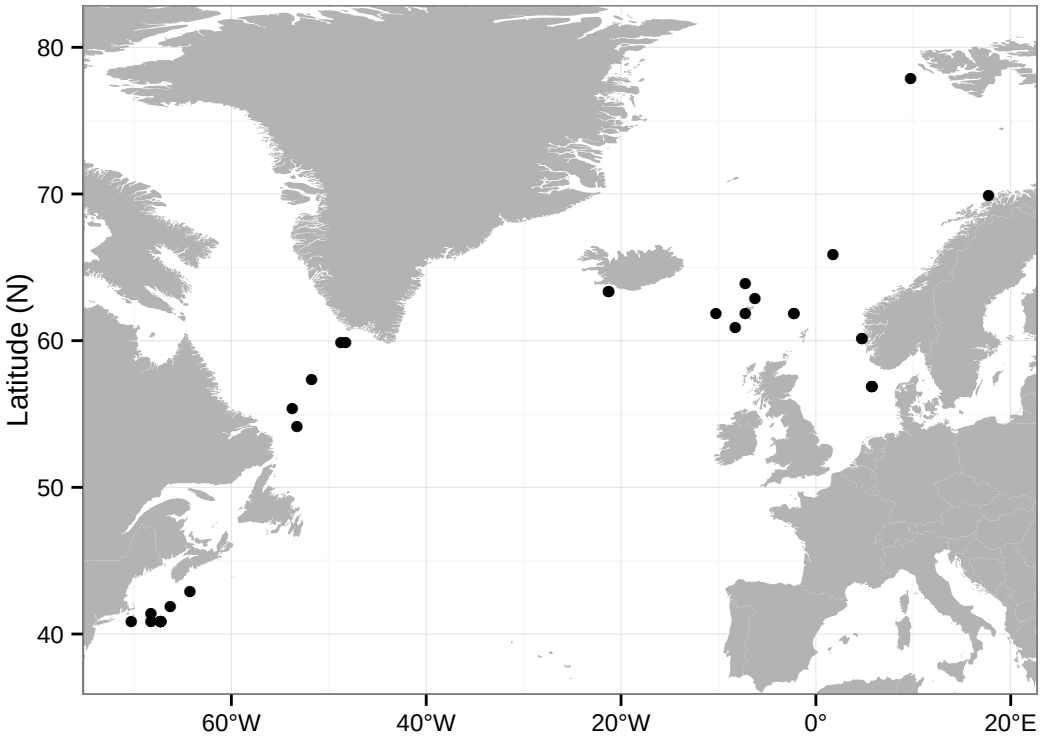


FIGURE 5.3: Map of locations where *C. finmarchicus* prosome lengths were recorded in papers compiled for testing model predictions of prosome length. Field estimates were compiled using data from the following papers: Jønasdøttir et al. (2008); Rey et al. (1999); Campbell et al. (2001); Head et al. (2013a); Jønasdøttir et al. (2005); Diel and Tande (1992); Jønasdøttir et al. (2002); Gabrielsen et al. (2012); Niehoff et al. (1999); Niehoff (2004); Durbin et al. (2000); Runge et al. (2006); Jønasdøttir and Koski (2011); Madsen et al. (2008b); Tande (1982).

5.A Appendix: Model summary

5.A.1 State variables

The model is adapted from Speirs et al. (2006), which modelled *C. finmarchicus*. The geographic domain covers the North Atlantic from 30 to 80°N and from 80°W to 90°E. This domain is further divided into cells of size 0.25°N by 0.5°E. Each cell is represented by a vector address $\mathbf{x} = \{\text{N,E}\}$, where N and E represent the latitude and longitude of the centre of each cell.

In each model cell, we divide the population into 3 groups: surface developers, diapausers, and adults. Surface developers includes all development stages from egg to the end of the C5 stage. Diapausers are C5 individuals overwintering in deep waters. Adults (C6s) are animals in the surface who have completed development and can reproduce. Each group is further divided into 10 body size classes. For the surface developers, we define a development class q, which takes a value of 0 for eggs and 1 at the end of C5. This allows us to divide the surface developers into a set of n classes of equal width Δq, and each overwintering body size class into m classes of width δq. Egg to adult development time is dependent on food and temperature. However, the relative durations of the inter-molt period remains constant. There is therefore a one-to-one relationship between the constant-width classes of the model and the observable physiological stages, shown in Table 5.2.

TABLE 5.2: Stage classes and mortality parameters.

Stage	E	N1	N2	N3	N4	N5	N6	C1	C2	C3	C4	C5
C. finmarchicus												
Surface												
last class	2	5	8	11	14	17	20	25	30	35	41	57
Diapause												
last class	-	-	-	-	-	-	-	-	-	-	-	100
C. helgolandicus												
Surface												
last class	1	4	6	11	15	19	27	31	36	42	47	57
$\mu_q^E(d^{-1} \times 100)$	18.2	33.6	33.6	14.9	2.6	2.6	2.6	1.5	0.0	2	2	15
$w_q^C(\mu g$	0.5	0.33	0.49	1.0	1.5	2.1	2.8	4.2	13	23	64	170

$C_{i,B,x,t} \equiv$ No. of class i developers of body size B in surface cell **x** at time *t* (5.1)

$D_{i,B,x,t} \equiv$ No. of class j diapausers of body size B in surface cell **x** at time *t* (5.2)

$A_{i,B,x,t} \equiv$ No. of adults of body size B in surface cell **x** at time *t* (5.3)

5.A.2 Body size

Adult prosome length (mm) is assumed to be determined at birth. For computational purposes we have 10 body size classes. First we divide temperature space into 10 equally spaced classes between lower and upper ecologically relevant temperature thresholds T_{B_L} and T_{B_U}. Eggs are then placed into the relevant temperature class, with body size being determined by the mean temperature in the temperature class. If the temperature at birth is below the lower threshold or above the upper threshold we place the egg into the first or last temperature class respectively. The relationship between adult length, L (mm) and temperature, T (°C) is that reported by Campbell et al. (2001), with a rescaling to account for non food-saturated conditions.

$$L = \frac{\alpha_L(m_L T + c_L)}{1000} \tag{5.4}$$

For adults we convert length to body weight, w_c^A (μg C) using the equation from Runge et al. (2006),

$$w_c^A = 4.39L^3.57 \tag{5.5}$$

We follow Speirs et al. (2006) and use the dry weights, $w^C_{B,q}$, of each stage from Lynch et al. (2001) as our body weights for each pre-adult stage. However, these numbers are adjusted for the temperature scaling of body size above, assuming that the animals caught by Lynch et al. (2001) (weights shown in Table 5.2) were grown at a temperature of 10 °C.

5.A.3 Transport updates

We simulate the physical transport of animals from one cell to another by redistributing the contents of each cell to a set of destination cells a set of times separated by the transport update interval Δg. Using subscript - and + to denote the system state infinitesimally before and after the update, we can write:

$$C^+_{i,B,x,t} = \sum_{\text{all y}} \Psi^S_{x,y,t} C^-_{i,B,y,t} \tag{5.6}$$

$$D^+_{i,B,x,t} = \sum_{\text{all y}} \Psi^S_{x,y,t} D^-_{i,B,y,t} \tag{5.7}$$

$$A^+_{i,B,x,t} = \sum_{\text{all y}} \Psi^S_{x,y,t} A^-_{i,B,y,t} \tag{5.8}$$

$\Psi^S_{x,y,t}$ and $\Psi^S_{x,y,t}$ are the transfer distributions, representing the proportion of individuals in the surface and deep layers of cell **y** at time $t - \Delta t$ that are transported to the same layer of cell **x** by time t. Thus, using $L \in [S, D]$, we define:

$$\Psi^L_{\mathbf{x},\mathbf{y},t} \equiv \text{Pr}\{\text{particle at } \mathbf{y} \text{ at time } t - \Delta t \text{ is at } \mathbf{x} \text{ at time } t\ \}$$

This quantity was determined by releasing 100 particles at the centre of each cell and tracking their positions from $t - \Delta t$ to t, assuming that the deterministic part of velocity is given by the NEMO model (Madec, 2012).

5.A.4 Biological updates

The state of the surface developer population in cell **x** is updated at a set of times $\{u^c_{\mathbf{x}}$, such that:

$$\Delta q = \int_{u^C_{x,i-1}}^{u^C_{x,i}} g^C_{\mathbf{x}}(\tau) d\tau$$

where $g^C_{\mathbf{x}}(\tau)$ is the development rate of surface developers in cell **x** at time τ (see equation). At the end of each update time, individuals are moved one class to the right. In the case of final stage CV, individuals are either moved to adult or diapause stage. The egg stage then receives the eggs produced by surviving adults. Diapause entry is described using a function $\theta_{i,x,t}$ which returns the fraction of individuals who transfer to the first diapause class. We let Ex,t denote the per capita egg production from the previous update to the one taking place at time t in cell **x**. Further, if $\xi^A_{B,x,t}$ and $\xi^C_{i,B,x,t}$ denote the respective survival of adults and surface developers, then we can write the surviviving developers and adults as: $S^C_{i,B,\mathbf{x},t} \equiv \xi^C_{i,B,x,t} C^-_{i,B,\mathbf{x},t}$ and $S^A_{B,\mathbf{x},t} \equiv \xi^A_{B,x,t} A^-_{\mathbf{B},x,t}$. We therefore have:

$$C_{i,j} = \begin{cases} E_{B,\mathbf{x},t} S^C_{i-1,\mathbf{x},t} & i = 1 \\ (1 - \theta_{i-1,\mathbf{x},t}) S^C_{i-1,\mathbf{x},t} & \text{otherwise} \end{cases} \tag{5.9}$$

$$D^+_{0,B,\mathbf{x},t} = D^+_{0,B,\mathbf{x},t} + \sum_{i=1}^{n} \theta_{i,\mathbf{x},t} S^C_{i,B,\mathbf{x},t} \tag{5.10}$$

$$A^+_{B,\mathbf{x},t} = (1 - \theta_{n,\mathbf{x},t}) S^C_{B,n,\mathbf{x},t} + S^A_{B,\mathbf{x},t} \tag{5.11}$$

The diapausing population of cell **x** is updated, in a similar way, at a set of times $(u^D_{B,x})$ related to each other such that:

$$\delta q = \int_{u^D_{B,x,i-1}}^{u^D_{B,x,i}} g^D_{\mathbf{x}}(\tau) d\tau \tag{5.12}$$

where $g^D_{B,x}$ is the development rate of diapausing individuals of body size class B in cell **x** at time τ (see equation 5.16). Our update process requires that all survivors in all classes, but the last, are moved one class to the right. Diapausers become adults when they have reached the end of the final diapause stage. Let $\xi_{B,x,t}$ be the survival of individuals in class j in model cell **x** from the last update to the one at time t, so that ${S^+}^D_{j,B,\mathbf{x},t} \equiv \xi^D_{j,B,\mathbf{x},t} D^-_{j,B,\mathbf{x},t}$ is the number of surviving diapausers just before the update. Diapausers are therefore updated according to:

$$D^+_{j,B,\mathbf{x},j} = \begin{cases} 0 & j = 1 \\ S^D_{j,B,\mathbf{x},t} & \text{otherwise} \end{cases} \tag{5.13}$$

and at the same time, adults are updated:

$$A^+_{0,B,\mathbf{x},t} = A^-_{0,B,\mathbf{x},t} + D^+_{m,B,\mathbf{x},t} \tag{5.14}$$

5.A.5 Update strategy

We have two types of updates: biological and transportation. Transportation updates occur at a set time, every 7 days. In between this there are a number of biological updates that must occur. This is performed by updating the biological state of each cell until the next update time is after the next transportation time. Once the biological updates are complete, we then perform the transport update.

5.A.6 Growth and development

Development times under food saturated conditions for both species are as calculated by Wilson et al. (2015).

Carbon weight is defined as w_c, and growth rate under food saturated conditions is defined as follows:

$$\dot{w}_c = {w_c}^{0.75} \left(\frac{P_5 A E \mu}{1 + \exp\left(\frac{P_3}{T+273.15} - \frac{P_3}{P_1}\right) + \exp\left(\frac{P_4}{P_2} - \frac{P_4}{T+273.15}\right)} - {Q_{10}^S}^{(T/10)} \lambda \right) \quad (5.15)$$

First we parameterize our model completely for *C. finmarchicus*, using the development times at 4, 8 and 12°C under food-saturated conditions reported by Campbell et al. (2001). The parameterization of development to C5 was performed by minimising the least squares of our model fit. Development time for *C. helgolandicus* was estimated assuming that the only inter-species difference is the response of ingestion to temperature.

Individuals were assumed to molt to the next stage when their carbon weight reaches the respective critical molting weight. We estimated the relationship between molting weight for C5 individuals and temperature using published data on length-weight (Hygum et al., 2000b) and temperature-length relationships (Campbell et al., 2001). C5 molting weight was therefore assumed to relate to temperature using the equation $C_m = 2.307 \cdot 10^{-10} \cdot (-27.4 * T + 2084)^{3.52}$, where C_m is the C5 molting carbon weight (μg), and T is temperature (°C).

Development time to adult under food saturated conditions, DT, was calculated assuming the equiportionality defined by Campbell et al. (2001). Finally, we define the development rate $g_{\mathbf{x}}^C(t)$ to be

$$g_{\mathbf{x}}^{C}(t) = \frac{1}{\mathrm{DT}}\left(1 - \exp\left[-\frac{F_{\mathbf{x}}(t)}{F_G}\right]\right) \tag{5.16}$$

where F_G is the half saturation coefficient from Campbell et al. (2001).

5.A.7 Diapause duration

We model diapause duration assuming that individuals start diapause with length dependent wax ester levels implied by the upper 95th percentile reported by Pepin and Head (2009). Diapause is assumed to end when wax ester levels are three times nitrogen weight. This is an approximate estimate derived from the limited data for the energetic requirements of molting and gonad formation (Rey-Rassat et al., 2002a). Respiration rates are assumed to have allometric scaling of 0.75 (Maps et al., 2014) and to have a Q_10^D of 2.8 (the mean value from (Hirche, 1983; Saumweber and Durbin, 2006; Ingvarsdøttir et al., 1999)).

The relationship between prosome length and wax esters available for respiration during diapause, WE_d, is therefore

$$\mathrm{WE}_d = aL^y \tag{5.17}$$

where $a = 3.66$ and $y = 4.6$, and L is prosome length.

Metabolism is assumed to relate strictly to structural (nitrogen) weight, which is assumed that structural weight is fixed throughout diapause. This assumption means that respiration rates are constant throughout diapause under fixed temperatures, which results in a more elegant model formulation.

Respiration rate, r (μmol O_2gN^{-1}hr^{-1}) is estimated using the data of Saumweber and Durbin (2006), and follows the equation:

$$r = \mu_d {w_N}^{0.75} Q_{10}^d T/10 \tag{5.18}$$

where μ_d is a constant, w_N is nitrogen weight (μg), and T is temperature in °C.

Nitrogen weight, w (μg), is related to prosome length, L (mm) using the following equation derived from Runge et al. (2006),

$$w_N = \alpha L^\beta \tag{5.19}$$

where $\alpha = 2.014$ and $\beta = 2.7$.

Using the weight-specific respiration data of Saumweber and Durbin (2006), we get the following estimate, μ_d = 280.

We then convert the oxygen respiration rate into a carbon respiration rate,

$$R = \frac{24 \cdot \text{RQ} \cdot 12.011 \cdot r}{10^6} \tag{5.20}$$

where R is the carbon respiration rate (μg CμN^{-1}d^{-1}) and RQ is the respiratory quotient.

This can be simplifed to the form

$$R = \xi {w_N}^{0.75} {Q_{10}^d}^{T/10} \tag{5.21}$$

where

$$\xi = \mu * 24 * RQ * 12.011 * 10^{-6} = 0.06$$

Therefore diapause duration is of the form

$$\begin{aligned} \text{Duration} &= \frac{aL^y}{\xi {w_N}^{0.75} \cdot {Q_{10}^d}^{T/10}} \\ &= \frac{aL^y}{\xi (\alpha L^\beta)^{0.75} \cdot {Q_{10}^d}^{T/10}} \\ &= \frac{a \cdot L^{y-0.75\beta}}{\xi \alpha^{0.75} {Q_{10}^d}^{T/10}} \end{aligned} \tag{5.22}$$

We then have the final equation which relates diapause duration with body size and temperature,

$$\text{Duration } = \gamma_d L^{\lambda_d} \cdot {Q_{10}^d}^{-T/10}$$

where $\gamma_d = 36.08$ and $\lambda = 2.58$.

5.A.8 Diapause entry

Individuals are assumed to enter diapause at the end of stage C5, and that the fraction, $\theta_{q,\mathbf{x},t}$, of the population entering diapause is related to growth rate. The proportion of animals that stay at the surface, F_s relates to a reference growth rate $\dot{w}_{de}$

$$\theta_{q,\mathbf{x},t} = \begin{cases} 0 & \text{if } \dot{w} < 0 \\ 1 & \text{if } \dot{w} > \dot{w}_{de} \\ \frac{\dot{w}_c}{\dot{w}_{de}} & \text{otherwise} \end{cases} \tag{5.23}$$

5.A.9 Mortality

Let u_n denote the nth update time in $u_{\mathbf{x}}^K$, where $K \in [A, C, D]$ denotes the target population. We write:

$$\xi_{q,B,\mathbf{x},u_i} = \exp[-m^K_{q,B,\mathbf{x},u_i}(u_{i-1})] \tag{5.24}$$

We assume that there is simply a constant background mortality rate for diapausers:

$$m^D_{i,B,\mathbf{x},t} = \mu^D \tag{5.25}$$

We assume that mortality for surface developers and adults consists of a temperature dependent background rate, together with density-dependent and starvation elements. Let $T^s_{\mathbf{x}}(t)$, $W_{\mathbf{x},t}$, and $F_{\mathbf{x},t}$ are surface temperature, biomass of *C. finmarchicus* or *C. helgolandicus*, and food in cell $\mathbf{x}$ at time t, then:

$$m^C_{i,B,\mathbf{x},t} = \gamma(T^S_{\mathbf{x}}(t))\mu^C_i(1 + \phi W_{\mathbf{x},t}) + \mu_F \tag{5.26}$$

$$m^A_{B,\mathbf{x},t} = \gamma(T^A_{\mathbf{x}}(t))\mu^C_i(1 + \phi W_{\mathbf{x},t}) + \mu_F \tag{5.27}$$

with temperature dependence being given by:

$$\gamma(T^S_{\mathbf{x}}(t)) = \gamma_0 + (1 - \gamma_0)(T/T_c)^z \tag{5.28}$$

The parameter λ_0 is the fraction of the mortality at some characteristic temperature T_c that is experienced at 0°C, and z determines how quickly mortality increases with temperature.

We relate starvation mortality to weight specific growth rate. If weight specific growth rate is above a threshold, there is no starvation mortality. However, below this threshold, starvation mortality increases linearly as growth rate decreases.

$$\mu_F(F_{\mathbf{x}}(t), T(t)) = \begin{cases} 0 & \text{if } \dot{w} > \dot{w}_c \\ \frac{w_c - w^{-1}\dot{w}}{\mu_c} & \text{otherwise} \end{cases} \tag{5.29}$$

Total biomass density in cell **x** is given by the sum over all develop classes of the number of individuals in each class multiplied by the dry weight of each individual plus a similar sum over the adult population, divided by the surface area of the cell ($\alpha_{\mathbf{x}}$):

$$W_{\mathbf{x},t} = \frac{1}{\alpha_{\mathbf{x}}} \left[\sum_{i=1}^{n} \sum_{j=1}^{B} w_{i,j}^{C} C_{i,j,x,t} + \sum_{j=1}^{B} w_{j}^{A} A_{j,x,t} \right] \tag{5.30}$$

5.A.10 Egg production

We assume that egg production is equivalent to growth, as defined above. Furthermore, we assume that the carbon weight of eggs is related to temperature as reported by Campbell et al. (2001). Thus

$$E_{B,x,t} - \beta_{B,x,t}(u_n - u_{n-1}) \tag{5.31}$$

where $\beta_{B,x,t}$ is the per capita EPR. This is modelled assuming a saturating function of food.

$$E_{B,x,t} = \frac{F_{\mathbf{x}}(t)}{F_h + F_{\mathbf{x}}(t)} \dot{w} \frac{1}{-0.00255T + 0.216} \tag{5.32}$$

This model provides a very close fit with the experimental data of Hirche et al. (1997).

TABLE 5.3: Summary of model equations. Part 1.

Equation	Comment
State variables	
$C_{i,B,x,t} \equiv$ No. of class i developers of body size B in surface cell **x** at time t	
$D_{i,B,x,t} \equiv$ No. of class j diapausers of body size B in surface cell **x** at time t	
$A_{i,B,x,t} \equiv$ No. of adults of body size B in surface cell **x** at time t	
Body size	
$L = \frac{\alpha_L(m_L T + c_L)}{1000}$	L is adult prosome length (mm) We assume that L is determined by temperature at birth
$w_c^A = 4.39 \times L^{3.57}$	w_c^A is carbon weight of adults (μg C)
Growth and development	
$\dot{w}_c = {w_c}^{0.75}\left(\frac{P_5 AE\mu}{1+\exp\left(\frac{P_3}{T+273.15}-\frac{P_3}{P_1}\right)+\exp\left(\frac{P_4}{P_2}-\frac{P_4}{T+273.15}\right)} - {Q_{10}^S}^{(T/10)}\lambda\right)$	$\dot{w}_c$ is carbon growth rate (μgC h^{-1})
$C_m = 2.307 \cdot 10^{-10} \cdot (-27.4 * T + 2084)^{3.52}$	C_m is molt weight (μg C) assumed for CV in development model
DT = development time (d) under food saturated conditions	
$g_{\mathbf{x}}^C(t) = \frac{1}{\mathrm{DT}}\left(1 - \exp\left[-\frac{F_{\mathbf{x}}(t)}{F_G}\right]\right)$	$g_{\mathbf{x}}^C$ is development rate (d^{-1}), F is food concentration (mg C m^{-3}) and F_G = half saturation of food (mg C m^{-3})
$\Delta q = \int_{u_{x,i-1}^C}^{u_{x,i}^C} g_{\mathbf{x}}^C(\tau) d\tau$	Update times, $\{u_{\mathbf{x}}^c\}$ satisfy this equation
Fecundity	
$E_{B,x,t} = \frac{F_{\mathbf{x}}(t)}{F_h + F_{\mathbf{x}}(t)} \dot{w} \frac{1}{-0.00255T + 0.216}$	$\beta_{B,x,t}$ is the per capita EPR (eggs^{-1}individual^{-1}d^{-1})

TABLE 5.4: Summary of model equations. Part 2.

Equation	Comment
Diapause	
Duration $= \gamma_d L^{\lambda_d} \cdot Q_{10}^{d\ -T/10}$	Diapause duration (d) is related to size and temperature
$\theta_{q,\mathbf{x},t}(F_{\mathbf{x}}(t), T(t)) = \begin{cases} 0 & \text{if } \dot{w} < 0 \\ 1 & \text{if } \dot{w} > \dot{w}_{de} \\ \frac{\dot{w}_c}{\dot{w}_{de}} & \text{otherwise} \end{cases}$	$\theta_{q,\mathbf{x},t}$ is proportion diapausing at the end of C5
Mortality	
$\xi_{q,B,\mathbf{x},u_i} = \exp[-m^K_{q,B,\mathbf{x},u_i}(u_{i-1})]$	ξ is proportion surviving, m is mortality rate
$m^D_{i,B,\mathbf{x},t} = \mu^D$	Simple background mortality rate, μ^D, is assumed for for diapausers
$m^C_{i,B,\mathbf{x},t} = \gamma(T^S_{\mathbf{x}}(t))\mu^C_i(1 + \phi W_{\mathbf{x},t}) + \mu_F$	$m^C_{i,B,\mathbf{x},t}$ is mortality rate for developers, ϕ is density dependence
$m^A_{B,\mathbf{x},t} = \gamma(T^A_{\mathbf{x}}(t))\mu^C_i(1 + \phi W_{\mathbf{x},t}) + \mu_F$	$m^A_{B,\mathbf{x},t}$ is mortality rate for adults, ϕ is density dependence
$\gamma(T^S_{\mathbf{x}}(t)) = \gamma_0 + (1 - \gamma_0)(T/T_c)^z$	γ gives the temperature dependence of mortality
$\mu_S(F_{\mathbf{x}}(t), T(t)) = \begin{cases} 0 & \text{if } \dot{w} > \dot{w}_c \\ \frac{\dot{w}_c - w^{-1}\dot{w}}{\mu_c} & \text{otherwise} \end{cases}$	μ_S is starvation mortality
$W_{\mathbf{x},t} = \frac{1}{\alpha_{\mathbf{x}}}\left[\sum_{i=1}^{n}\sum_{j=1}^{B} w^C_{i,j} C_{i,j,x,t} + \sum_{j=1}^{B} w^A_j A_{j,x,t}\right]$	$W_{\mathbf{x},t}$ is biomass (μg C) for density dependence. See table 5.2 for stage biomasses.

TABLE 5.5: Model parameters. Bracketed value shows *C. helgolandicus* parameter.

Parameter	Symbol	Value	Units	Reference
Surface developers				
Ingestion scaling with temp.	P_1	293 (289)	-	Møller et al. (2012)
	P_2	284(275)	-	Møller et al. (2012)
	P_3	13,282 (14,123)	-	Møller et al. (2012)
	P_4	29,725 (39,429)	-	Møller et al. (2012)
	P_5	6.05 (12.12)	-	Møller et al. (2012)
Assimilation efficiency	AE	0.488	-	Wilson et al. (2015)
Q_{10} of surface respiration	Q_{10}^S	3.19	-	Wilson et al. (2015)
Ingestion scaling	μ	0.0415	-	Wilson et al. (2015)
Respiration scaling	λ	0.000101	μgCμgC^{-1}d^{-1}	Wilson et al. (2015)
Development saturation coeff.	F_g	29.2	mg C m^{-3}	Campbell et al. (2001)
Nominal mortality	μ_q^E	Table 5.2	d^{-1}	Eiane et al. (2002)
Starv. and density dependence				
Starv. growth threshold	$\dot{w}_c$	0.0012	μgCμgC^{-1}d^{-1}	Fitted
Starv. ref. growth	μ_c	0.01		Fitted
Density dependence	ϕ	3×10^{-6}	d^{-1}m^3μg^{-1}	Fitted
Fraction back. mort. at 0 °C	γ_0	0.65	-	Speirs et al. (2006)
Characteristic temp.	T_C	8	°C	Fitted
Temp. power coeff.	z	7 (4.1)	-	Fitted
Stage specific dry weight	w_q^C	Table 5.2	μg	Lynch et al. (2001)
Adults				
Fecundity half saturation food	F_h	82.02	mgCm^{-3}	Hirche et al. (1997)
Body size				
Temperature-body size coeff.	α_L	0.9	-	Fitted
	m_L	-39.1	-	Campbell et al. (2001)
	b_L	3073	-	Campbell et al. (2001)
Lower temp. threshold	T_{B_L}	0 (7)	°C	Fitted
Upper temp. threshold	T_{B_L}	15 (20)	°C	Fitted
Adult mortality	μ_y^A	0.01	d^{-1}	Speirs et al. (2006)
Diapausers				
Diapause reference growth	$\dot{w}_{de}$	0.1	μgCgC^{-1}d^{-1}	Fitted
Diapause duration factor	γ_d	36.08	d	Fitted
All. scaling of diapause dur.	λ_d	2.58	-	Fitted
Diapause temperature scaling	Q_10^d	2.8	-	Assumed
Mortality rate	μ_D	0.05	d^{-1}	Speirs et al. (2006)

Chapter 6

Population model results

First we report results for the baseline model. In this version of the model, the only interspecies difference, other than those relating to development and EPR, is the response of mortality to temperature, with only a single parameter, z, being different between each species.

We then perform a sensitivity analysis of our model. This is principally composed of an analysis of the importance of diapause assumptions to model results, and of the sensitivity of model results to mortality assumptions.

6.1 Summary of differences with Speirs et al. (2006)

Before showing the model results, we will briefly summarize the differences our model and that of Speirs et al. (2006), on which this model is based. Speirs et al. (2006).

We maintained the stage-structured methodology of Speirs et al. (2006). However, each stage is now divided into 10 body size classes, with body size determined by temperature at birth. This allows the influence of body size on diapause duration and fecundity to be modelled more credibly.

In our baseline model diapause duration is related strictly to prosome length and temperature experienced during winter. In contrast, Speirs et al. (2006) assumed that diapause exit was triggered by a photoperiod cue.

Speirs et al. (2006) modelled development time and egg production rate assuming relationships between temperature and food concentration from experimental studies. Their assumption was that egg production rate increases monotonically with temperature. In contrast, we use the growth rate model developed by Wilson et al. (2015) to produce new development time and egg production rate models. In our model, development time has a U-shaped response to temperature, whereas egg production rate has a dome-shaped response.

Mortality is modelled in the same way as Speirs et al. (2006), with the exception of starvation mortality. The relationship between ingestion rate and temperature for both species indicates that starvation should be related to food and temperature, whereas Speirs et al. (2006) only used food. We therefore model starvation mortality as a function of growth.

6.2 Testing the baseline model

A fundamental requirement is that our model reproduces the geographic distribution and seasonal cycle revealed by the CPR. Figures 6.1 and 6.2 compare predicted and bimonthly abundance derived from CPR for *C. finmarchicus* and *C. helgolandicus* respectively. As stated in the previous chapter CPR abundance (m^{-3}) is multiplied by a factor of 20 to give a number that is comparable with our modelled abundance (m^{-2}).

The model of *C. finmarchicus* reproduces the large scale geographic pattern of annual abundance in comparison with CPR. The correlation coefficient between modelled average annual abundance in each 2°E by 1°N cell is 0.75. Bimonthly comparisons show a similarly good fit between modelled *C. finmarchicus* abundance and CPR (Figure 6.1).

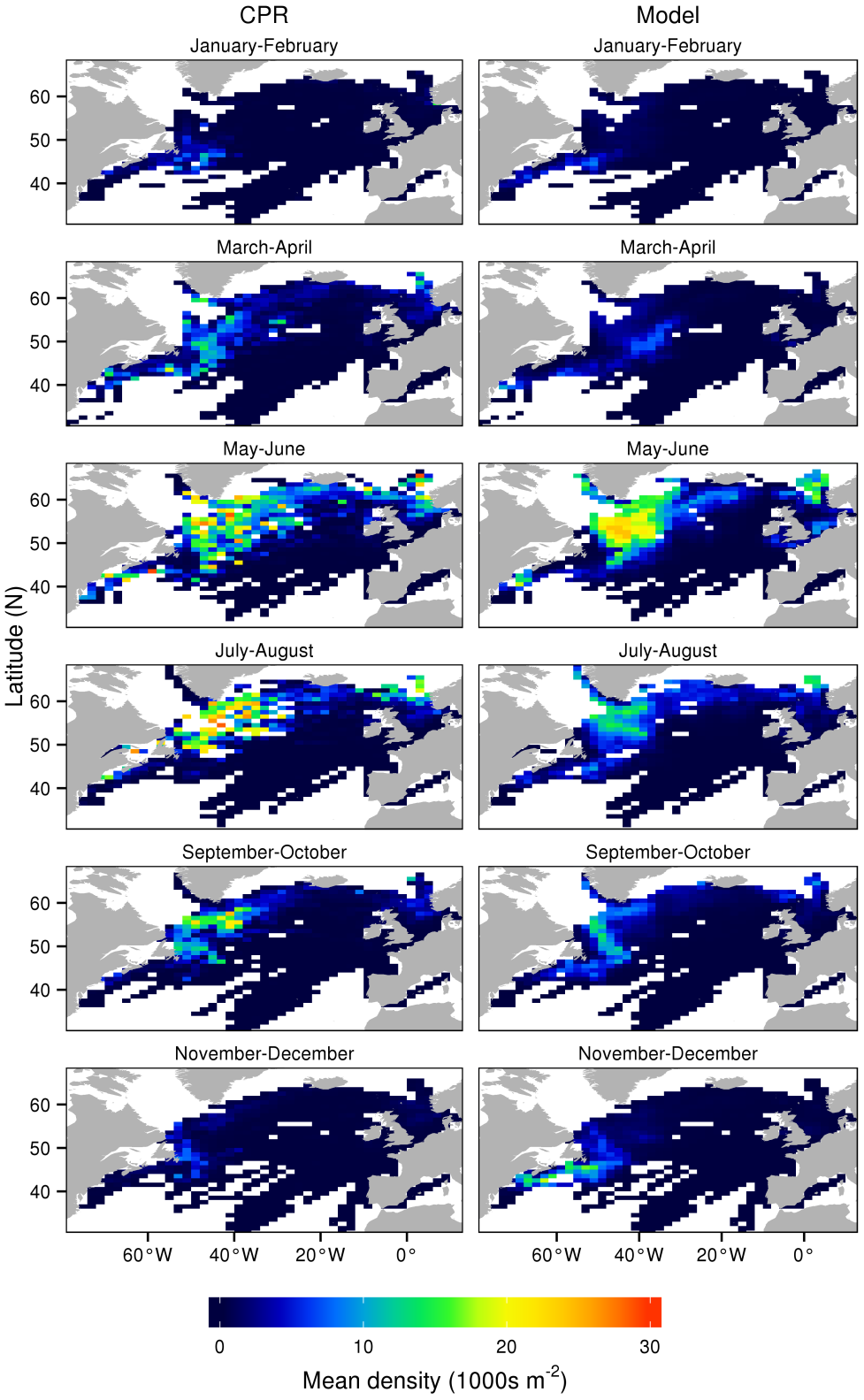


FIGURE 6.1: Comparison of bimonthly *C. finmarchicus* abundance as recorded by CPR and by the model. Density is averaged C5 and adult abundance

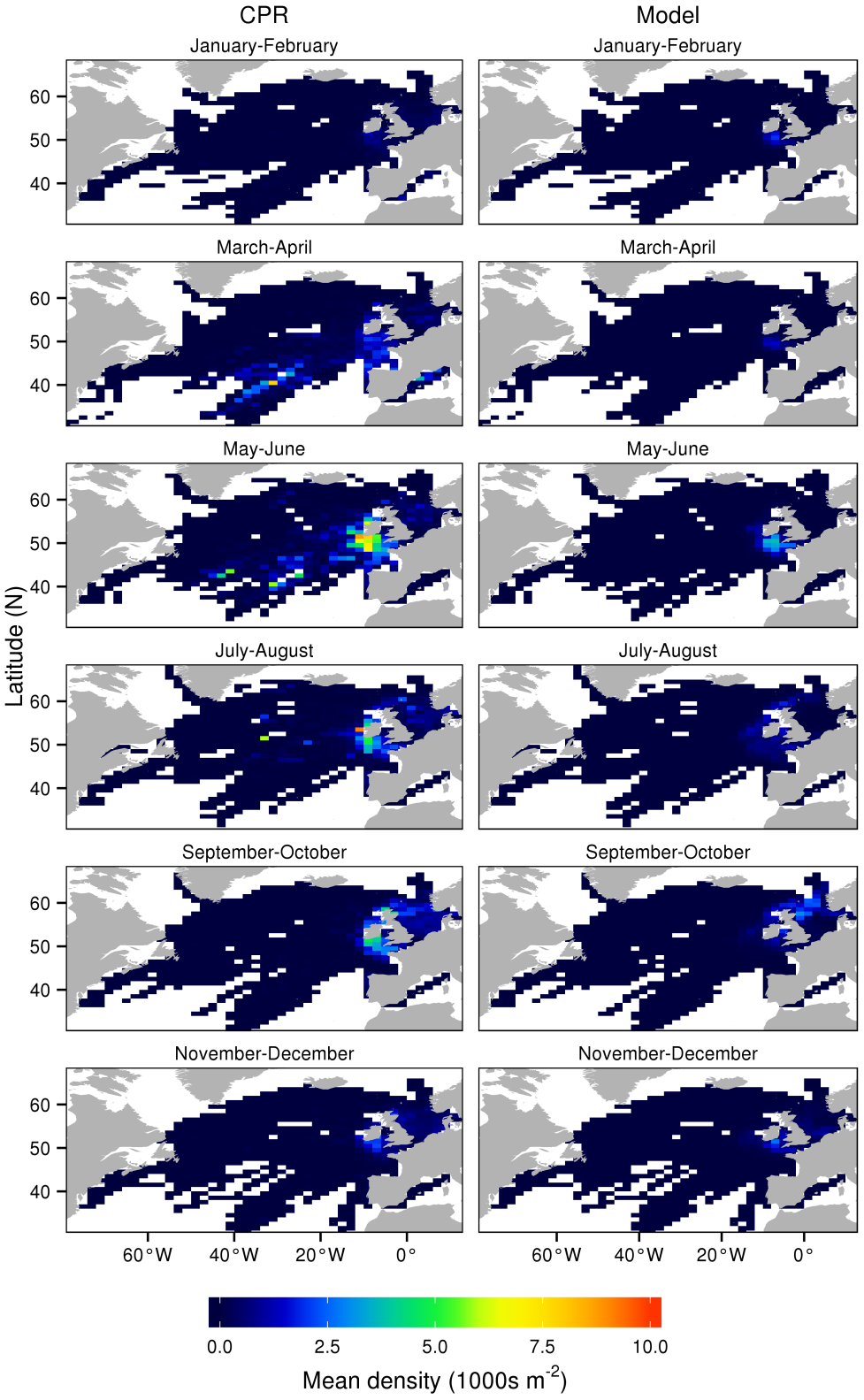


FIGURE 6.2: Comparison of bimonthly *C. helgolandicus* abundance as recorded by CPR and by the model. Density is averaged C5 and adult abundance

Importantly the model reproduces the relatively high abundance of *C. finmarchicus* in the West Atlantic in autumn. In addition, the model predicts a year round surface population in coastal waters in the West Atlantic, in accordance with CPR. However, it perhaps over-predicts abundance in November and December.

Similarly, our model of *C. helgolandicus* compares reasonably well with CPR abundance data. The correlation coefficient between modelled average annual abundance in each 2°E by 1°N cell is 0.76. The model appears to reproduce the geographic and seasonal cycles with reasonable fidelity compared with CPR (Figure 6.1). In particular, it succeeds in restricting *C. helgolandicus* to the continental shelf. However, the model over predicts abundance in November and December. The model also succeeds in reproducing the apparent bloom of C. helgolandicus in the North Sea in autumn.

Comparisons with time series show reasonable model results for *C. finmarchicus*. However, there are some notable differences between predictions and the time series. Figure 6.3 shows predicted abundances of the combined C1 to C4 stages for *C. finmarchicus* versus those from time series data. The model fits are good, with some exceptions. Timing of the first generation in our model is very similar to that shown by the time series for OWS I, Murchison and the Westmann Islands. However, there appears to be significant delays in the timing of the first generation in the Gulf of Maine and at OWS M. Modelled peak abundance is within a factor of 2 at all locations, except at Westmann Islands where the peak abundance in our model is significantly lower than that observed in the time series data.

We then compared modelled combined abundance for stage C5 and adult with that in the time series (figure 6.4). As with the C1-4 stages, modelled peak abundances of *C. finmarchicus* are within a factor of 2 of those recorded in the time series, with the exception of the Westmann Islands. OWS I is notable for getting the scale of the first generation very accurate, but our model predicts a much larger second generation than is apparent in the time series. Our model fails to show the apparent sharp increase in

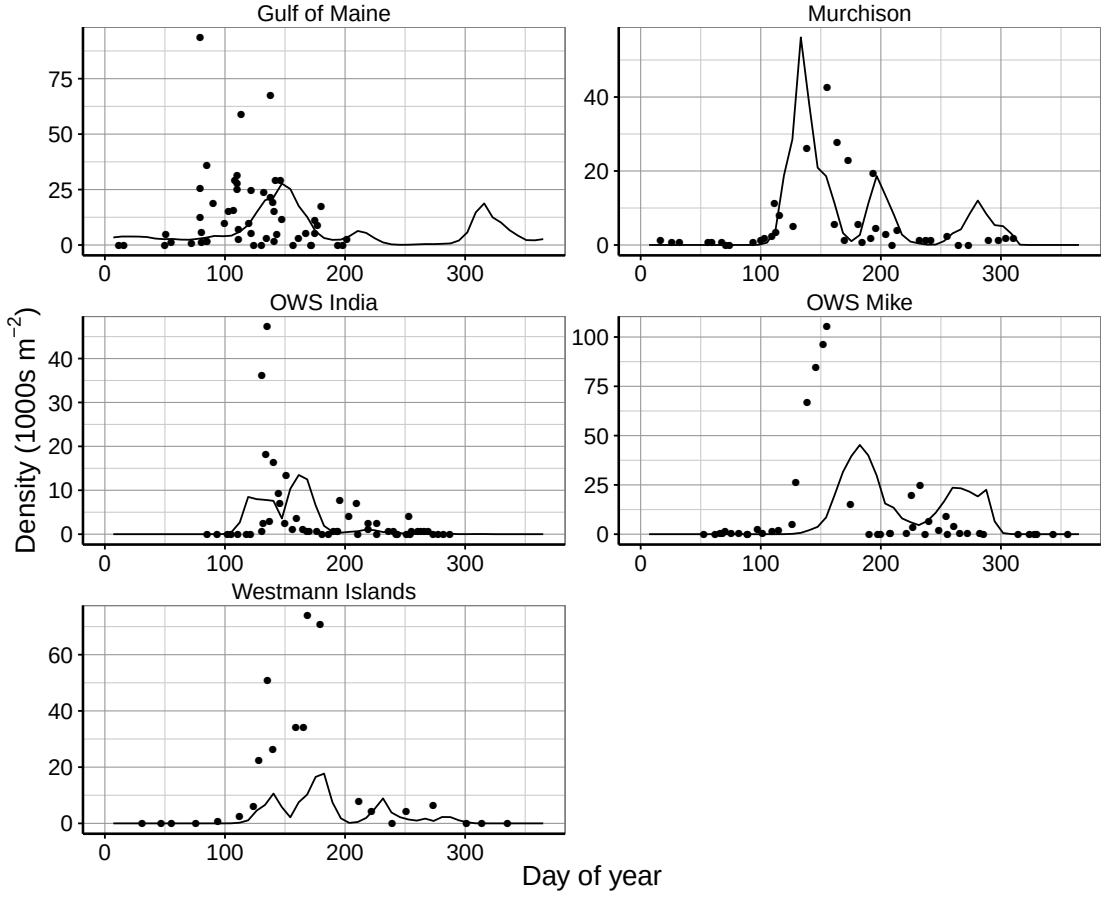


FIGURE 6.3: Comparison of modelled *C. finmarchicus* abundance for combined states C1 to C4 with time series data. Lines represent model output; points represent time series data. Abundance is depth integrated over the top 100 m of the water column.

C5 and adult at OWS M before day 100. Additionally, the second peak in C5 and adult abundance at OWS M appears to be time shifted by approximately 50 d.

Predicted abundance of diapausing C5s were then compared with time series estimates in the Gulf of Maine and OWS M (figure 6.5). Peaks in modelled diapause abundance are comparable with those in the time series. However, predicted diapause abundances are relatively large year round at OWS M. In particular, they are above 10,000 ind m^{-2} from day 100 to 150, which is contradicted by the time series. Similarly, we expect diapause populations to decrease sharply after day 100, which does not occur in our model.

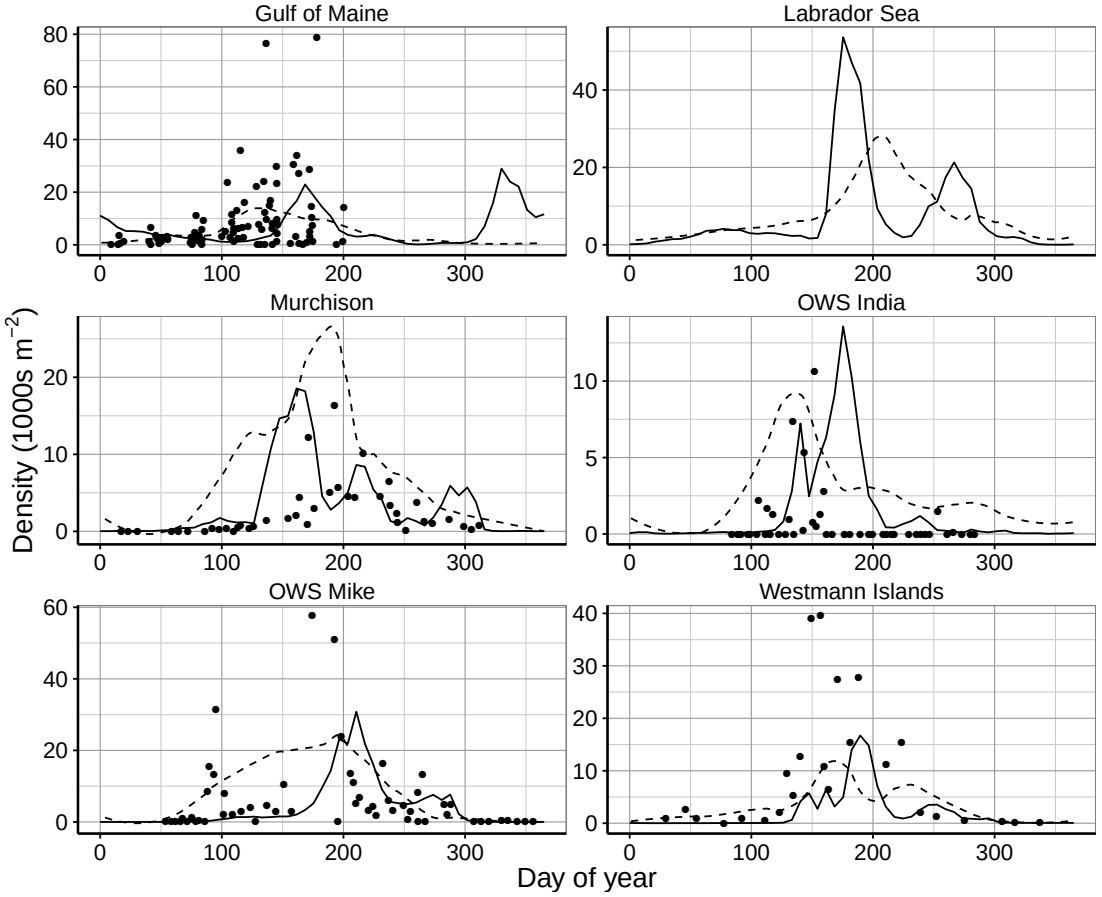


FIGURE 6.4: Comparison of modelled *C. finmarchicus* abundance for combined states C5 and adult with time series data. Lines represent model output; points represent time series data. Abundance is depth integrated over the top 100 m of the water column.

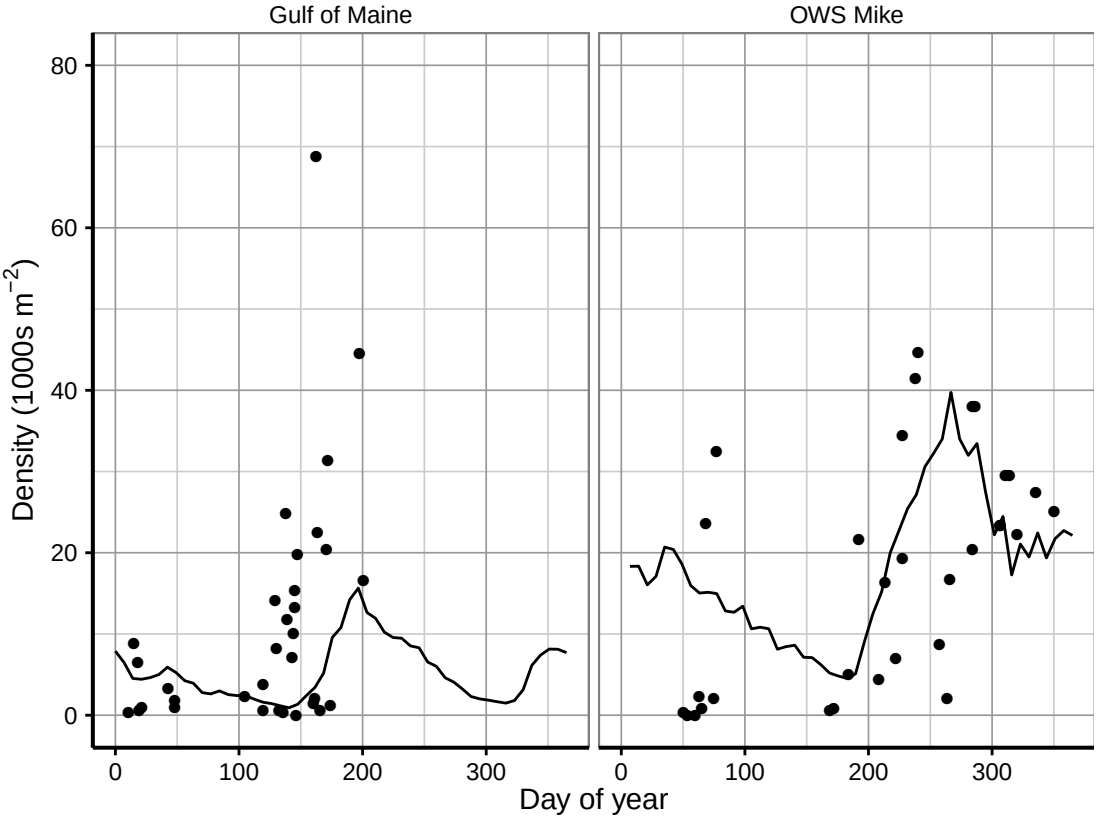


FIGURE 6.5: Comparison of modelled abundance for diapausing C5 with time series data. Lines represent model output; points represent time series data. Abundance is depth integrated over the top 100 m of the water column. Dots represent locations where there there are samples of diapause abundance.

Our final comparison of population predictions for *C. finmarchicus* is between predicted and observed diapausers (6.6). Predictions in the East Atlantic are very good and compare very well both in terms of absolute diapauser numbers and in the spatial distribution of diapausers. Our model appears to over predict abundance of diapausers in the West Atlantic. However, the relative lack of field estimates mean that we cannot be very confident the field estimates are a fully accurate reflection of diapauser abundance.

The overall spatial fit of the *C. helgolandicus* model is slightly better than for *C. finmarchicus*. However, the baseline predictions show some notable departures from time series data. Figure 6.7 compares model predictions with field time series and time series derived from CPR. The model is reasonably successful at L4 and Stonehaven in

terms of broad patterns of abundance. Notably the model successfully reproduces the timing of the autumn peak of *C. helgolandicus* abundance at Stonehaven. However, the model fails to reproduce the small bloom in *C. helgolandicus* abundance in spring. Seasonality at L4 is good in terms of timing of peak and absolute abundance. However, the model appears to over predict abundance during winter. Importantly, the baseline model is unsuccessful at the Vigo station, failing to reproduce the pattern of time series abundance with any success. This is in line with the broad failure of the baseline *C. helgolandicus* model at southern locations, with the model failing to predict any abundance in the Mediterranean.

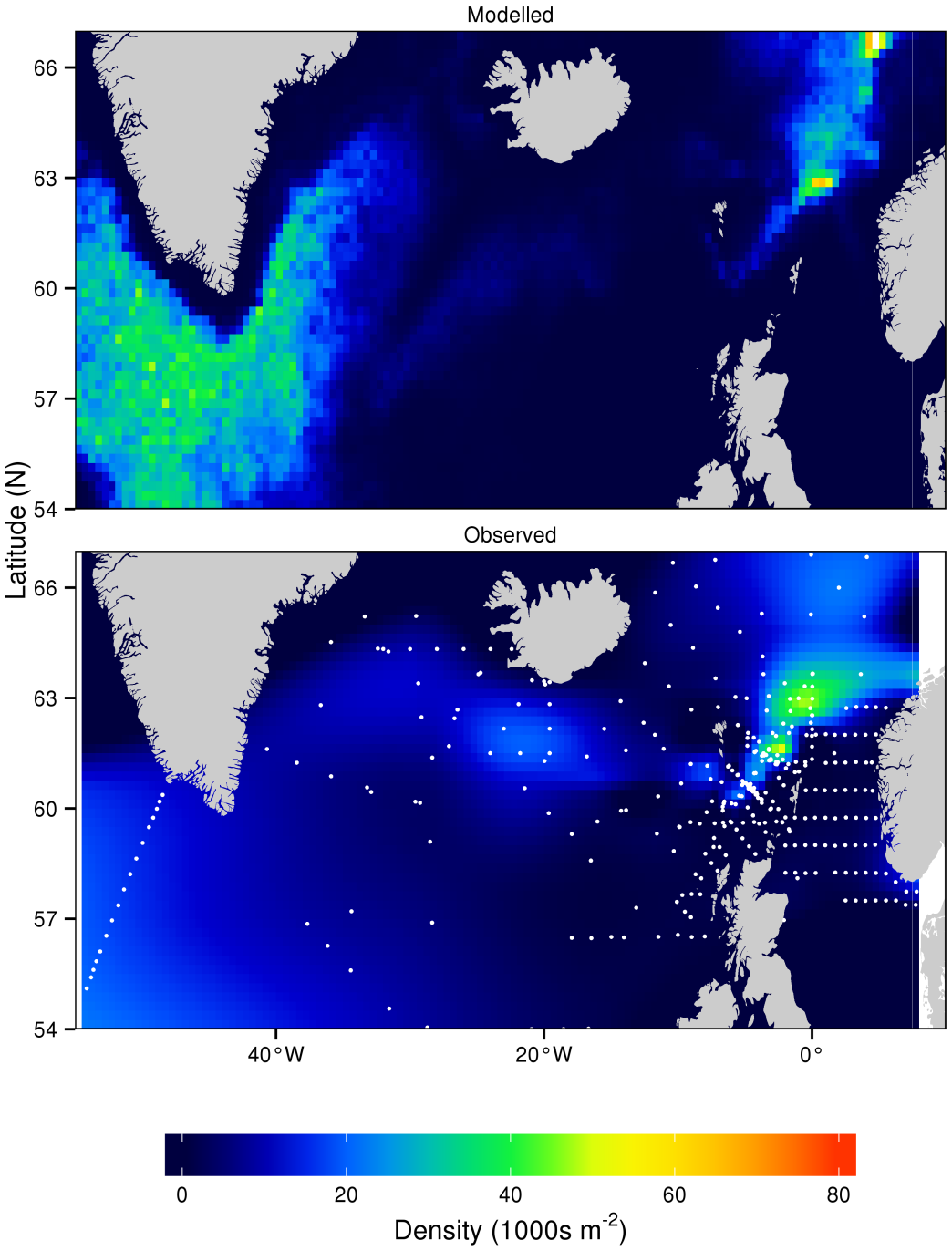


FIGURE 6.6: Comparison of predicted and observed abundance of diapausing C5. Abundance is integrated over the entire water column at a depth of below 100 m.

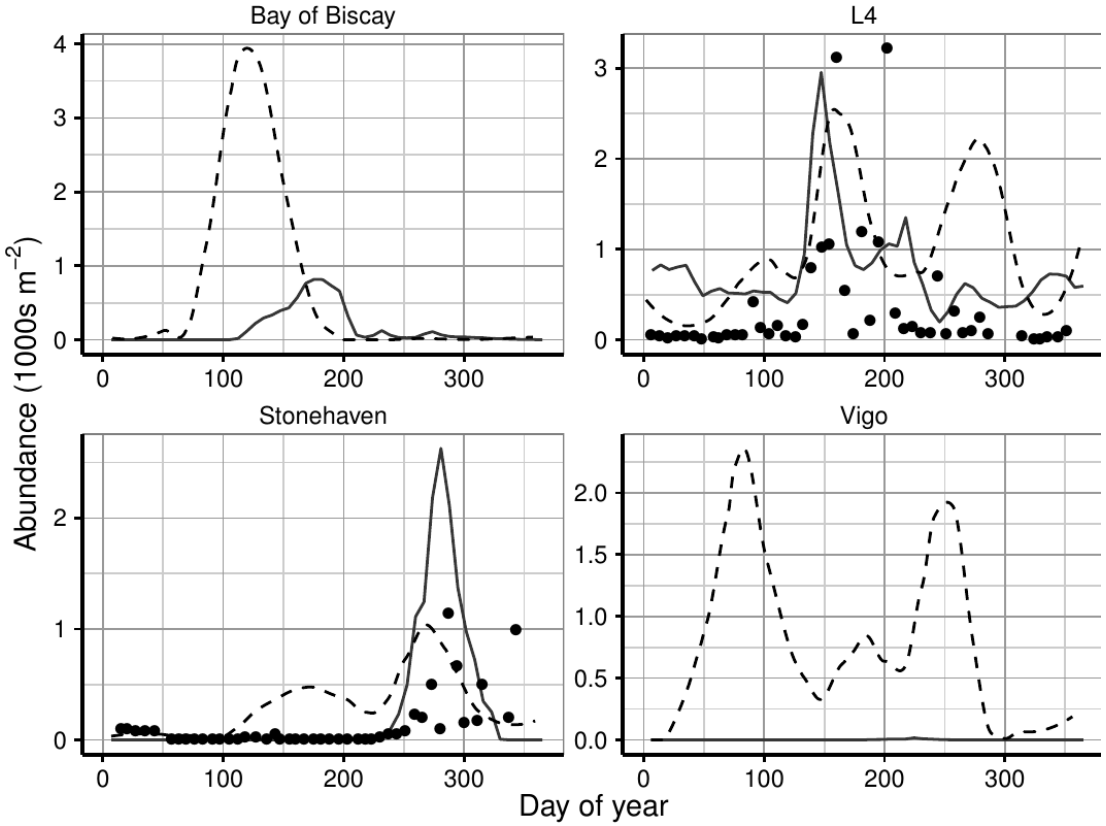


FIGURE 6.7: Comparison of modelled abundance of *C. helgolandicus* for combined states C5 and adult with time series data. Solid lines represent model output; dashed lines represent smooths of CPR abundance; points represent time series data. Abundance is depth integrated over the top 100 m of the water column.

6.3 Body size

We modelled prosome length using the simplified assumption that temperature at birth determines adult body size. The ability of our model to realistically represent body size was tested by comparing modelled body sizes with published body sizes for *C. finmarchicus*.

Female prosome length data for *C. finmarchicus* was compiled from published literature, largely from EPR studies. Insufficient body size data is available for our year of study. We therefore compiled data over all available years. Body size predicted at the relevant month was then compared with that from our model output.

The results are shown in Figure 6.8. Model data was compared with field data using a linear model ($R^2 = 0.24$). This indicates that our model provides a reasonably realistic representation of the large scale patterns of body size, and the model does not appear to be geographically skewed.

We then considered the geographic and seasonal cycle in body size. This was done by considering the pattern in body size for stage C5 for *C. finmarchicus*.

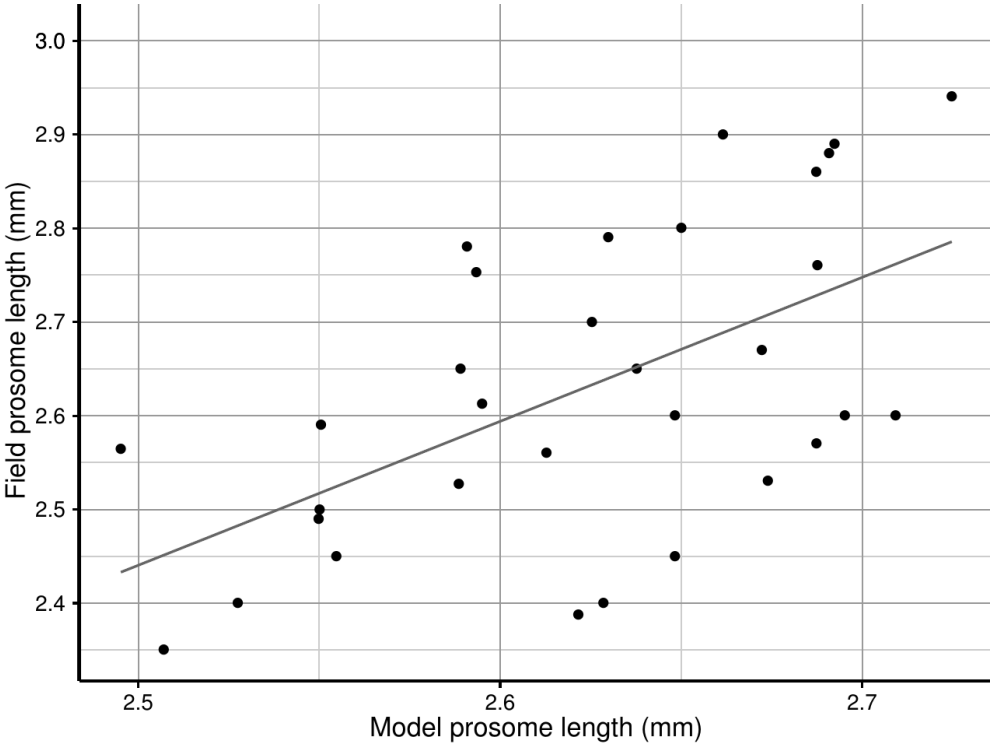


FIGURE 6.8: Comparison of model predictions female prosome length with field estimates. Model predictions are mean prosome length at the month of year and location of the field estimate. References for field estimates are given in figure 5.3.

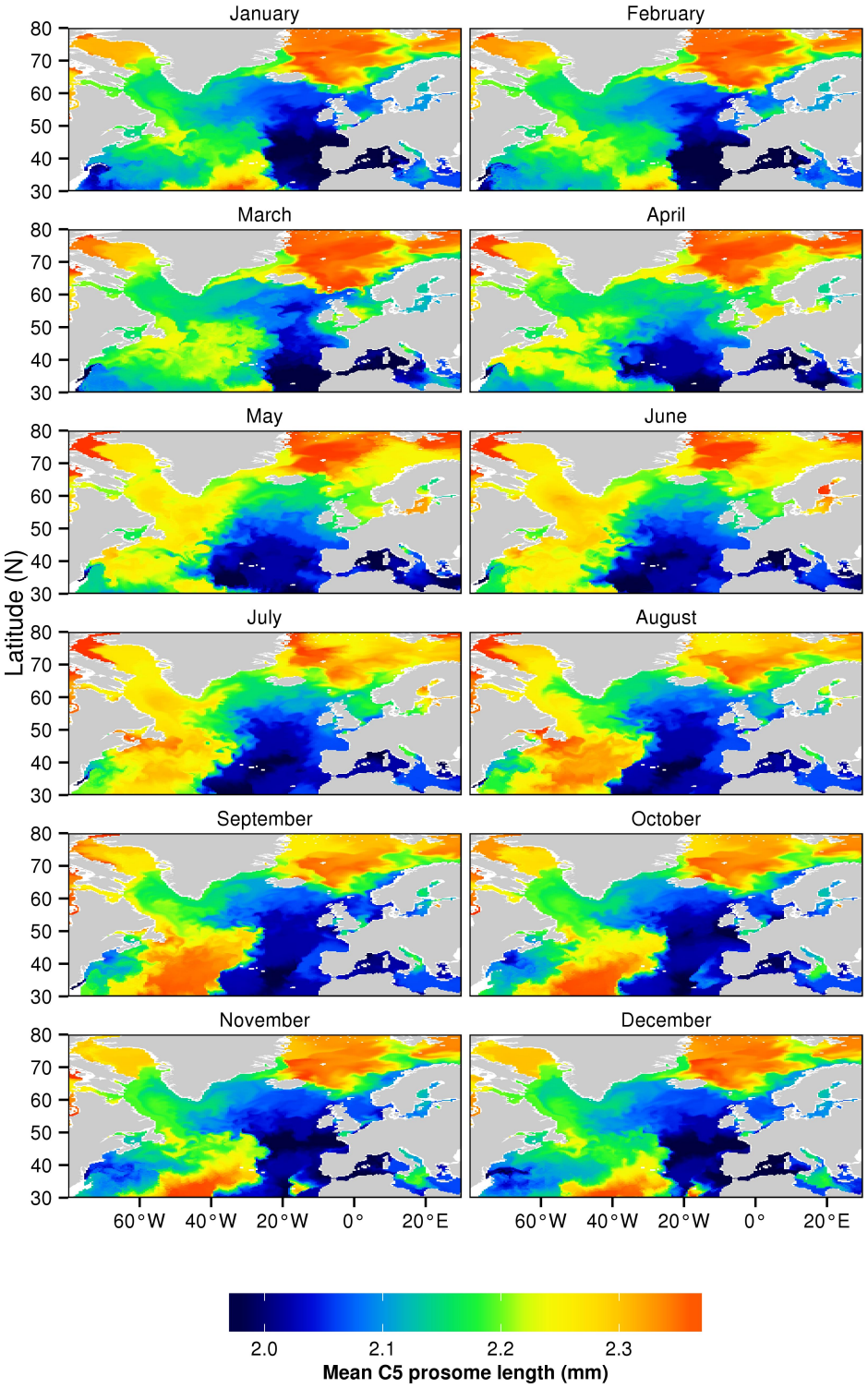


FIGURE 6.9: Mapped predicted mean C5 prosome length for the *C. finmarchicus* model in each month of the year

6.4 Fecundity

Figure 6.10 shows a comparison between predicted and field estimates of EPR. Comparison of the EPR for *C. finmarchicus* at L4 indicates that the model is relatively successful in the first half of the year, with modelled EPR tracking time series EPR with reasonable fidelity, but the under predicts EPR slightly. However, in the second half of the year modelled and actual EPR depart significantly at L4, with modelled EPR being significantly higher than time series EPR.

The pattern of predicted *C. finmarchicus* EPR at OWS from days 80 to 170 are reasonable in comparison with the time series. In the time series, EPR peaks at approximately day 140, and our predicted EPR is very close to the mean and median EPR at that time in the time series. Notably, our model does not predict a decline in EPR around day 150, which is apparent in the time series.

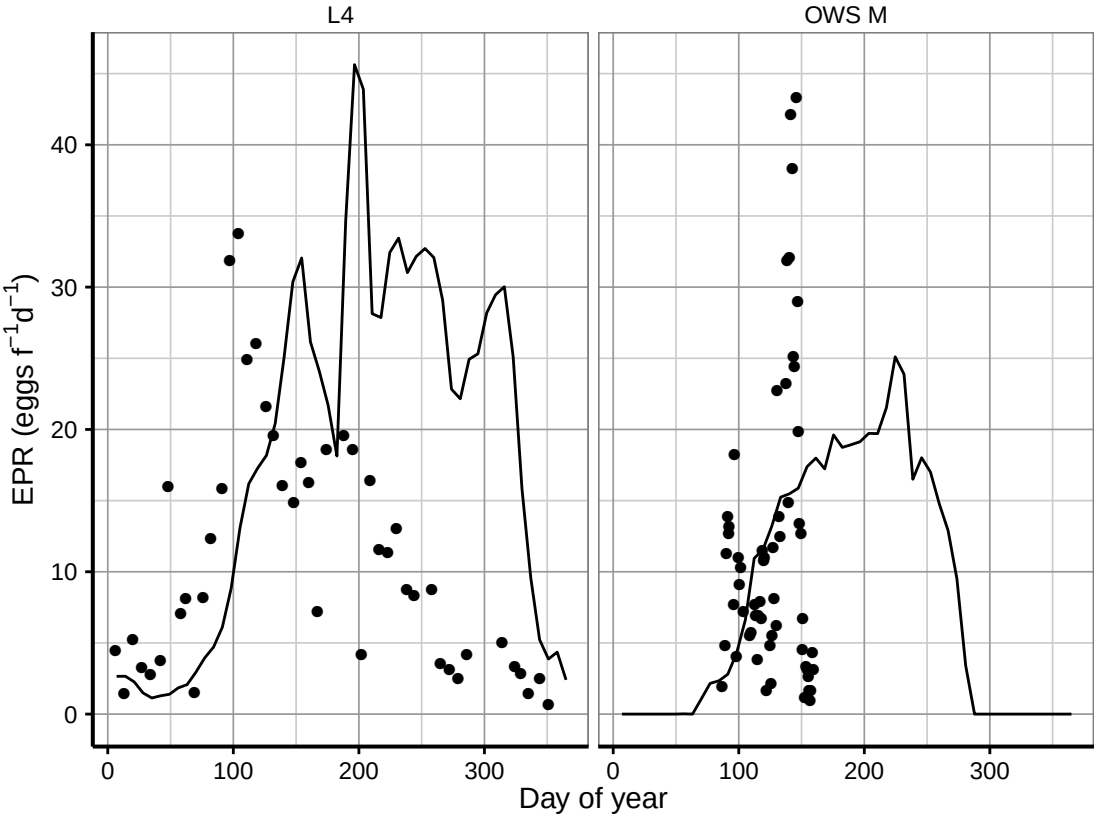


FIGURE 6.10: Predicted EPR for *C. helgolandicus* at L4, English Channel and for *C. finmarchicus* at OWS M compared with field estimates. Solid lines are modelled EPR; points are field estimates.

6.5 Sensitivity analysis

6.5.1 Sensitivity of the *C. finmarchicus* model to choice of OCGM

OCGMs can be spatially biased in terms of temperatures (Sévellec and Fedorov, 2013). We therefore tested the sensitivity of our model to surface temperature. This was performed by running our model using the surface temperatures used by Speirs et al. (2006), which came from the OCCAM OCGM, and comparing the performance of the model, both at the scale of spot time series and at the domain scale. The NEMO transport fields and deep temperatures were maintained in this sensitivity analysis.

First, we compared the time series for C5 and adults at the probe locations for *C. finmarchicus* (Figure 6.11). The model performed less well in comparison with CPR data (the correlation coefficient declined from 0.75 to 0.71), but strikingly the model improved significantly when compared with time series data (the sum of correlation coefficients increased from 2.1 to 2.7). This indicates the choice of OCGM can have a significant influence on the phenology of *C. finmarchicus*.

This is particularly pronounced at OWS M. Seasonal peak of *C. finmarchicus* C5 and adults is approximately 50 d later in our baseline model run than in the run using OCCAM surface temperatures. Surface temperatures for the NEMO model are significantly lower, which results in longer development times and hence a delayed seasonal peak. Comparison of model temperatures with physical measurements at OWS M indicates that the OCCAM model is more realistic at this location, with NEMO temperatures being approximately 2°C lower than was recorded at OWS M in 1997 by Irigoien et al. (1998). The inability of our model to reproduce the seasonal peak in *C. finmarchicus* abundance at OWS M therefore appears to largely be a result of spatial biases on the NEMO model.

In most of the other probe locations the sensitivity of phenology to OCGM is less pronounced. However, the scale of peaks can vary significantly using NEMO and OCCAM. Peak abundance at Murchison is approximately 2 times greater when using NEMO surface temperatures. In contrast, OWS I sees a peak abundance 2 times greater when the surface temperature from OCCAM is used.

We then explored the sensitivity of large scale differences to choice of OCGM by considering phenology. This was done by mapping the difference in timing of seasonal peak in total C5 and adults when using NEMO and OCCAM. Figure 6.12 shows phenology of *C. finmarchicus* using NEMO and OCCAM surface temperatures, and also shows temperature differences between NEMO and OCCAM.

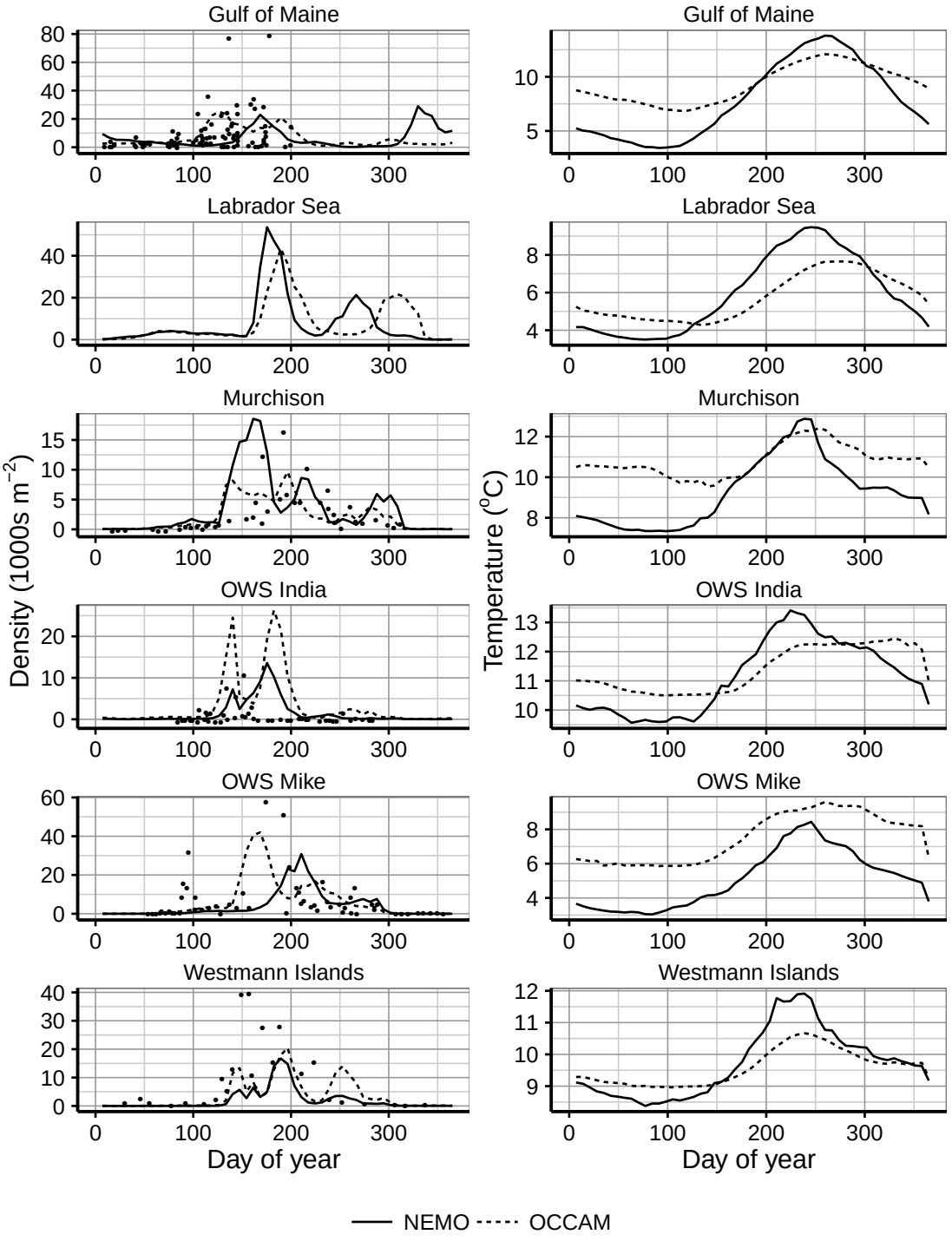


FIGURE 6.11: Comparison of *C. finmarchicus* model predictions using Nemo and Occam models as surface temperature. Left panel is predicted abundance at time series locations of C5 and adults using each OCGM. Right panel is modelled temperature at these locations using each OCGM.

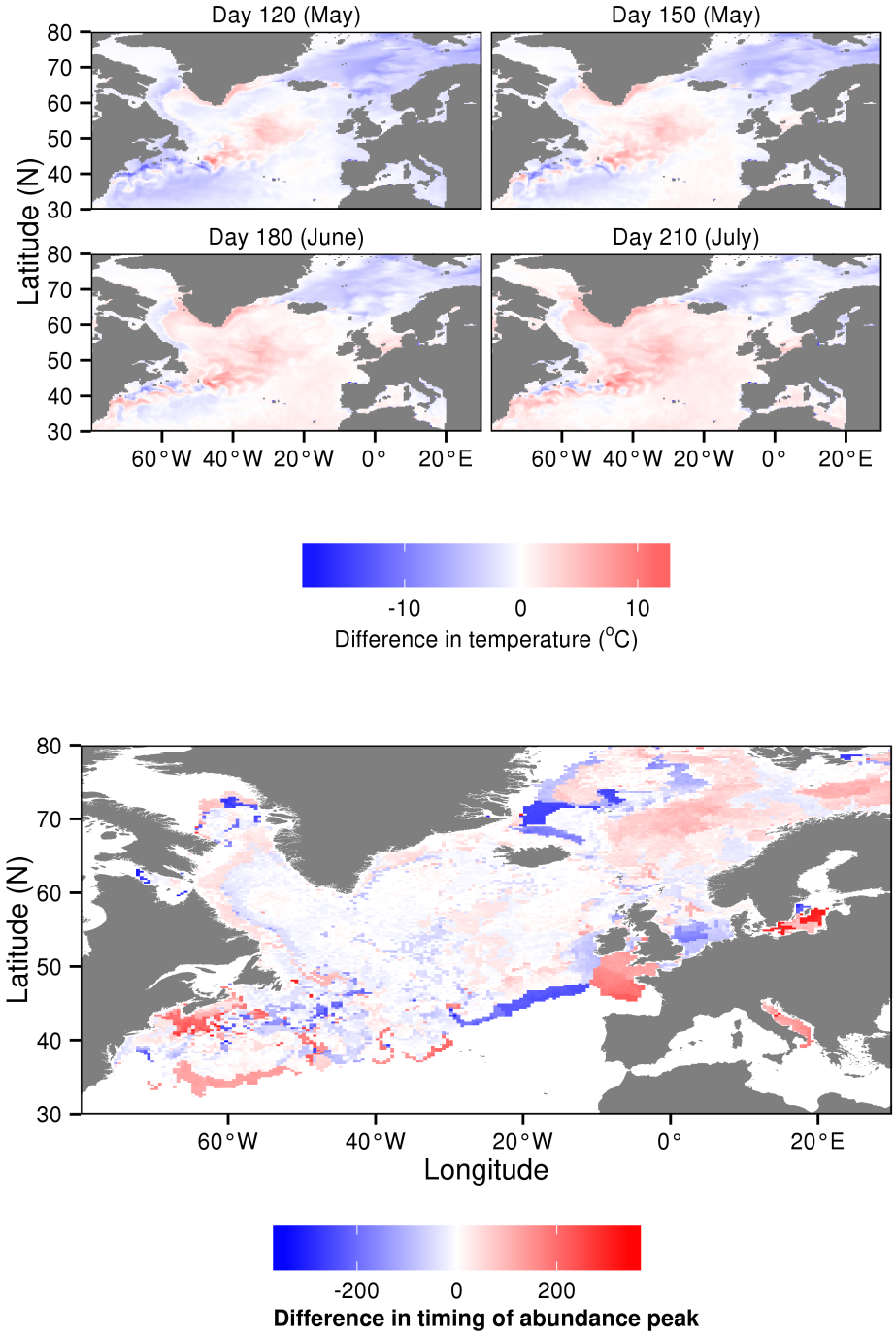


FIGURE 6.12: Mapped difference in timing of day of abundance peak of C5 and adults for *C. finmarchicus* when the model is run using NEMO and OCCAM temperatures. Red means that abundance peaked later in the NEMO run.

Figure 6.12 shows significant spatial differences in the temperature predictions of the OCCAM and NEMO models. In particular, there is a notable departure between the models north and south of the Iceland-Scotland ridge. North of the ridge NEMO tends to predict significantly lower temperatures; whereas south of the ridge NEMO predicts higher temperatures. This apparent bias in the NEMO model in the region surrounding OWS M further confirms that the inability of our model to reproduce *C. finmarchicus* phenology near OWS M is probably a result of spatial bias in NEMO temperatures.

We quantified the influence of choice of OCGM by calculating the mean difference in day of peak C5 and adult abundance weighted by total modelled abundance in our baseline model. This indicates that on the scale of the entire model domain the choice of OCGM for surface temperature does not result in significant differences in phenology. Mean difference between the day of peak C5 and adult abundance in the NEMO and OCCAM runs is 3 d. However, the mean absolute difference in day of peak is 30 d. Choice of OCGM therefore appears to have a significant influence on the regional scale behaviour of *Calanus* models.

Finally, we considered the influence of OCGM on body size. Figure6.13 shows the influence of surface temperature on C5 prosome length. Predicted C5 prosome lengths are uniformly larger in the Norwegian Sea, when using NEMO as surface temperature. There is also a notable improvement in the model fit of predicted prosome length with observed. The pattern is less consistent in the West Atlantic. In the Labrador Sea, body sizes are bigger in spring and winter when using OCCAM, but the reverse is true in summer. In addition, when the model is run with OCCAM surface temperatures the R^2 of the linear model relating observed and predicted female prosome lengths improves from 0.24 to 0.33. Body size is therefore significantly influenced by the choice of ocean model.

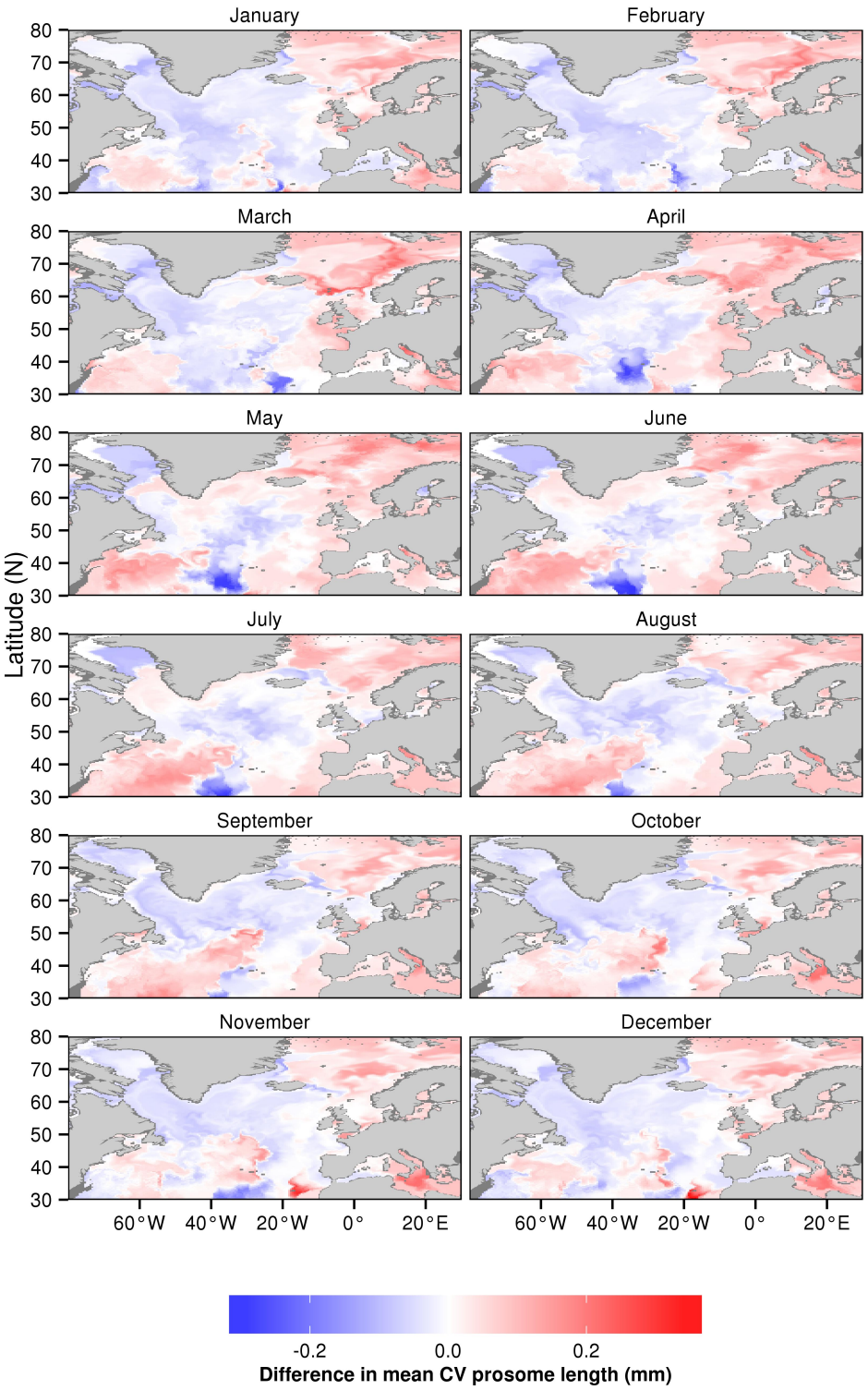


FIGURE 6.13: Mapped difference in C5 prosome length for *C. finmarchicus* when the model is run using NEMO and OCCAM temperatures. Red means that prosome length is larger in the NEMO run.

6.5.2 Diapause

C. finmarchicus

Speirs et al. (2006) modelled diapause assuming that individuals only exited diapause when a particular photoperiod threshold was crossed. This was necessary to reproduce the occurrence of a large number of C5 and adult in the OWS M time series. However, our baseline model uses a purely physiological diapause model, with duration being determined purely by body size and temperature.

This baseline model failed to reproduce C5 and adults at OWS M around day 90. Therefore, we tested the sensitivity of the *C. finmarchicus* model to diapause exit assumptions. 2 runs were performed. One is the baseline model with the addition of the photoperiod cue from Speirs et al. (2006). In the second we assumed that diapause exit was only triggered by photoperiod. Figure 6.14 shows the comparison between the 3 models. The addition of a photoperiod cue alone makes minimal difference to the seasonal cycle at OWS I and Westmann Islands. This indicates that there are very few diapausers remaining in this population after the time of the photoperiod cue. OWS M's seasonal cycle changes notably with the addition of the photoperiod cue. The peak in C5 and adult abundance around day 90 is reproduced successfully, and the peak later in the season is time shifted to earlier in the year.

The Gulf of Maine and Labrador Sea time series see only minor changes to their phenology as a result of these changes. The removal of the physiology cue results in a more pronounced peak in abundance before day 150 for both Westmann Islands and OWS I. This suggests that our model under predicts diapause duration near the Westmann Islands and OWS I; whereas it overestimates diapause duration near OWS M.

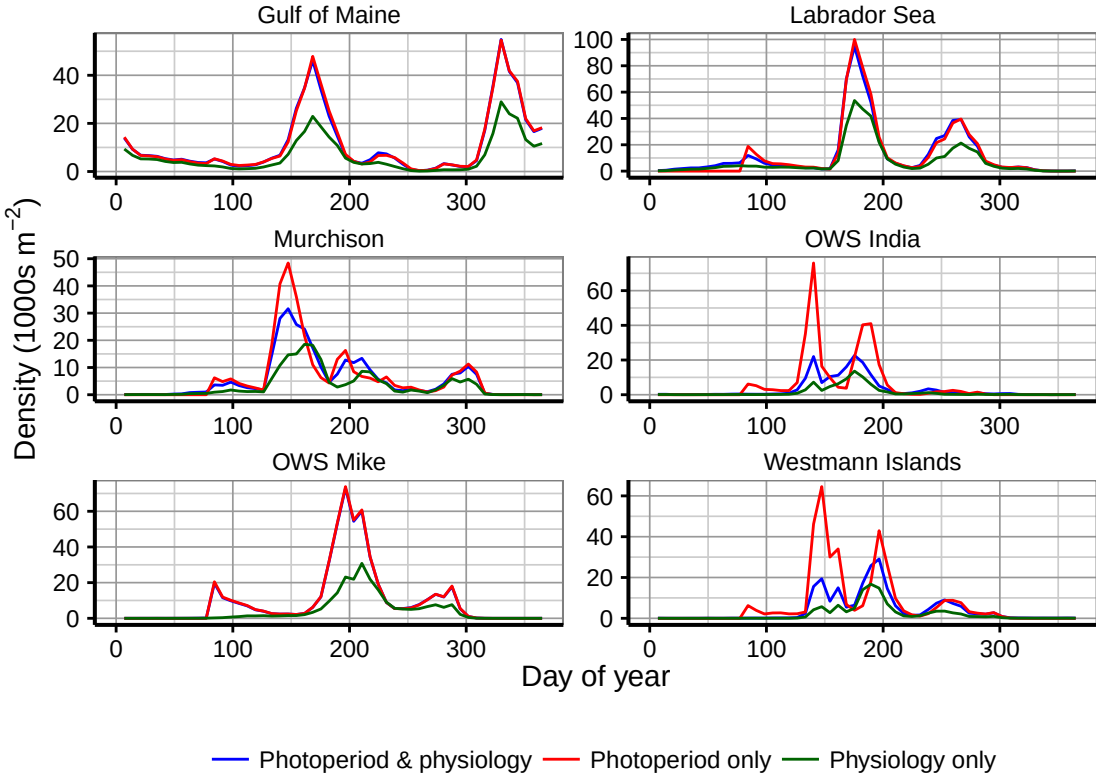


FIGURE 6.14: Comparison of time series data predicted assuming 3 different models of diapause exit. Photoperiod cue means that individuals exit diapause at a time determined by photoperiod. Physiology cue means that diapause duration is determined by body size and overwintering temperature.

C. helgolandicus

A simple question: Does *C. helgolandicus* need to diapause? This question was considered by simply switching off diapause in our *C. helgolandicus* model and considering the effect. This results in a model that performs remarkably well. In fact, it arguably performs better than our baseline model. The key features of the distribution of *C. helgolandicus* are largely reproduced, with the correlation coefficient (0.78) of model performance compared with CPR actually improving in comparison with our baseline model. Figure 6.15 illustrates the annual cycle of combined C5 and adult abundance of *C. helgolandicus* in our baseline model with diapause switched off. The population of *C.*

helgolandicus in the North Atlantic therefore appears to be largely reproducible under the assumption that *C. helgolandicus* does not diapause.

More importantly, the state of North Atlantic populations of *C. helgolandicus* in our baseline model is highly sensitive to assumptions relating to diapause. A sensitivity analysis indicates that small perturbations to the system can result in a switch from *C. helgolandicus* being a shelf to being an oceanic species. Figure 6.16 shows the correlation coefficient between model predictions and CPR under varying assumptions for diapause duration and the scaling of mortality with temperature. Our baseline model shows that the optimal model is when z is approximately 4.1. However, a marginal reduction in z results in a drastic reduction in the performance of the model, with *C. helgolandicus* becoming an oceanic species. Notably, the high sensitivity to perturbations is not evident in the model run when diapause duration is 60% of that in the baseline model.

In contrast, the model of *C. finmarchicus* is relatively insensitive to changes to the temperature scaling of mortality. Figure 6.17 shows that the correlation coefficient between model predictions and CPR essentially varies continuously as z is varied.

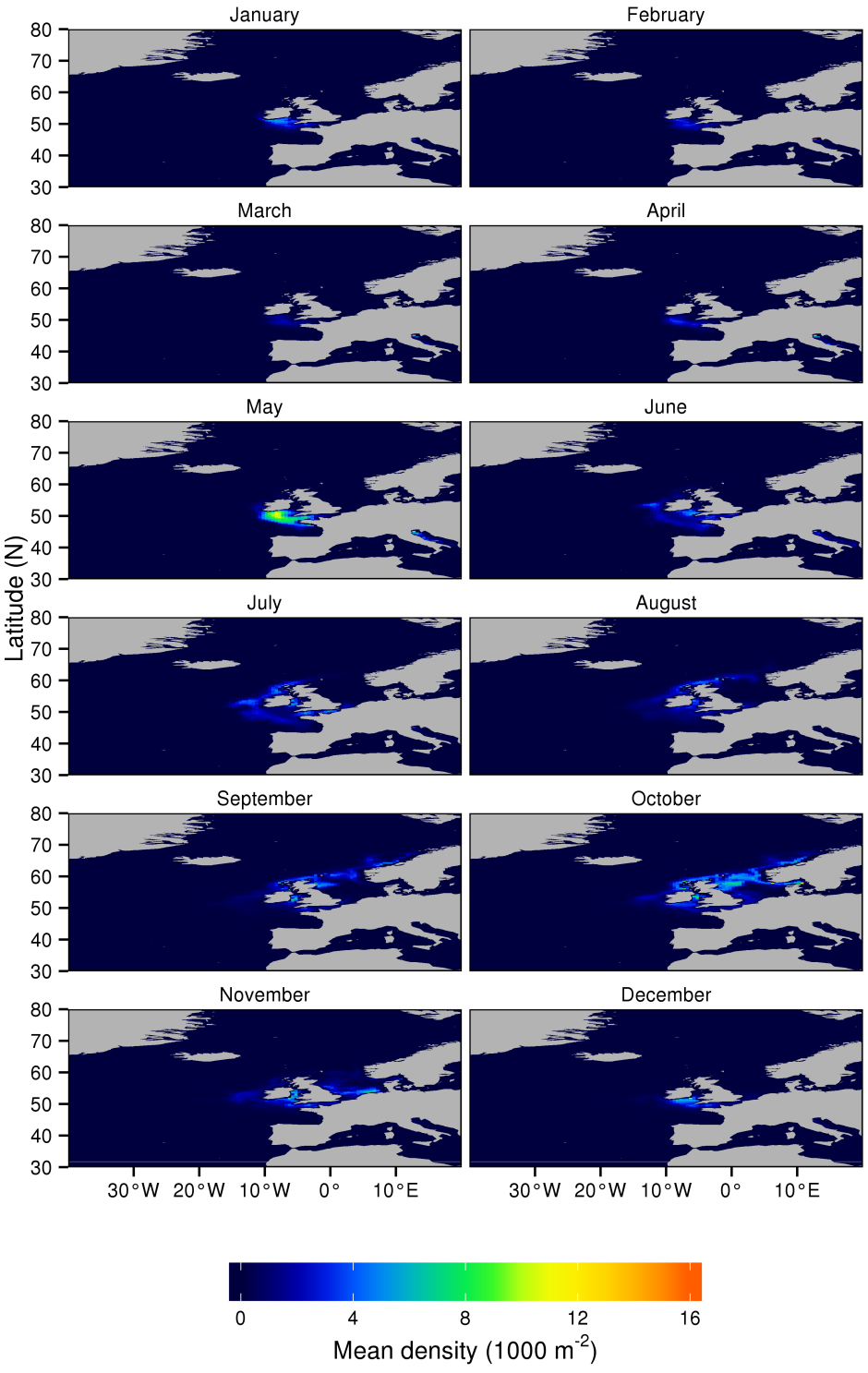


FIGURE 6.15: Seasonal cycle of *C. helgolandicus* abundance in baseline model without diapause. In this model run *C. helgolandicus* remains surface waters year round.

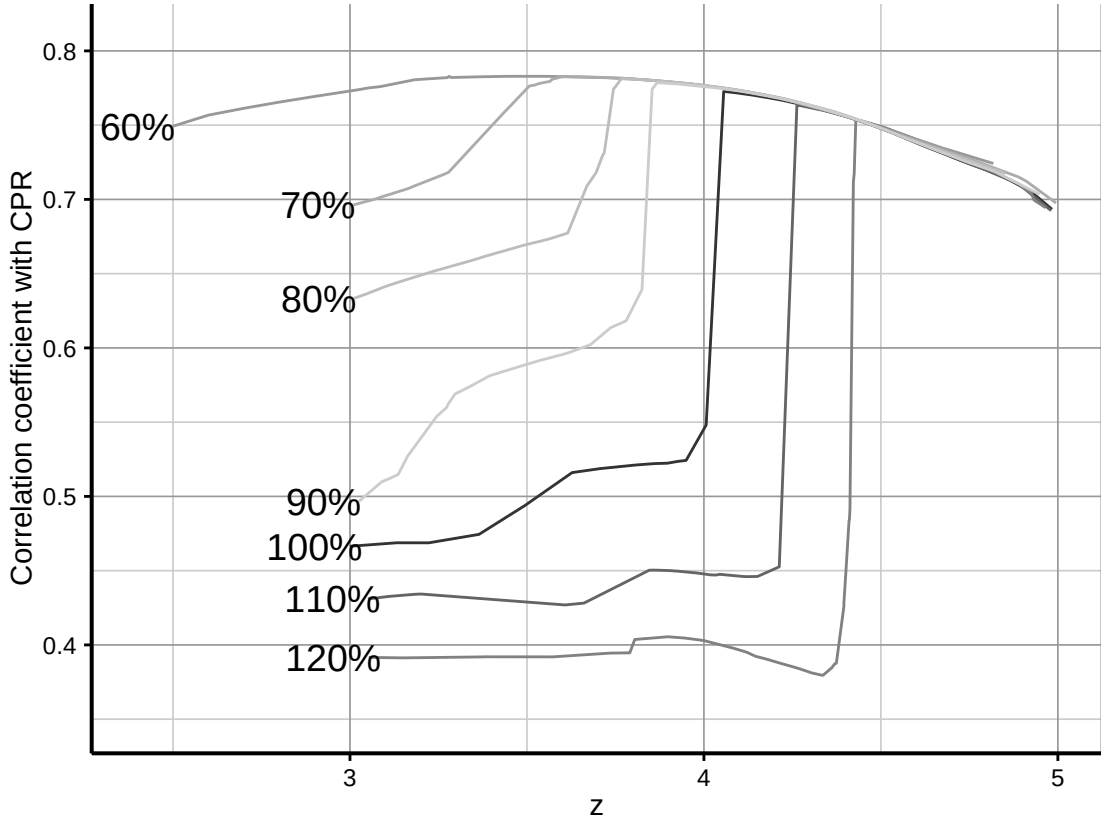


FIGURE 6.16: Sensitivity of *C. helgolandicus* model to diapause duration. Diapause duration was altered by a fixed percentage throughout the model domain, and the temperature scaling of mortality was varied. Abrupt changes in model fit close to the optimum indicates that *C. helgolandicus* switches from being a shelf to an oceanic species.

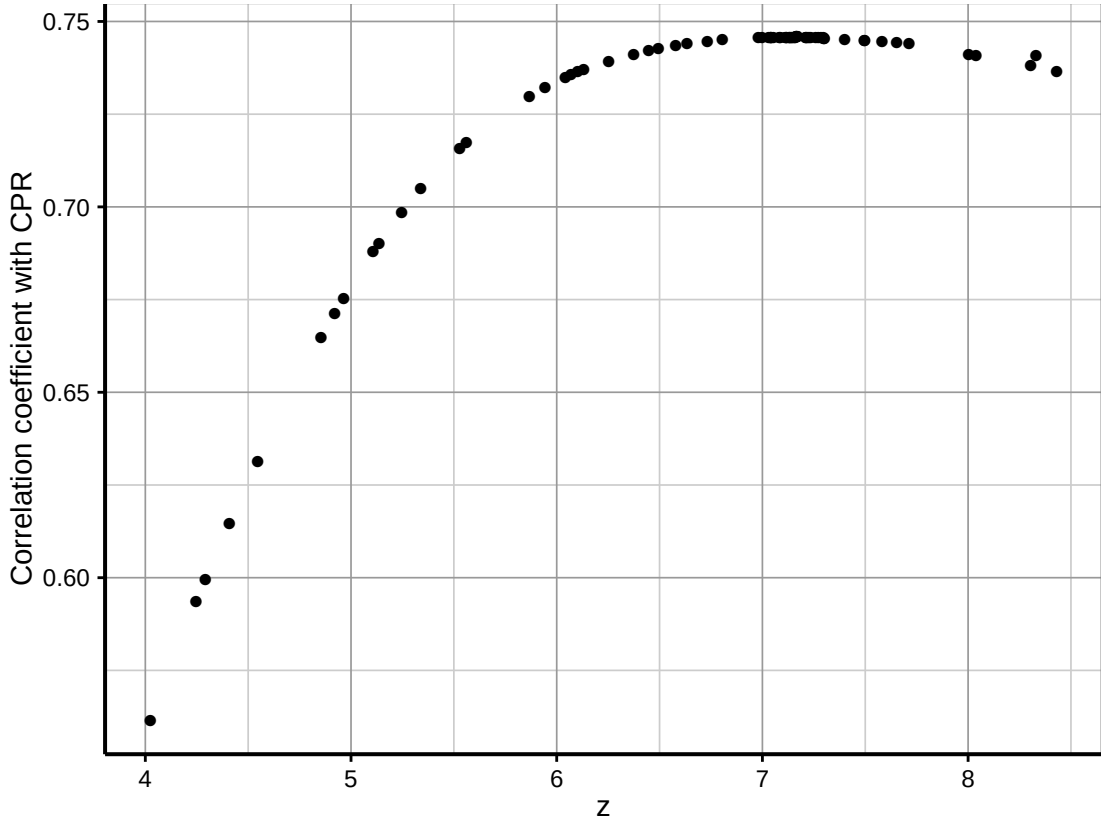


FIGURE 6.17: Sensitivity of *C. finmarchicus* model to scaling of mortality with temperature. Reductions to z lowers mortality at high temperatures and results in *C. finmarchicus* having a too southerly distribution.

6.6 The role of transport for *C. helgolandicus* in the North Sea

Previous modelling and field research has demonstrated that the *C. finmarchicus* population in the North Sea is highly dependent on the transportation of diapausing populations into the North Sea through the Faroe-Shetland Channel (Heath and Jønasdøttir, 1999; Heath et al., 1999; Heath, 1999). However, it is unclear what the source of the autumn bloom in *C. helgolandicus* is. This population may result from in situ production or it may result from transportation of populations into the North Sea.

We partially address this question by performing model runs where transport is shut down at the northwest entrance to the North Sea. This is only a partial and tentative answer because our *C. helgolandicus* failed to reproduce the apparent spring bloom of *C. helgolandicus* in Stonehaven.

First, we ran our baseline model to a steady state, and then in the next year we shut down transport as shown in Figure 6.18. There were four scenarios. Transport was blocked from weeks 26, 30, 34 and 38 onwards. Blocking transport from day 182 results in a drastic reduction in the autumn bloom of *C. helgolandicus* at Stonehaven. Blocking transport after day 210, approximately 70 d before the bloom, results in a significant reduction in the bloom. This implies that a large proportion of the autumn *C. helgolandicus* bloom results from transportation of populations into the North Sea from the northwest.

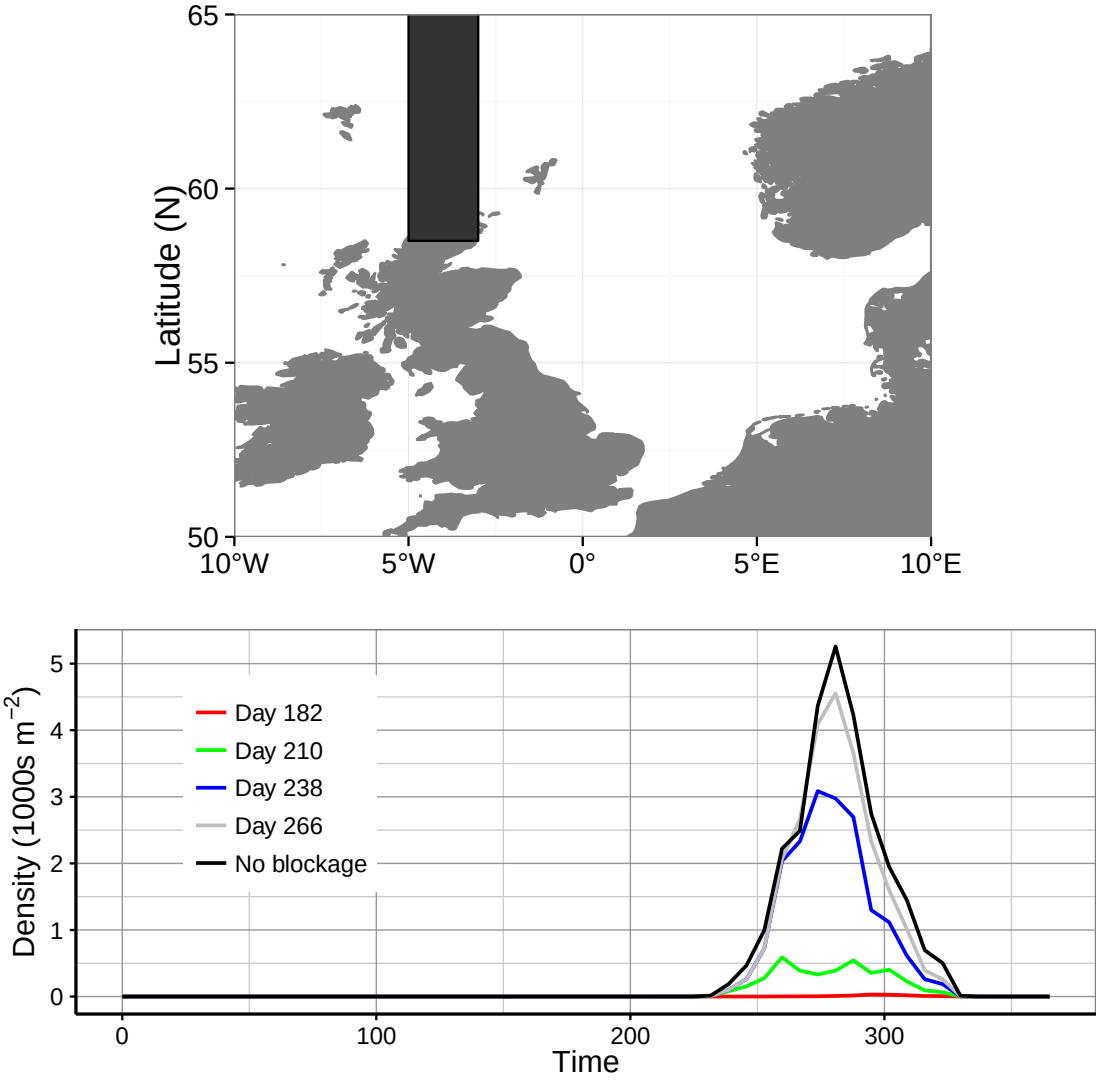


FIGURE 6.18: Impact of blocking transport into the North Sea on the Stonehaven time series. Model was run to a steady state and then transport was blocked from weeks 182, 210, 238 and 266 onwards respectively. Time series shows model predictions in first year block is applied. The black area in the map is the area where transport is blocked.

6.7 Conclusions

The key conclusions of this chapter are as follows:

- The baseline models are shown to provide successful reproductions of the geographic distributions of both species.
- The seasonal cycles predicted for both species are credible when compared with field data at time series locations.
- The abundance and geographical distribution of *C. finmarchicus* diapausers are reasonable in comparison with field data.
- Our prosome length provides realistic predictions of female prosome length for *C. finmarchicus*.
- Egg production rate predictions are reasonable. However, our model significantly over predicts *C. helgolandicus* egg production rate in the second half of the year in comparison with field estimates from L4 in the English Channel.
- Model runs using the surface temperatures from the OCCAM OCGM instead of the NEMO OCGM provide more realistic predictions of *C. finmarchicus* seasonality at OWS Mike. This highlights the impact biased OCGM's can have on the predictions of zooplankton population models.
- Geographical distribution of *C. helgolandicus* is very sensitive to diapause duration assumptions, with small increases in diapause duration resulting in it becoming an oceanic species. This shows the importance of better quantification of *C. helgolandicus*'s diapause capabilities.
- A run where we switched off transport into the North Sea demonstrates that a large part of the autumn bloom in *C. helgolandicus* is a result of advection of populations into the North Sea.

Chapter 7

Predicting the future distribution of *C. helgolandicus*: challenges and uncertainties

To date, there have been a limited number of studies of the impact of future climate change on populations of *C. finmarchicus* and *C. helgolandicus* (Maar et al., 2013; Skaret et al., 2014; Reygondeau and Beaugrand, 2011). However, none of these studies has considered the potential future changes in the geographic distribution of *C. helgolandicus*. In fact, our modelling study is the first model of the large scale geographic distribution of *C. helgolandicus* in the North Atlantic.

Increased oceanic temperatures are almost certain to result in a further northward shift in the distribution of *C. helgolandicus*. However, a more fundamental question is whether *C. helgolandicus* will remain a shelf species, or if it will become an oceanic species in response to climate change. Any forecast of the future distribution of *C. helgolandicus* will be uncertain. And this chapter will not make specific forecasts. Instead,

it will consider the uncertainties that need to be resolved before we can make reasonably confident forecasts of the change in the distribution of *C. helgolandicus* under future climate change. These uncertainties have two key elements: our relatively poor understanding of mortality and of diapause behaviour in *C. helgolandicus*.

7.1 A conceptual view of the difference between an oceanic and shelf *C. helgolandicus*

A simplified phenology of *C. helgolandicus* helps us understand the potential causes of *C. helgolandicus* being a shelf species. In this simplified view, life for *C. helgolandicus* simply consists of two parts, a reproductive season and a diapause season.

This reproductive season is spent in surface waters, while the diapause season is spent in deep waters. For *C. helgolandicus* to persist in a particular region, the reproductive season and the diapause season must overlap, otherwise there will be no diapause population to become the reproductive population.

This conceptual view helps clarify the potential impacts of increasing oceanic temperatures at high latitudes. Increases in temperature will result in a lengthening of the reproductive season for *C. helgolandicus*. However, increases in temperature in deep waters will reduce the diapause season. The probability of *C. helgolandicus* becoming an oceanic species therefore may largely result from the relative changes in surface and deep temperatures in oceanic regions, and also the changes in surface food availability.

7.1.1 Simplified forecasts of the influence of climate change on *C. helgolandicus*

Recent and future oceanic warming has not and will not be uniform (Collins et al., 2013). Regions of the North Atlantic may warm significantly less than other regions,

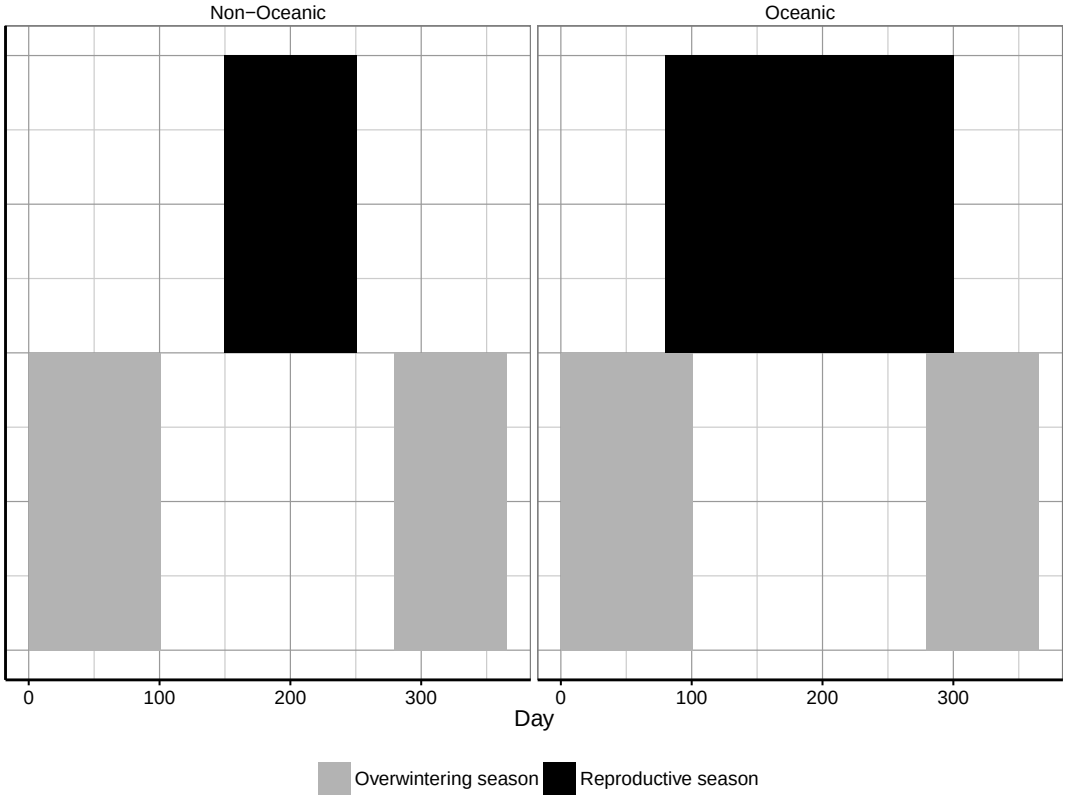


FIGURE 7.1: A simple conceptual model of the difference between an oceanic and non-oceanic *Calanus* species. Phenology is divided into two parts: diapause and reproductive seasons. These periods must overlap for a species to be oceanic.

or even cool (Drijfhout et al., 2012). Warming at surface and deep waters will occur on different time scales, with warming lagging that in warmer waters (Li et al., 2013). In addition, weakening of the Atlantic Meridional Overturning Circulation (AMOC) may result in cooling in some high latitude regions (Banks and Gregory, 2006). These complexities are likely to result in difficult to predict regional changes in *Calanus* communities, but it is relatively clear that they will result in general northward shifts in distributions (Reygondeau and Beaugrand, 2011). A key question is whether these distribution shifts will result in large scale regime shifts (Rocha et al., 2014) and whether there will be a tipping point which results in *C. finmarchicus* becoming an oceanic species.

The existence of tipping points in ecological systems at a global scale is an issue of

current scientific controversy; however their existence at local and regional scales is less so (Brook et al., 2013; Lenton and Williams, 2013). In the marine environment local regime shifts are typically related to abiotic and biotic processes and changes to habitat (DeYoung et al., 2008). In the case of *Calanus*, the regime shift in the North Sea has been linked to changed oceanic temperatures (Lindley and Reid, 2002).

However, tipping points are both hard to predict and understand (Boettiger and Hastings, 2013). Put simply, we often have a poor understanding of why an ecosystem is in its current state, and predicting the future will therefore not be easy. There is a reason why some researchers prefer to talk of anticipating and not predicting tipping points (Scheffer et al., 2012). And this is true for *Calanus*. Our model shows that we have a poor understanding of what limits the southern distribution of *C. finmarchicus*. Similarly, we are not fully confident of what causes *C. helgolandicus* to be restricted almost entirely to shelf regions. Predictions of the future should be made cautiously.

Can we predict whether future ocean warming will create a tipping point beyond which *C. helgolandicus* becomes an oceanic species? The influences of future climate change are likely to have a number of key influences on *C. helgolandicus*. Surface warming is likely to significantly reduce its development times at the northern fringe of its distribution. Surface warming in northerly regions, then, improves conditions for *C. helgolandicus* development. However, surface warming will also reduce the size of *C. helgolandicus*, which will reduce its diapause duration. Similarly, any warming in deep water will further reduce *C. helgolandicus*'s diapause duration. The ability of *C. helgolandicus* to become an oceanic species will therefore rest on the combined effects of improved development conditions at the surface and potentially worsened diapause conditions.

We will now consider what happens to the distribution of *C. helgolandicus* under simplified climate change scenarios. Four scenarios were run: uniform warming of surface

waters in the North Atlantic of 1 and 2°C, with either no deep water cooling or an identical amount of deep warming. In all cases, development time, diapause duration and all other temperature-dependent processes were driven by the modified temperatures.

The model used is our baseline model. However, the baseline model showed sensitivity to the temperature scaling of mortality. We therefore run all of our scenarios using a range of temperature scalings for mortality. As with our original model, we report the correlation coefficient of the model in comparison with CPR. This metric indicates when C. helgolandicus becomes an oceanic species. The results are shown in figure 7.2.

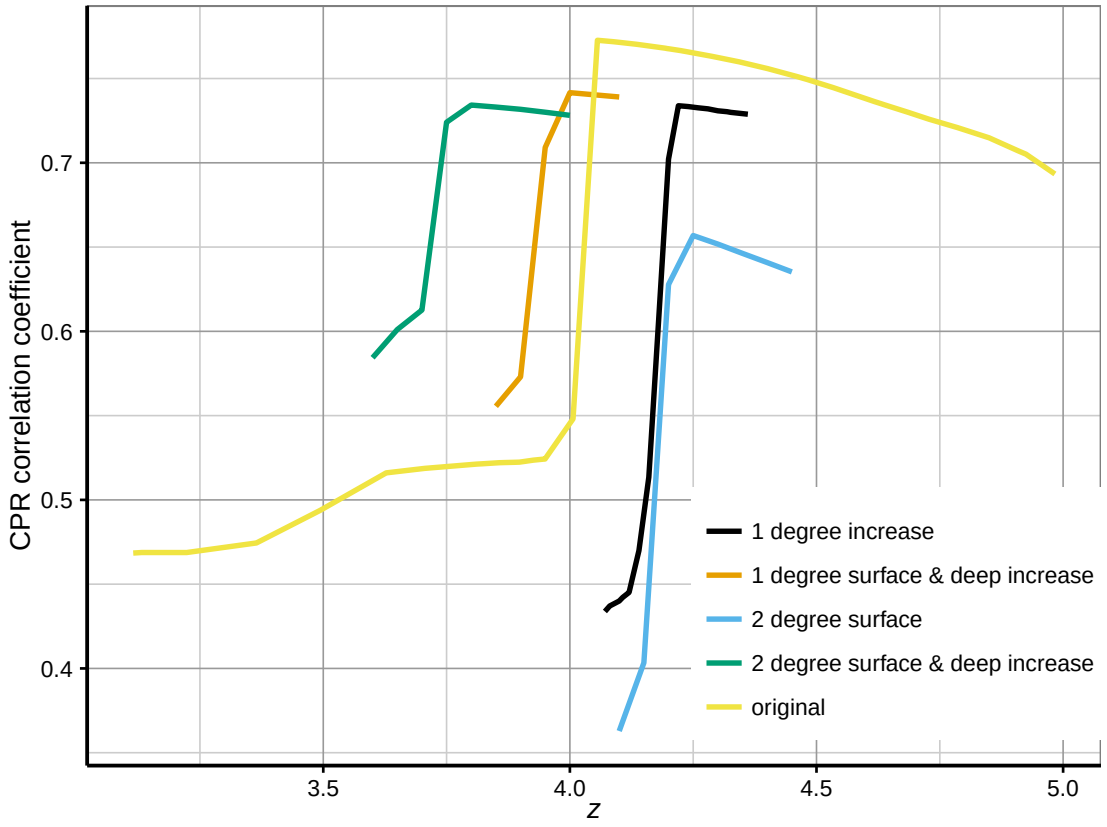


FIGURE 7.2: The influence of increased oceanic temperature on the distribution of *C. helgolandicus* under simplified climate change scenarios. Results shown are the correlation coefficient between CPR abundance and the temperature scaling of mortality.

If temperatures increase by the same amount in surface and deep waters, then *C. helgolandicus* remains a shelf species. However, when surface warming exceeds deep

warming by 1 or 2°C, then C. helgolandicus may become an oceanic species. However, this is sensitive to the assumptions relating to temperature dependent mortality.

This sensitivity appears to disappear when we assume that *C. helgolandicus* can diapause for a shorter period of time. Reducing diapause times by 40% results in a model where minor perturbations to mortality do not result in a state shift from *C. helgolandicus* being a shelf to being an oceanic species.

7.1.2 Limits of niche models

These deep uncertainties indicate that we should not rely too heavily on conventional ecological niche or species distribution models when predicting the future distribution of *C. helgolandicus*. Ecological niche modelling, such as we performed in chapter 3, is almost certain to be unable to predict *C. helgolandicus* becoming oceanic. The restriction of *C. helgolandicus* to the continental shelf is likely to be a forced feature of any such model. The limits of species distribution models to predict shifts in distribution under climate change has long been discussed in the literature (Davis et al., 1998), with some researchers suggesting that traditional species distribution models should be combined with process based models when assessing the potential future shift in species distributions (Morin and Thuiller, 2009). This seems to be a sensible path to pursue. However, we cannot make particularly strong claims for the advantages of using our model of *C. helgolandicus* to predict its future distribution.

A similar northward shift in the distribution of *C. finmarchicus* is expected. However, we must recognize the failure of our model to give a satisfying explanation of the reasons for the current distribution of *C. finmarchicus*. Something limits the southern distribution of *C. finmarchicus*, but we do not understand what. Our model is similar to (Speirs et al., 2006) in that we assume that mortality increases rapidly at higher temperatures. This is arguably nothing more than a mathematical construction put in

place to stop *C. finmarchicus* going too far south. However, without it, *C. finmarchicus* will go too far south.

Our model indicates that the future distribution of *C. helgolandicus* may be particularly sensitive to predation pressures, which are influenced by anthropogenic influences (Richardson, 2008; Berge et al., 2012). However, the influence of predation pressures is often poorly understood. Berge et al. (2012) have argued that Arctic *Calanus* communities were shaped heavily by the existence of baleen whales.

7.2 Projected changes in North Atlantic temperatures under a high green house gas emissions scenario

We will now briefly consider projected changes in North Atlantic ocean temperatures, and how they may impact *C. helgolandicus*. Our aim here is to highlight possible future directions for research.

The future evolution of atmospheric and oceanic temperatures is generally considered using the IPCC's Reference Concentration Pathways (Moss et al., 2010). These scenarios cover a range of possible futures, and it is questionable to attach a probability to any of them. Long term changes in atmospheric concentration of greenhouse gases will be determined largely by changes in patterns of global energy consumption, but our ability to forecast future changes in global energy with confidence is limited (Smil, 2000). This can be demonstrated most starkly by comparing previous forecasts of China's future CO_2 emissions with what they actually are today. In 1999, the International Energy Agency (IEA) forecast that China's energy related CO_2 emissions would reach 5.3 Gt CO_2 in 2010 and 7.1 Gt CO_2 in 2020 (Birol and Argiri, 1999). However, China's actual energy related CO_2 emissions had reached 8.3 Gt CO_2 by 2010 (Boden et al., 2010), which was 57% higher than forecast by the IEA.

Here we consider changes in oceanic temperatures when atmospheric conditions match those in the IPCC Reference Concentration Pathway (RCP) 8.5. Of the IPCC RCP scenarios (Meinshausen et al., 2011), this is a relatively high greenhouse gas emissions scenario (Riahi et al., 2011). Global primary energy supply rises from approximately 400 EJ in 2000 to 17,000 EJ in 2100, with annual anthropogenic CO_2 emissions rising from just over 20 Gt CO2 in 2000 to just over 80 Gt CO_2 in 2100 (Riahi et al., 2011). Atmospheric CO_2 levels therefore rise from current levels of approximately 400 ppm to approximately 950 ppm in 2100 (Meinshausen et al., 2011).

Yool et al. (2013) used the RCPP 8.5 scenario to estimate future oceanic temperatures. The projected changes in surface and deep water temperature between 2000 and 2099 are shown in figure 7.3. There are a number of noticeable features. Oceanic warming is not uniform. Most notably, the Norwegian Sea experiences cooling in deep waters in contrast to most of the rest of the North Atlantic.

The region close to the Gulf of Maine sees extreme levels of warming, which may have a significant influence on *C. finmarchicus* populations. In addition, large parts of the Mid Atlantic do not see significant warming in spring, which is likely to limit the possibility of *C. helgolandicus* surviving in these regions.

These changes in conditions are best illustrated with reference to OWS M (Figure 7.4). Temperatures during the reproductive season increase by approximately 3°C. In fact, temperatures in this region in 2099 become comparable with those in the Celtic Sea today. In contrast, temperatures in deep water slightly decrease. Surface conditions therefore appear to improve significantly for *C. helgolandicus*, whereas deep water conditions stay approximately the same.

We hypothesize that these conditions in the Norwegian Sea are possibly sufficient for *C. helgolandicus* to no longer be restricted to shelf regions in a future warmer Atlantic. The high levels of warming in surface waters, but slight cooling in deep waters will significantly improve conditions for *C. helgolandicus* populations in the North Sea. Future

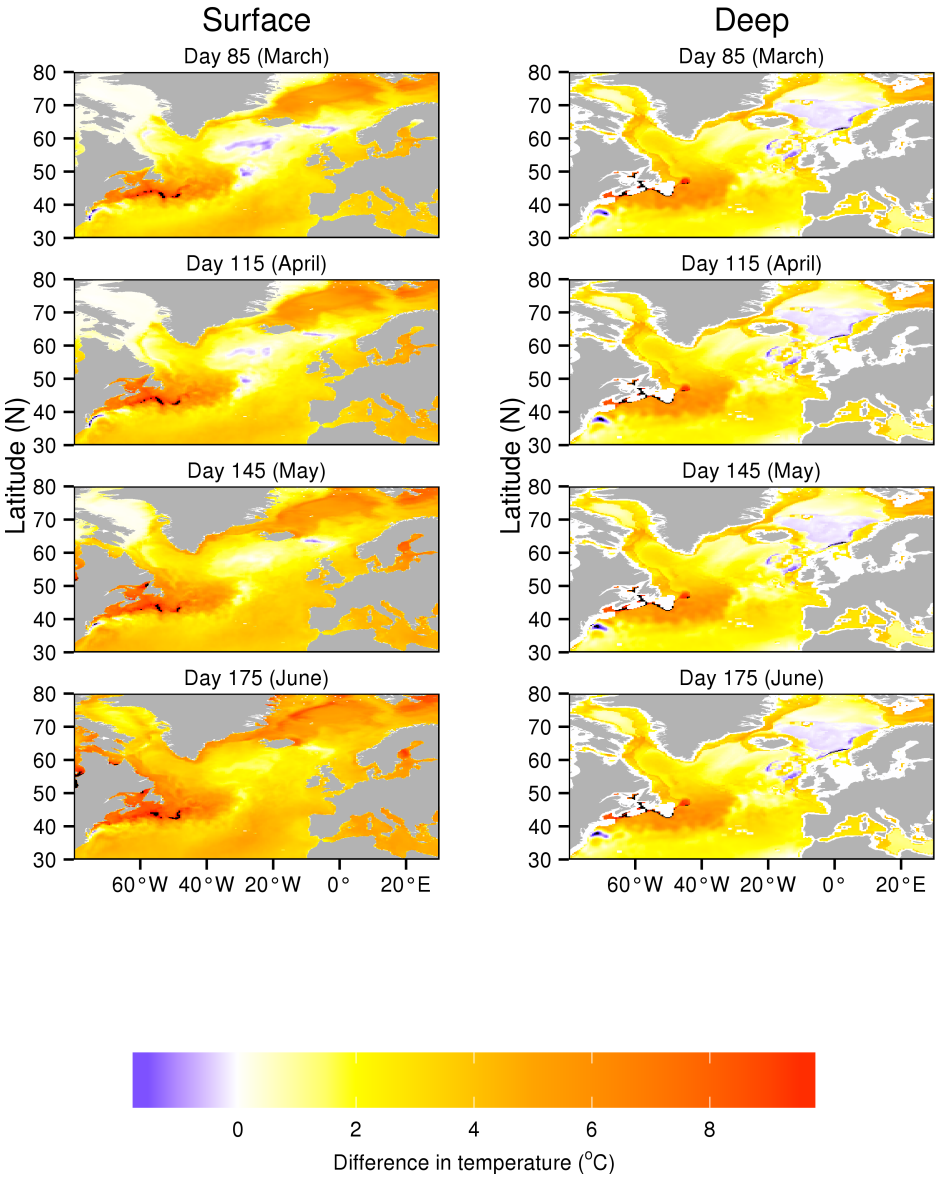


FIGURE 7.3: Changes in decadal average oceanic temperature (2000-2009 to 2090-2099) using IPCC RCP8.5. Details of the model forcings and set up are given in Yool et al. (2013).

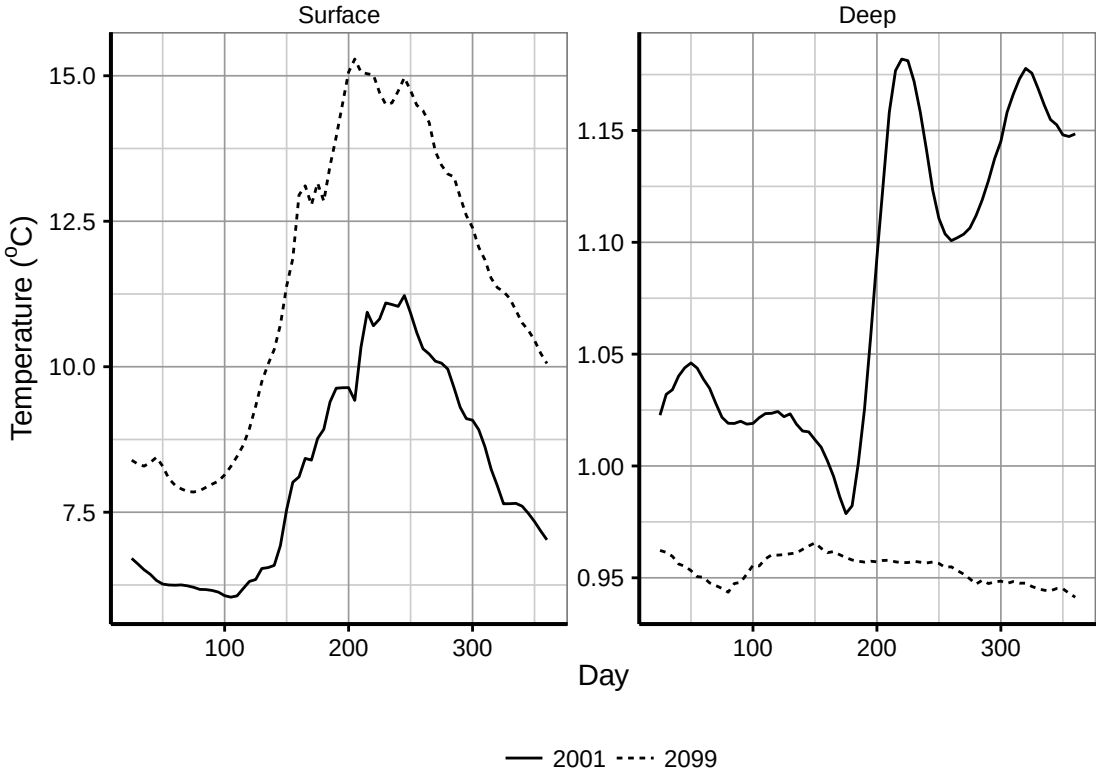


FIGURE 7.4: Projected changes in oceanic temperature at OWS M in the Norwegian Sea from 2000 to 2099 under IPCC scenario RCPP8.5.

modelling studies may help to resolve this question. However, an important knowledge gap is the diapausing capabilities of *C. helgolandicus*. A fuller understanding of lipid levels accumulated by *C. helgolandicus* in northern regions and the diapause respiration rates of *C. helgolandicus* are needed.

7.3 Conclusions

The key conclusions of this chapter are as follows:

- We used a simple climate change scenario to show that predicted changes in the distribution of *C. finmarchicus* are highly sensitive to the assumptions used for mortality and diapause.
- Considerations of future surface and deep temperatures in the Norwegian Sea highlight the possibility that C. helgolandicus may become an oceanic species in this region.

Chapter 8

Population model discussion

The underlying goal of what has come before has been to answer a simple question: Why do *C. finmarchicus* and *C. helgolandicus* have distinct geographical distributions? We have created a model which reasonably successfully reproduces the geographic distribution. It does so under the assumption that a difference in the response of mortality with temperature is the only interspecies difference, with the exception of those indicated by our review in chapter two. We will now critically evaluate what our model does and does not tell us, and highlight the areas of the biology of both species that need to be more fully understood.

8.1 Mortality

In chapter two we suggested that the apparent U-shaped response of development time to temperature result in *C. finmarchicus* and *C. helgolandicus* being restricted to specific temperature bands. Further, we hoped that each species' geographic distribution could largely be explained with reference to its development time. Similarly, we hoped that the very pronounced influence of temperature on mortality assumed by Speirs et al. (2006) could be dispensed with. This hope was not borne out.

Instead, we essentially maintained the temperature dependence of mortality used by Speirs et al. (2006) for *C. finmarchicus*. Restricting the distribution of *C. finmarchicus* to plausible regions still requires an ad hoc formulation of mortality, where mortality increases rapidly at higher temperatures. We were therefore unable, against our hopes, to provide a more biologically grounded explanation for the southerly limit of *C. finmarchicus*'s distribution. Our model therefore disappointingly fails to advance our understanding of what limits the southern distribution of *C. finmarchicus*.

8.1.1 Comparative mortality

To achieve credible predictions of the geographic distribution of both species we were forced to assume that the scaling of mortality with temperature was much greater in *C. finmarchicus* than in *C. helgolandicus*. This is deeply unsatisfying, but without advances in our understanding of what limits the southern distribution of *C. finmarchicus* it appears unavoidable.

The problem can be understood by considering the Celtic Sea. Figure 8.1 shows a reconstruction of the Celtic Sea *Calanus* community over the period 1958-2002. The *Calanus* community has been consistently dominated by *C. helgolandicus*, with *C. finmarchicus* populations being so low as to imply they are sink populations. However, the biological and ecological reasons for this are unclear.

Environmental conditions in the Celtic Sea do not appear to favour *C. helgolandicus* over *C. finmarchicus*. In fact, it is arguably the opposite. Figure 8.2 shows the development time from egg to adult implied by our development time models close to L4. With the exception of summer, development conditions appear to be better for *C. finmarchicus* than for *C. helgolandicus* throughout the year.

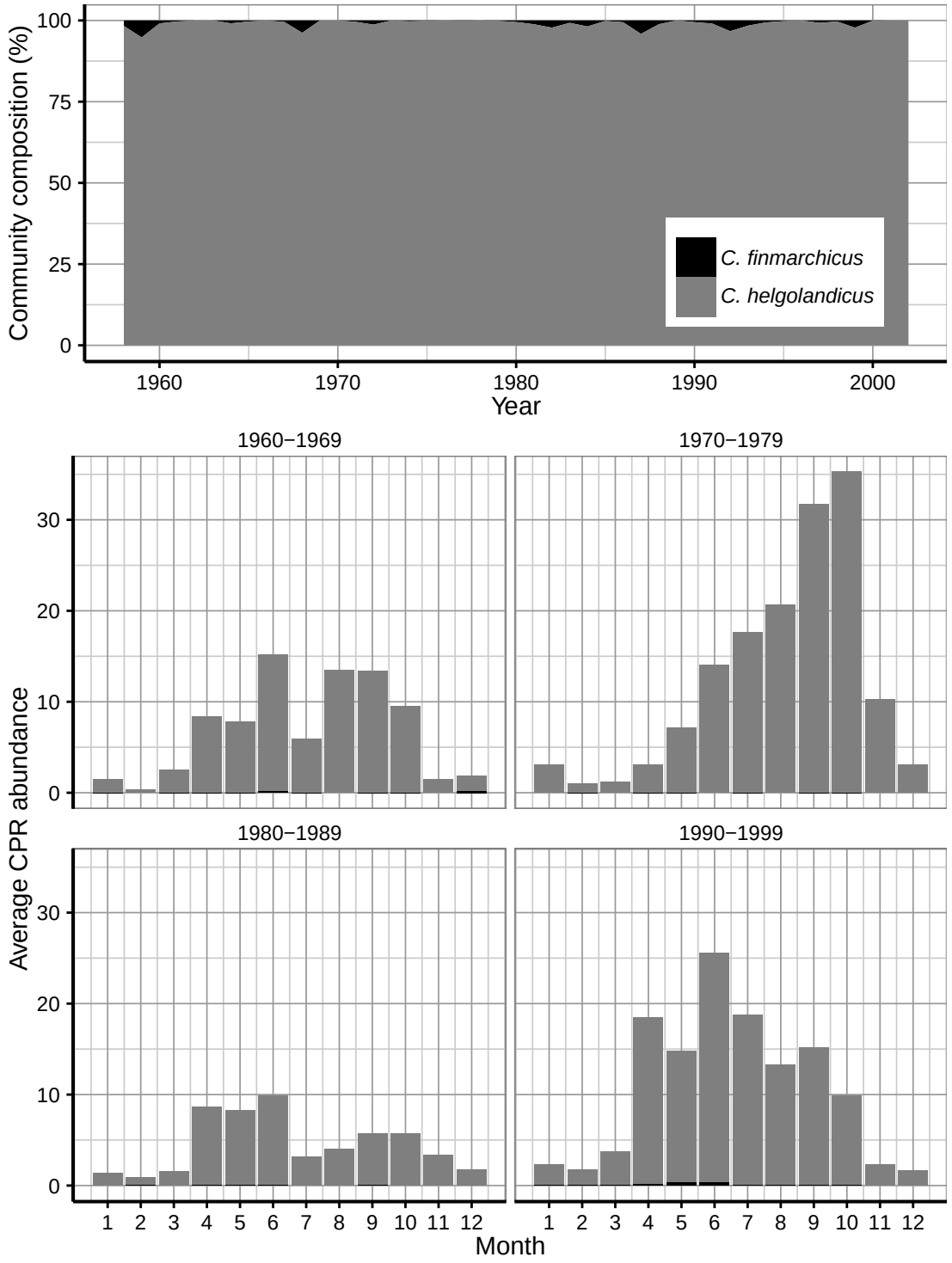


FIGURE 8.1: Long term trend in *Calanus* composition in the Celtic Sea. Trend is derived from combined C5 and adult *C. finmarchicus* and *C. helgolandicus* in CPR data.

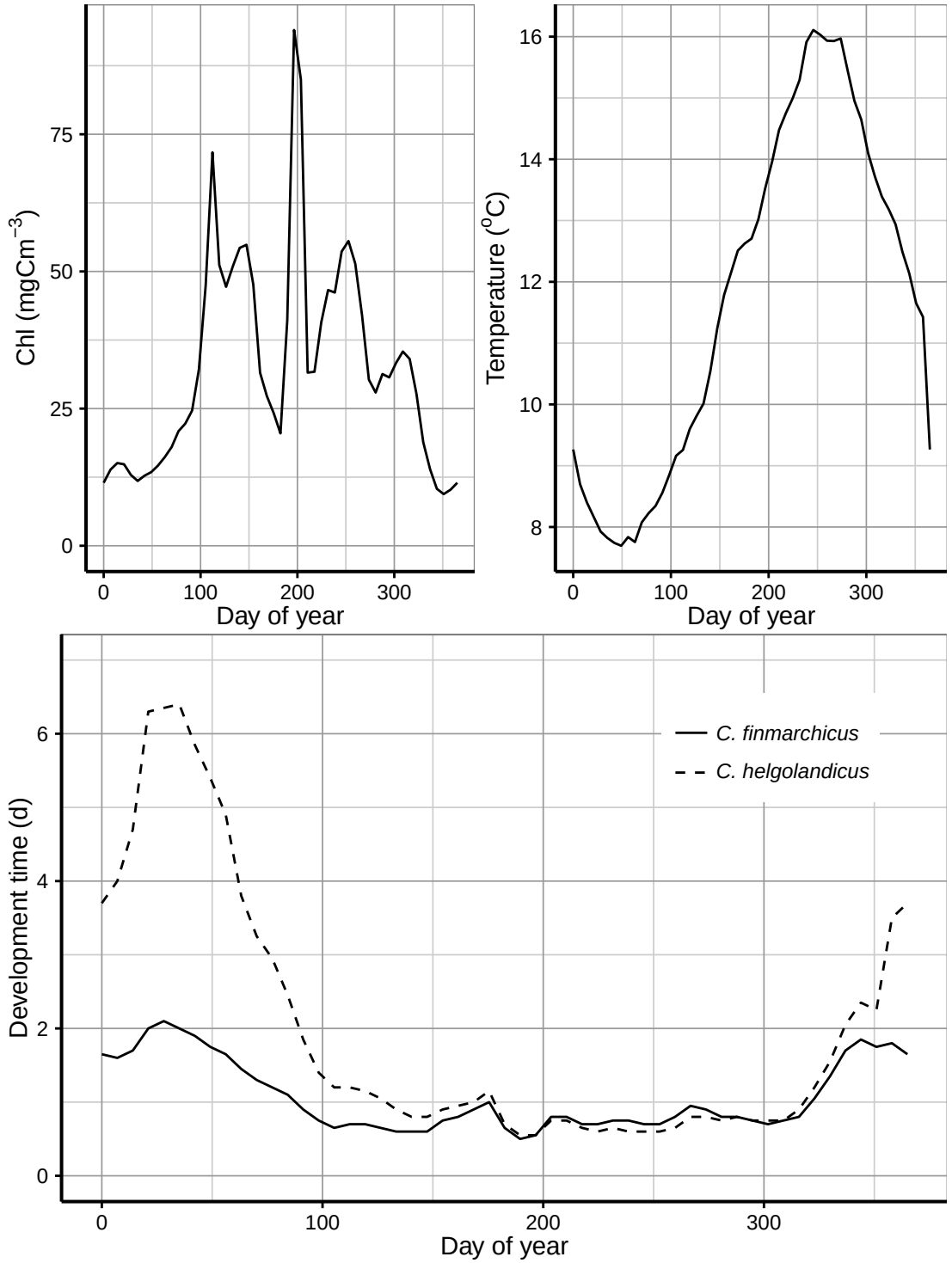


FIGURE 8.2: Comparison of food concentration, sea surface temperature and modelled development times in the model cell closest to the L4 time series.

8.1.2 Egg hatching success

Our model of mortality suggests that populations at the southern fringe of *C. finmarchicus*'s distribution should be very sensitive to increased temperature. However, a recent incidence of extreme warming in the Gulf of Maine did not result in a significant decline in the abundance of *C. finmarchicus* (Runge et al., 2014). Temperatures exceeded 20°C in this region in the summer of 2012, compared with a climatological maximum of 16-17°C (Mills et al., 2013). The co-occurrence of this extremely high temperature and a surface population is inconsistent with the temperature dependent mortality in our model.

Preziosi and Runge (2014) recently found that hatching success of *C. finmarchicus* was significantly reduced at temperatures above 19°C. This effect, if incorporated into our model, is likely to help restrict the southern edge of the distribution of *C. finmarchicus*. Figure 8.3 shows a map of annual maximum temperatures in each cell our model. In the western Atlantic the inclusion of egg hatching success has the potential to successfully restrict the southern limit of *C. finmarchicus*'s distribution. However, in the East Atlantic lowered egg hatching success is unlikely to have any impact at latitudes greater than 42°N. Therefore the inclusion of a temperature dependent hatching success rate in our model is likely to be redundant, as we will still need to maintain the extreme scaling of mortality with temperature.

Published laboratory data is consistent with *C. helgolandicus* not having temperature dependent hatching success rate over ecologically relevant temperatures. Laboratory studies over temperature ranges of 7-13°C (Mayor et al., 2012) and 5-24°C (Laabir et al., 1995) indicate that there is no temperature influence on egg hatching success.

A future *Calanus* model could therefore explicitly model hatching rate as a function of temperature. Hatch rate is likely to have a dome-shaped response with temperature. This is indicated by the work of Preziosi and Runge (2014) and further by work on

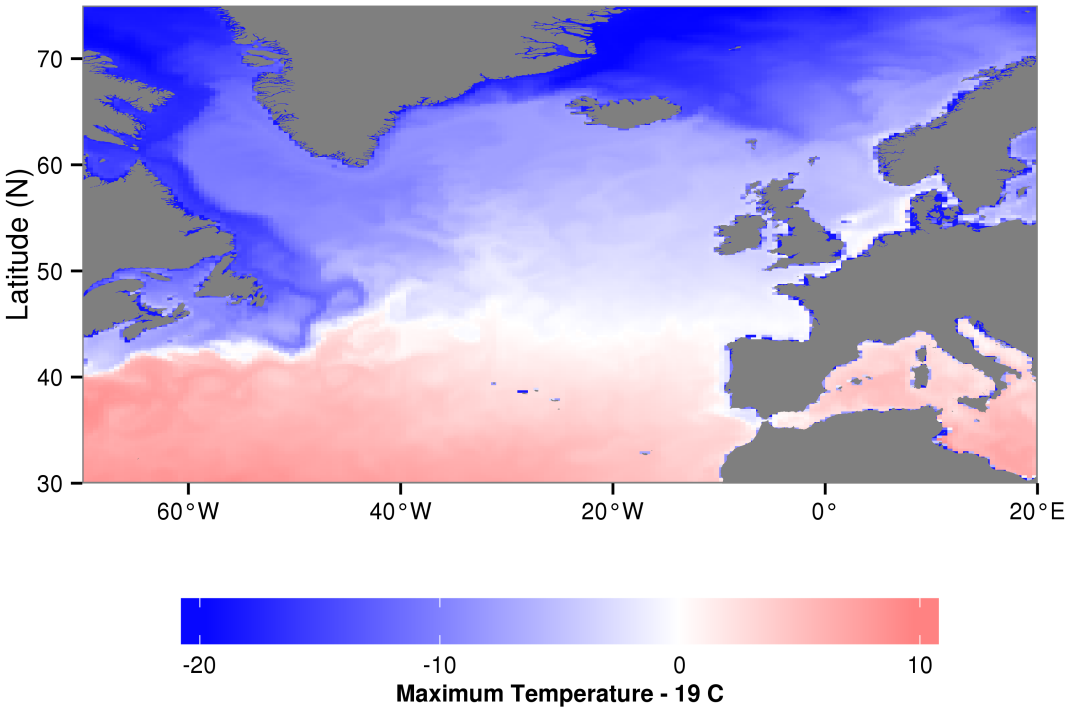


FIGURE 8.3: Mapped annual maximum sea surface temperatures in each model cell less 19°C. Temperatures used are for 1997 using the NEMO OCGM.

Arcatia species (Milione and Zeng, 2008; Holste and Peck, 2006). However, it remains unclear if its inclusion would merit the additional computational expense.

8.1.3 Starvation mortality

A fundamental requirement of our model was to restrict *C. helgolandicus* to shelf regions. This was achieved through the combination of a diapause duration model which related diapause duration to size and temperature, and to model of starvation mortality based on growth. Relating mortality to growth makes conceptual and theoretical sense, and has been carried out in previous *Calanus* models (Tittensor et al., 2003).

However, the form of our model is indisputably ad hoc. Further, there is no clear way to either test or validate our starvation mortality model for *C. helgolandicus*. Our principal problem is that we want to know its starvation mortality in oceanic regions, but *C. helgolandicus* is essentially never found in these regions. The uncertainty in our starvation model must therefore be recognized.

8.2 Performance of the *C. helgolandicus* model in the North Sea

CPR and the Stonehaven time series show a clear phenology for *C. helgolandicus* in the North Sea. There are 2 annual peaks; the first is in spring, typically between day 100 and 150, while the second is in autumn, typically around day 250. Our model successfully reproduces the second peak, and it provides evidence that a large proportion of this second peak results from transport of populations into the North Sea.

However, we failed to reproduce the spring bloom of *C. helgolandicus* in the North Sea. This could be put down to a number of factors. The Stonehaven time series indicates that the spring bloom of *C. helgolandicus* in 1997 was noticeably weak in comparison with other years. It is therefore possible that a significant spring bloom is not a permanent feature of phenology in the North Sea. However, this is not a particularly credible argument. It would require that either temperatures or chlorophyll levels were particularly detrimental to *C. helgolandicus* development in 1997. There is no evidence that this is the case. Spring temperature and chlorophyll levels at Stonehaven were not lower in 1997 than the typical conditions over the period between 1997 and 2008. It is therefore questionable to invoke the environmental conditions of 1997 as the reason for the failure of our model to reproduce the spring bloom in *C. helgolandicus* in the North Sea.

More generally, the apparent phenology of *C. helgolandicus* is difficult to reconcile with what is known about the influence of temperature on *C. helgolandicus* development time. The first Stonehaven bloom typically occurs before day 130. However, temperatures are always below 9°C before this day. The only published study of *C. helgolandicus* development from egg to adult at this temperature failed to development them beyond C1 (Bonnet et al., 2009). Similarly, Møller et al. (2012) used the same ingestion rate data as we have to create a development model, finding that modelled development time was greater than 120 d for temperatures below 8°C. In addition, ingestion rates for *C. helgolandicus* are less than half of those of *C. finmarchicus* at temperatures below 8°C (Møller et al., 2012).

Egg to adult development time for *C. helgolandicus* is therefore expected to be greater than 100 d up until around day 120 in the North Sea. This is shown graphically in Figure 8.4, which displays the first day of the year when *C. helgolandicus* development time is less than 100 d. This figure indicates that *C. helgolandicus* development times in the North Sea are too pronounced in the first 100 d of the year for a phytoplankton triggered bloom to occur.

We are therefore faced with two key possibilities. The apparent bloom in *C. helgolandicus* C5 and adults observed near day 100 may be post-diapausing *C. helgolandicus* individuals that are transported into the North Sea. In addition, the long delay, of over 100 d, between the first and second blooms in the North Sea suggests that if this is true that this is a sink population, which does not lead to a second generation.

Second, our modelled development times may be inaccurate in the North Sea. This is possible, however development time studies of *C. helgolandicus* of eggs from the offspring of females caught in the North Sea would be necessary to confirm if there are regional scale effects on development time.

Finally, it may be possible that the observed *C. helgolandicus* in the Stonehaven time series and CPR in spring are in fact hybrids of *C. finmarchicus* and *C. helgolandicus*. This

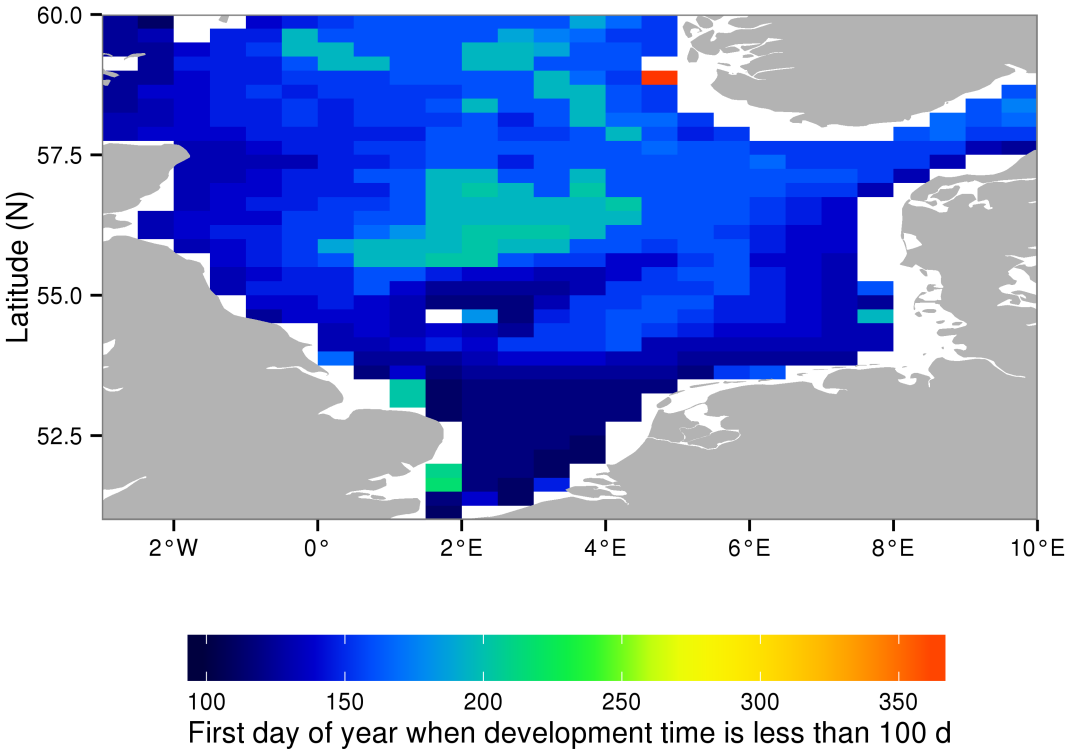


FIGURE 8.4: Map showing the first day of the year when modelled egg to adult development time for *C. helgolandicus* is less than 100 d in the North Sea.

is a speculative hypothesis. However, at the fringes of its northern distribution *C. finmarchicus* has been observed to hybridize with *C. glacialis* (Berchenko and Stupnikova, 2014; Parent et al., 2011, 2012), and we cannot rule out a similar phenomenon for *C. finmarchicus* and *C. helgolandicus*.

8.3 Influence of choice of ocean model

Large scale population models of zooplankton population must be driven by the temperatures and flow fields of OCGM. However, the potential for these models to lead to biases in zooplankton models has not been considered in existing literature. In fact, to

our knowledge, the work of Sinha et al. (2010) is the only published study to consider the behaviour of a marine ecological model when driven by two different OCGMs.

Historically, zooplankton models, and marine ecosystem models in general, are only forced by one OCGM. The reasons for this are obvious and understandable. Computation of the transport in an ocean model is a time consuming process. In our case, it takes 3 days to simply run the code which produces the transition matrices for surface and deep transportation. However, this code must be first be set up, then tested and debugged, a process which takes longer than most researchers would like. Having to do this for two ocean models, let alone setting up the relationships necessary to acquire the relevant data to run two models, is clearly a much too arduous task, given that there is little guarantee the end result will be anything more than a barely noticed caveat in a modelling paper. We were able to consider the influence of choice of OCGM because of the switch between using the OCCAM and the NEMO model with our enhancements to Speirs et al. (2006). The necessary data for OCCAM already existed, so not much extra work was needed to compare the *Calanus* models when driven by temperature from each OCGM.

So, we cannot recommend that modellers run zooplankton models using output from different OCGMs. The time spent is likely too great for what might be a research output of limited interest. What we can recommend is that modellers consider the potential influence of OCGM bias in further biasing zooplankton models. This bias should first be highlighted and then taken into account when comparing model results with data.

Ocean model bias can be detected in a number of ways. First, OCGM temperature output can be compared with global data sets (Rayner et al., 2003; Levitus et al., 2013)). These comparisons could take many forms. Phenology can be particularly sensitive to temperature around the time of the phytoplankton bloom. Therefore a comparison of surface temperatures in spring may reveal important biases. Similarly, deep temperatures can be compared with observations. In this case observational data is less reliable,

however comparisons can potentially demonstrate if modelled patterns of diapause duration can simply be a result of inaccurate deep temperatures.

Temperatures in time series locations can also be compared with temperature records at these locations, which are normally available (Heath et al., 2000a). Taken together, these comparisons will indicate to a researcher whether they should rely heavily on time series. This will require some subjective choices to be made. In our case, modelled phenology at the OWS M location was heavily distorted by underestimates of temperature. The underestimate of temperature was so significant that you might argue that the data at this location should not be used for model testing or parametrization. However, this is perhaps going too far. Visual inspection of modelled and observed time series can show the difference between predicted and observed abundance peaks. In turn approximate adjustments can be made to estimate what the timing would be if the temperatures were fully accurate.

However, the influences of these biases are likely to be complex, and difficult to untangle on a regional scale. Temperature biases will demonstrate temporal and spatial autocorrelation (Diniz-Filho et al., 2003). The extent of this autocorrelation will be made more difficult to interpret due to ocean transportation. A key source of North Sea *C. finmarchicus* comes from the diapausing population in the Norwegian Sea (Heath et al., 1999; Rullyanto et al., 2015). The population in this region is therefore likely to be influenced by biases on a reasonably large geographic scale.

Misrepresentation of the environmental conditions in one region will likely influence the seasonal cycle of *Calanus* in some other locations. However, the extent of these influences is not well understood. For example, if temperature is underestimated in the Norwegian Sea what influence will it have in all of our East Atlantic time series? Diapause centres such as the Norwegian Sea play key roles in determining the geographic distribution of *C. finmarchicus*. Understanding what happens when we mis-characterize temperatures at diapause centres may be a useful question for future research.

8.4 Diapause

The influences on the timing and duration of diapause in *C. finmarchicus* have been considered in a number of modelling and field studies (Ingvarsdøttir et al., 1999; Johnson et al., 2008; Saumweber and Durbin, 2006). And the existing modelling studies of Ingvarsdøttir et al. (1999) and Saumweber and Durbin (2006) share many characteristics with ours.

In our baseline model, diapause duration was influenced by two variables: prosome length and diapause temperature. This baseline model was able to produce good spatial predictions of annual abundance of *C. finmarchicus*, but its predictions of the phenology of diapausers in some locations, in particular at OWS M, were notably inaccurate.

Field estimates of diapause duration by Melle et al. (2014) indicate that timing of diapause exit does not vary significantly. This does not appear consistent with the causes of diapause duration being purely physiological, as in our model.

We formulated a number of proxies for diapause exit. However, they all showed significant spatial variations in diapause exit timing. Our model shows that, with the exception of the region north of the Iceland-Scotland ridge, the timing of diapause exit is relatively synchronous across the model domain. However, there is a stark difference between the timing of diapause exit in the Norwegian Sea in comparison with the West Atlantic, which does not accord well with field estimates of the timing of diapause exit (Melle et al., 2014).

The reasons for this disparity appear to be the much lower temperatures in the Norwegian Sea. Diapause temperatures north of the Iceland-Scotland ridge are approximately 4°C lower than anywhere else in our model domain. This difference has a pronounced effect on diapause duration. In effect, we assume that diapause duration decreases with a factor Q_{10} with each increase in temperature of 10°C. A 4°C change in temperature will therefore result in an approximate change in diapause duration of 40%.

Modelled estimates of diapause duration also depart significantly from those at spot locations reported by Melle et al. (2014). OWS M diapause was estimated to be approximately 200 d, in comparison with our estimate of approximately 300 d. A strict physiological model of diapause duration therefore appears to fail in the important diapause basin of the Norwegian Sea.

An emergent property of our model is that diapause duration is higher at lower temperatures. Paradoxically, Johnson et al. (2008) found no relationship between estimated diapause duration and diapause temperatures. This was despite finding evidence of a significant relationship between surface temperature at the onset of diapause and diapause duration. The data of Johnson et al. (2008) implied a 46% reduction in diapause duration when surface temperature was 6°C compared to 12°C. The indirect influence of surface temperature in our model through prosome length would imply a 25% reduction, much lower than shown by Johnson et al. (2008).

The two major diapause regions for *C. finmarchicus* are the Southern Norwegian Sea and the Irminger Sea/Labrador Sea Subpolar Gyre (Melle et al., 2014). Temperatures at 1000 m are approximately 4°C lower in the Norwegian Sea diapause centre (Figure 8.5). Similarly, surface temperatures are lower in the Norwegian Sea. Field data indicates that there should be approximately a 20% difference in diapause duration between these regions (Melle et al., 2014). However, this is much smaller than that implied by our model of diapause duration and the relative environmental conditions of both basins.

A diapause duration model of the type assumed by our model therefore appears incapable of reproducing existing observed patterns of diapause duration. The theory that lipid modulation determines diapause duration may still be valid. However, it needs to be reconciled with the low diapause temperatures observed in the Norwegian Sea and the apparent lack of the implied prolonging of duration.

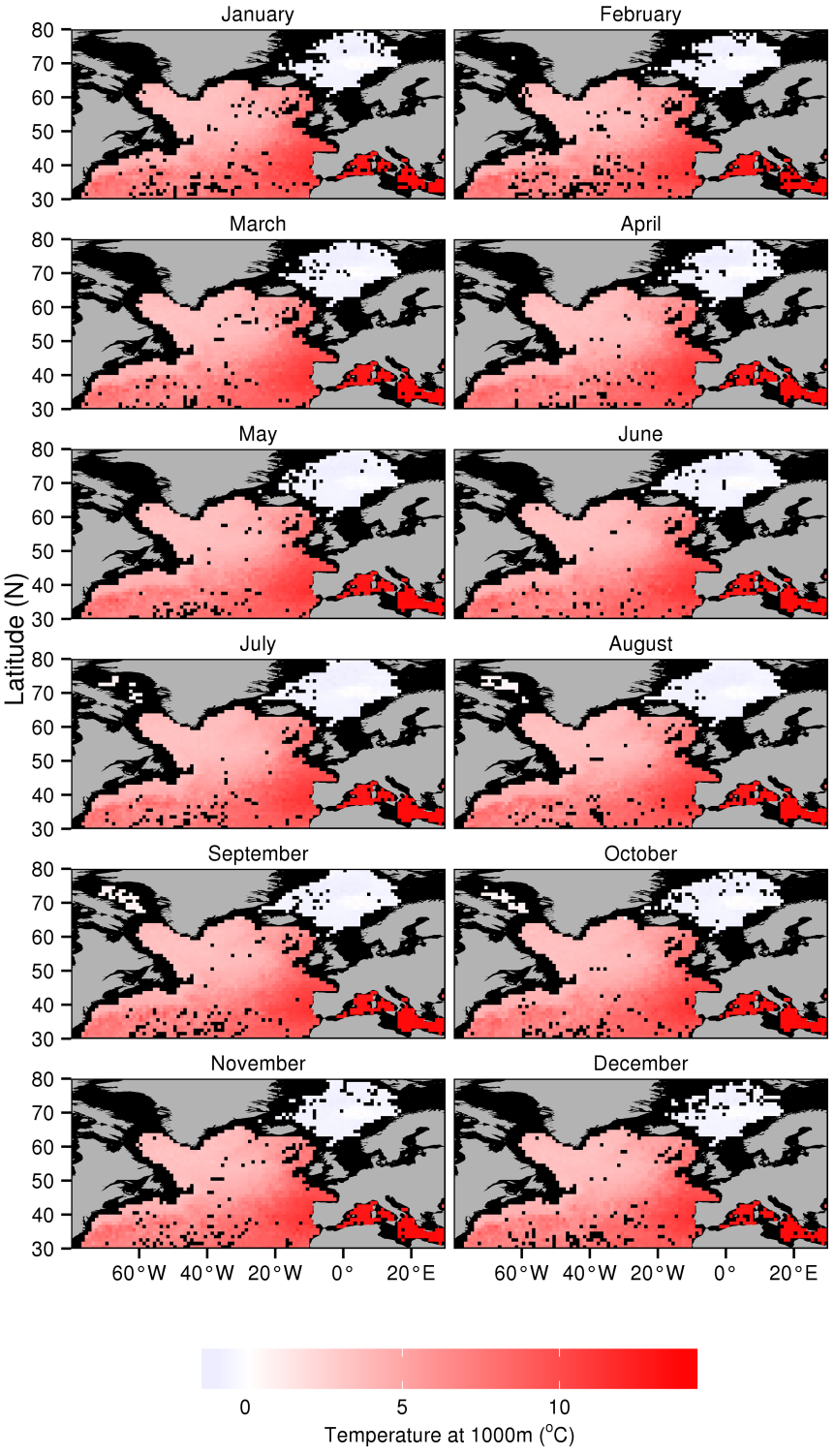


FIGURE 8.5: Monthly temperatures at a depth of 1000 m. Temperatures are decade averages from the World Ocean Atlas 2013 (Locarnini et al., 2013).

8.5 Body size

Body size in *Calanus* has received little attention in the published literature. In fact, the compilation of body size data and the relating of it to temperature, in this thesis appears to be the first such attempt in the literature. This lack of attention appears to be a glaring gap in knowledge.

Long term changes in body size of zooplankton communities have been linked to changes at higher trophic levels (Beaugrand et al., 2003; van Deurs et al., 2014). Yet, quantitative knowledge of long term changes in size of individuals or communities is almost totally lacking. Further, our review and modelling study indicates that a more nuanced view of body size is needed when determining changes in size composition of communities.

Changes in size composition are often estimated by using species abundances and a single size for each species. For example, Pitois and Fox (2006) estimated long term changes in the size composition of zooplankton communities throughout the North Atlantic. However, they assumed that the size of zooplankton did not vary and space, and that there was a factor 3 difference in the body weight of *C. finmarchicus* and *C. helgolandicus* in every region. This will clearly result in erroneous conclusions about changes in size composition.

Large scale considerations of body size must consider both the influence of temperature and the extent of overlap between species. Only considering the size of species at the centre of its geographical distribution is likely to result in erroneous conclusions about what occurs when one species replaces another due to climate change.

8.6 Food quality

Food quality has a significant influence on EPR (Niehoff et al., 1999; Jønasdøttir et al., 2002) and development time (Diel and Klein Breteler, 1986). However, the effect of food quality has not been considered in our model or in previous models of *Calanus*.

Our model notably fails to reproduce the annual cycle of *C. helgolandicus* EPR at L4, with the result that modelled egg production is significantly higher in the second half of the year than expected. Consequently, our model over predicts late year abundance of *C. helgolandicus* in this region. Irigoien and Harris (2003) found a similar disparity between peak EPR and females, which they say suggested that the influence of diatoms reduces the viability of the early cohort. However, more research is needed to link the changes in phytoplankton composition in L4 (Widdicombe et al., 2010) with varying EPR.

Resolution of phytoplankton into functional groups from satellite data is not possible. However, a new generation of coupled physical-biogeochemical models can model the functional groups (reviewed in Chust et al. (2014)). This type of model can potentially be incorporate into a *Calanus* model to more fully incorporate the influence of food quality. However, for this to occur our understanding of the influence of diet on growth and fecundity will have to improve significantly.

8.7 Modelling the southern extent of *C. helgolandicus*

A notable feature of our model is the relative inability to reproduce the southern population of *C. helgolandicus* in the Atlantic. Population numbers at the Vigo station are significantly higher than our baseline model predicts. Our focus is on the Atlantic, however our baseline model also fails to reproduce Mediterranean *C. helgolandicus* populations despite them existing in reality (Bonnet et al., 2005).

In our baseline model, we were unable to produce credible predictions at the Vigo station without making significant reductions in the quality of model predictions at other locations. However, the relaxation of our assumptions relating to diapause duration can result in a better performance at the Vigo station without damaging the overall geographic performance of the model. Reducing diapause duration by 40% means that the overall fit of the model to CPR can be optimized while simultaneously lowering the scaling of mortality with temperature. This indicates that the failure of our baseline model to give credible predictions at Vigo is a result of excessive mortality at that location. Alternatively, modelled development time may be significantly higher than in reality.

8.8 Phenology as a driver of *Calanus* distributions

The role of phenology in limiting geographic distributions has been the topic of some discussion in the ecological literature (Chapman et al., 2014; Chuine, 2010). It has received little attention where zooplankton are concerned. However, our model for *C. helgolandicus* indicates that phenology plays a key role in limiting its geographic distribution.

Calanus phenology in oceanic environments can be simplified as follows. The spring phytoplankton bloom results in the first generation of *Calanus*, which will result in further generations. Adverse environmental conditions or other triggers result in *Calanus* moving to deep waters, where they will stay for months. They then return to surface waters to feed on a phytoplankton bloom and the phenological cycle is closed. However, in the case of *C. helgolandicus*, the cycle does not appear to close. It will exit diapause when surface conditions are deleterious to its growth and will therefore be incapable of generating a second generation.

8.9 The limits of current experimental knowledge

A fundamental feature of our modelling study, and most other *Calanus* models, is its reliance on experimental work. However, this experimental work is typically not carried out over a large enough temperature range for us to have high confidence that biological processes are accurately defined. This is most important for *C. finmarchicus*, where we are forced to assume an extremely strong relationship between temperature and mortality. It is unclear if this is a credible modelling assumption, or if the temperature dependence of one of our model elements departs significantly from reality. We therefore reviewed the maximum temperatures various traits for *C. finmarchicus* have been recorded at in experimental studies. The results are shown in table 8.1.

TABLE 8.1: Temperature ranges for measurement of *C. finmarchicus* rates. * indicates the reference with the highest report temperature.

Trait	Maximum temperature (°C)	Reference
Growth	12	3,4, 5, 9,19, 23
Development	12	4, 18, 19, 21, 23
Fecundity	13.5	2,3, 7*, 8, 12, 16
Egg hatching success	22	15
Ingestion rate	21	3, 11, 14*
Respiration rates	17.9	1,6, 10, 13*, 20
Costs of gonad formation	8	17

References: 1. Ingvarsdøttir et al., 1999; 2. Rey et al., 1999; 3. Harris, 2000; 4. Campbell et al., 2001 5. Hygum et al., 2000b; 6. Saumweber and Durbin, 2006; 7. Runge and Plourde, 1996; 8. Pasternak et al., 2013; 9. Carlotti et al., 1993; 10. Hirche, 1983; 11. Meyer et al., 2002; 12. Hirche et al., 1997; 13. Hirche, 1987; 14. Møller et al., 2012; 15. Preziosi and Runge, 2014; 16. Kjellerup et al., 2012; 17. Rey-Rassat et al., 2002a; 18. Cook et al., 2007; 19. Hygum et al., 2000a; 20. Ikeda et al., 2001; 21. Corkett et al., 1986; 22. Tande, 1988; 23. Diel and Klein Breteler, 1986.

In the East Atlantic, the surface temperature experienced by *C. finmarchicus* populations rarely exceeds 12 or 13°C. A full understanding of what limits the geographic distribution of *C. finmarchicus* therefore requires knowledge of the response of *C. finmarchicus* to temperatures above 12°C. For most traits, this knowledge is currently lacking.

Development times and growth rates have not been recorded at temperatures above 12°C. Our development time model was derived from the clearance rates reported by Møller et al. (2012), which reported clearance rates at temperatures up to 21°C. This model assumed that respiration rate followed a Q_10 response, and this number was parameterized. However, respiration rate data above 12°C is also relatively sparse. Hirche (1987) appears to be the only published study to report *C. finmarchicus* respiration rate above 12°C. They reported respiration rates at 15.1 and 17.9°C, but these estimates were only based 3 and 2 animals respectively.

Fecundity has also not been studied over a broad range of temperatures. The highest temperature at which EPR has been reported in an experimental study is 13.5°C (Runge and Plourde, 1996), whereas egg hatching success has been measured at temperatures up to 22°C (Preziosi and Runge, 2014).

Finally, the costs of molting from C5 to adult and gonad formation has only been estimated at 8°C (Rey-Rassat et al., 2002a). In addition, the estimate in Rey-Rassat et al. (2002a) is itself highly uncertain, as the researchers had to adjust their estimate of costs of gonad formation. We therefore have a very poor understanding of the potential influences of climate change on the lipid metabolism of post-diapause *C. finmarchicus*.

The key gaps in modelling *Calanus* therefore appear to be as much experimental as they are conceptual. Predicting the impact of a 2 or 3°C increase in temperature on populations first requires that we know what the influence will be on the biological and physical state of individual animals. But we clearly lack this knowledge. Experimental studies are therefore needed over a broader range of temperatures. The recent incident of summer temperatures exceeding 20°C in the Gulf of Maine (Preziosi and Runge, 2014) suggests that these high temperatures are now ecologically relevant.

Clear priorities therefore exist. We need to clarify the influence of temperature on growth, development and fecundity. We expect that such studies will show a dome-shaped response of growth rate and EPR to temperature. However, this hypothesis is

easily refuted. Similarly, the increase in development time at high temperatures may be more or less steep than in our model. Improvements in the accuracy of the EPR and development time models used for *C. finmarchicus* may potentially result in population models which can reproduce the geographic distribution of *C. finmarchicus* without recourse to an extreme scaling of mortality with temperature.

We proposed a new, more mathematically elegant, model for diapause. A key feature of this model is that smaller individuals have significantly lower relative lipid levels than larger individuals, which in turn significantly reduces their diapause durations. This assumption is derived from published lipid-length relationships. However, the reasons for this relationship are poorly understood. The influence of food quantity on lipid reserves has been studied experimentally (Hygum et al., 2000b), however the influence of temperature on lipid reserves has not been studied experimentally. A laboratory study of the accumulation of lipids of Calanus under varying temperatures would confirm if there is a pronounced influence of temperature or body size on lipid levels. In turn this information could potentially inform the assumptions of future population models.

This section highlighted knowledge gaps by focusing solely on *C. finmarchicus*. However, a key knowledge gap relates to the diapausing abilities of *C. helgolandicus*. We do not know the influence of temperature on diapausing *C. helgolandicus*. In fact, we do not know the influence of temperature on *C. helgolandicus* respiration. Similarly, we do not fully understand the relative lipid accumulation capabilities of both species. If we are to credibly model the future distribution of *C. helgolandicus*, we will need to expand our knowledge of the biological determinants of diapause in this species.

8.10 Conclusions

The key conclusions of this chapter are as follows:

- A key requirement of future Calanus research is to close vital gaps in our knowledge of the relationship between life cycle traits and temperature.
- Our model assumes that there is a dome-shaped response between growth and fecundity and temperature. Future research is needed to refine or refute these models.
- The causes of the spring bloom of *C. helgolandicus* in the North Sea should be an area of future study. Our model results and review in chapter 2 indicate that this bloom is inconsistent with known knowledge of development in *C. helgolandicus*.
- Understanding why *C. helgolandicus* exists in the Celtic Sea region, but *C. finmarchicus* is a question which may resolve our poor understanding of what limits the southern distribution of *C. finmarchicus*.
- Model over-predictions of EPR in the English Channel indicate an incomplete understanding of egg production rate. Future models of Calanus should consider whether food quality or other environmental drivers are needed to explain patterns of EPR.
- Our model highlights the importance of considering body size, which to date has been an understudied aspect of zooplankton ecology.
- The sensitivity of the *C. helgolandicus* model to diapause duration highlights the usefulness of future research on what drives lipid levels in *Calanus*. Future Calanus models should consider more complex formulations of the relationship between body size and lipid levels and environmental conditions.

8.11 Closing thoughts

When modelling animals, you tend to have two mental states: internally, you worry deeply about the uncertainties in the model, and externally you wish to highlight what the model does well. Worries about uncertainties can get a modeller down. But consider what this model has achieved with reasonable success. We have successfully reproduced the geographic distributions of two species over distances of thousands of kilometres. This model is driven by information acquired by satellites in the sky, and by a model of the ocean which is verified by information acquired from a fleet of ocean going research vessels. On a biological level, the model builds on the hard work of multiple research teams on multiple continents. The *Calanus* story is not complete, but scientists have now acquired a rich body of evidence that allows us to tell a credible story.

Furthermore, the chief uncertainties in the model are as you might expect. Understanding the behaviour of zooplankton at a depth of 1 kilometre in close to freezing water in the middle of the ocean is exceedingly challenging. From the relatively comfortable perspective of a modeller a wish list of data requirements can easily be drawn up. This wish list will inevitably look a lot different from the perspective of a field researcher sitting on a research vessel which is dodging gale force winds in a North Atlantic winter. The uncertainties revealed by our model must put be put in the context of the often harsh physical realities of collecting the data needed to resolve them.

These challenges were made clear to me when I spent two rather uncomfortable weeks on board the FRS Scotia in the North Sea and Faroe-Shetland Channel in December 2011. This provided me with a more realistic perspective. Marine biology is tough, and perhaps too tough for this desk bound modeller. So, instead of closing by chiding field researchers for not providing enough data to enable a “perfect” *Calanus* model, I will thank them for their, perhaps inexplicable, willingness to face tough physical conditions to collect the data in the first place.

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