UNIVERSITY OF STRATHCLYDE

Modelling the impact of environmental change on the physiology and ecology of sandeels

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It doesn't matter what temperature the room is, it's always room temperature.

Steven Wright, comedian

Abstract

Sandeels comprise a quarter of North Sea fish biomass and are vital prey for a number of marine mammals and birds. However, in recent decades there have been significant declines in sandeel abundance and energy value. These declines have been linked to climate change, however, it is unclear what the relative influence of changes in food and temperature is. Here we examine the role of these factors on different aspects of the sandeel lifecycle and determine how robust sandeels are to expected climate warming.

First, we review the evidence for climate impacts on sandeels and discuss the implications for higher trophic levels with particular reference to seabirds. Evidence summarised demonstrates that sandeels are a critical food source for many seabirds, and that declines in sandeel populations have negatively impacted seabird breeding populations. Lack of existing quantitative understanding of the influence of food and temperature on sandeels demonstrates the need for a new mathematical model to predict the outcome of climate warming on sandeel stocks.

Second, we model changes in spawning and hatch dates off the Scottish east coast, which have been proposed as a contributor to the long-term decline in sandeel energy content. Results indicate that spawning and hatch dates do not explain this decline. Instead, the timing of both lifecycle events is relatively fixed and is governed by predictable environmental cues. Moreover, given the weak temperature effect on spawning and hatching, future temperature rises appear unlikely to significantly affect hatch date.

The central part of this thesis is the development and use of a new dynamic energy budget model to unravel the influence of food and temperature on sandeel abundance and energy content. An important application of the model was the examination of mortality rates between 2001 and 2007, a period of pronounced stock decline off the Scottish east coast. The model was driven by food and temperature. Support was found for the hypothesis that overwinter starvation mortality contributed towards a recent decline in sandeels in northern UK waters. Highest over-winter mortality rates were recorded for juveniles and not individuals aged 1 or over due to the effect of weight-specific metabolism. However, a sensitivity analysis of the model suggests that mortality rates are more sensitive to changes in copepod abundance in the build up to overwintering rather than temperature during overwintering. We suggest that food-driven size-selective starvation mortality may have contributed to the stock decline off the Scottish east coast.

We therefore conclude that indirect food web effects of climate change are likely to be greater than direct physiological effects on sandeels.

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First, I want to thank Mike, Dougie and Simon for their support and guidance throughout my study. I'm grateful for their patience when things took longer than expected and for making me a more critical thinker and capable of doing independent research.

I wish to thank Phil Boulcott and Simon Greenstreet who provided the bulk of the data I got to play with in the last few years. Particular thanks goes to Simon for fruitful discussions. Over the years I have shared an office with Andisheh, Robert, Rhuraidh, Craig, Abdulmajeed and Hoa. Thanks must go to Robert who plied me with coffee on a daily basis to "get the brain going". Andisheh taught me much about life and politics for which I'm grateful. Hoa pushed me over the finishing line when I needed it and reminded me whats important. Technical assistance was provided by Robert and Ian Thurlbeck. I want to thank the Marine Alliance for Science and Technology Scotland and the University of Strathclyde for funding this project.

Most of all, I wish to thank my family, Mum especially, who supported me through the last 5 years and kept the question, "how's the PhD going?", to a minimum.

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Abbreviations

AIC	Akaikes information criteria
CPR	Continuous plankton recorder
CPUE	Catch per unit effort
CV	Calanoid copepod stage 5
DEB	Dynamic energy budget
DW	Dry weight
GAM	Generalized additive model
GEBCO	The General Bathymetric Chart of the Oceans
GMT	Greenwich mean time
GSI	Gonadosomatic index
IPCC	Intergovernmental Panel on Climate Change
JNCC	Joint Nature Conservation Committee
MCCIP	Marine Climate Change Impacts Partnership
MPA	Marine protected area
NAO	North Atlantic Oscillation
PL	Prosome length
SCR	Seabird colony register
SMR	Standard metabolic rate
SSB	Spawning stock biomass
SST	Sea surface temperature
TSB	Total stock biomass
WNAO	Winter North Atlantic Oscillation Index
WW	Wet weight

Part I

Introduction

Chapter 1

The North Sea sandeel fishery, and recent population changes

The growth of fish production and aquaculture in post-war Europe accelerated the need for cheap sources of fish meal and petroleum. Atlantic herring *Clupea harengus* were seen as the ideal source due to their high oil content and abundance. However, herring stocks in Southern North Sea collapsed in the 1950s due to overfishing, so an alternative was needed. During this time the Danish pig farm industry realised that sandeels, a small shoaling fish and vital prey for many UK seabirds, carried the same nutritional quality as herring (Dammers, 1958). Massively abundant, seemingly inexhaustible resources for fish meal and oil, sandeels were the ideal replacement for herring. And so the North Sea sandeel fishery began. Beginning in 1958, catches were taken primarily by Danish fishermen to provide fishmeal for the pig farm industry, and landings have been dominated by them ever since (Figure 1.1). North Sea sandeel landings remained fairly steady at around 130,000 tonnes during the 1960s but increased dramatically in the 1970s, partly because it became easier to get trawling concessions for sandeels (Figure 1.1, Lorentzen and Hannesson, 2004).

It was not long until concern was raised over the effect the fishery was having on sandeel top predators. In the 1980s, a decline in sandeel abundance and concurrent decrease in seabird breeding success led to a ban on sandeel fishing in Shetland (Poloczanska, 2004). This was the first incidence of a sandeel fishing embargo being imposed as a precautionary measure to protect seabirds. Although not a direct cause of a decline in sandeels, fishing may have exacerbated the stock decline in Shetland.

In 1981 sandeel landings accounted for 25% of annual fish landings (Figure 1.2). By 1989, North Sea sandeel landings exceeded 1 million tonnes for the first time. In 1990, a group of Danish fishermen located a dense aggregation of sandeels in waters inshore off the Firth of Forth. Lured by the high value of sandeels as fishmeal, the fishermen returned every year thereafter. An average of 39,000 tonnes were landed between 1990 and 1999, with a peak of 100,000 tonnes in 1993. At the same time, several seabirds at a nearby seabird colony demonstrated remarkably poor breeding success (Greenstreet et al., 2010), the first sign that the fishery was depriving seabirds of sandeel prey. By 1999 the fishery had reached uneconomic levels, characterised by a decline in sandeel abundance (Figure 1.5). During this time, kittiwakes, puffins, guillemots and razorbills on the Isle of May suffered breeding failures (Frederiksen et al., 2008). Concerns over the effect the fishery was having on seabirds led to the closure of the sandeel fishery in 2000. Since then, sandeel fishing off the Scottish east coast has been restricted, and only a small scientific monitoring survey has been allowed to catch sandeels (Greenstreet et al., 2010).

1.1 Recent changes in sandeel populations

Around 1998—1999 sandeel stocks collapsed on the scale of the North Sea, with a shift from an average biomass of $\sim$2 megatons to $\sim$1 megaton (Christensen et al., 2013). However, this was masked locally by variation in trends of the different sandeel stocks (Figures 1.3 and 1.4). Populations in the southern and central areas underwent a step decline in the late 1990s, before slowly recovering after 2005. However, sandeels off the Scottish east coast increased around 2000—2001, before undergoing a sustained decline. The continued decline in the absence of fishing suggests a strong environmental effect.

So, what is driving the decline in sandeels in this region?

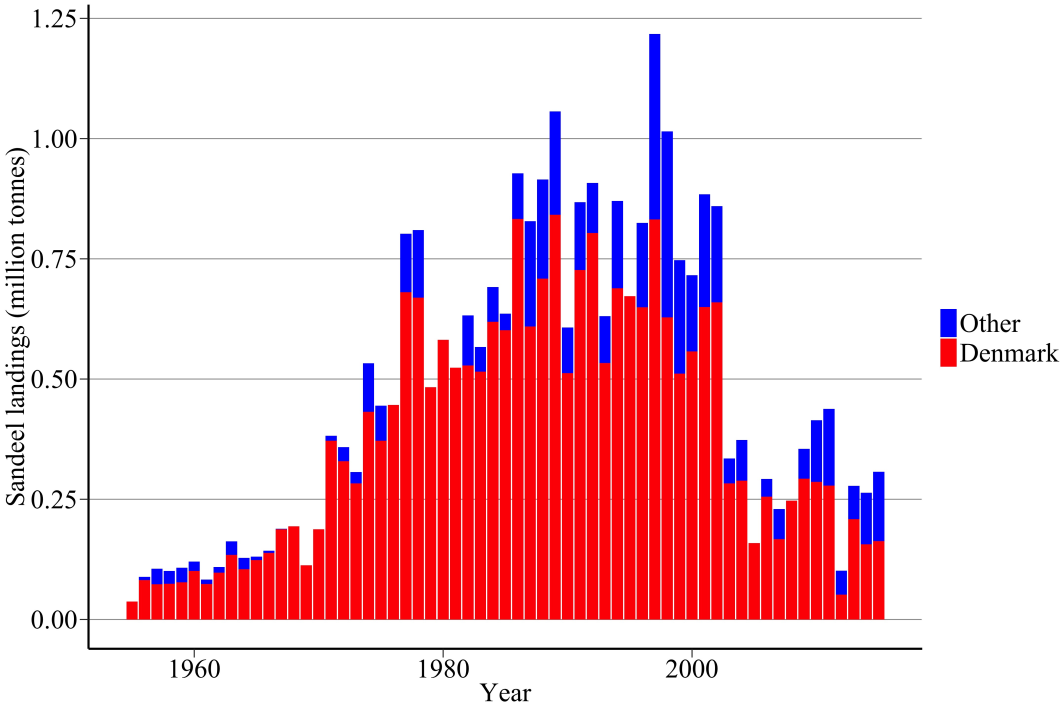


Figure 1.1: North Sea sandeel landings between 1955 and 2015. Shown are the magnitude of sandeel landings (million tonnes) (mainly *A. marinus*) and the contribution of total landings from Denmark. Data from ICES (2016).

1.2 Hypotheses for the sandeel stock decline

Here we address the possible reasons why sandeels have declined off the North-western North Sea. A number of hypotheses remain as to why sandeels have declined (Table 1.1).

Table 1.1: Potential factors which can lead to a reduction in sandeel abundance.

Factor	Reasons	Paper
Declining fecundity	Reduction in energy stores required for reproduction	Boulcott and Wright (2011)
Increasing overwinter mortality	Elevated metabolism due to temperature, insufficient energy reserves due to poor food availability in summer	van Deurs et al. (2011) van Deurs et al. (2011)
Increasing juvenile mortality	Predation, lack of food	Heath et al. (2012)
Egg mortality	Temperature, predation	
Larval mortality	Predation, poor food availability	Heath et al. (2012)
Changes in larval drift patterns e.g. being swept to unsuitable areas.	Hydrodynamic changes	Christensen et al. (2008)

Figure 1.2: Proportion of total fish landings in ICES divisions IV and III that were sandeels (mainly *A. marinus*) between 1950 and 2010. Fish landings data extracted from http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx

1.2.1 Has overwinter mortality increased?

Two main factors have been proposed as responsible for the decline in sandeel abundance, increases in overwinter and predation mortality. Sandeels show significant weight loss during the overwintering period (Boulcott et al., 2007; Boulcott and Wright, 2008), and it is speculated that increased temperature will increase this rate of loss due to elevated metabolism. The energy required by overwintering animals must be accumulated the previous summer, so unless warming is accompanied by increased scope for summer feeding, which does not appear to be the case (Wanless et al., 2004; Boulcott et al., 2007), then the net effect is likely to be reduced overwinter survival (van Deurs et al., 2011).

There are several pathways that can increase overwinter mortality. Across fish species, the probability of starvation decreases with increasing size (Schultz et al., 1998; Oliver

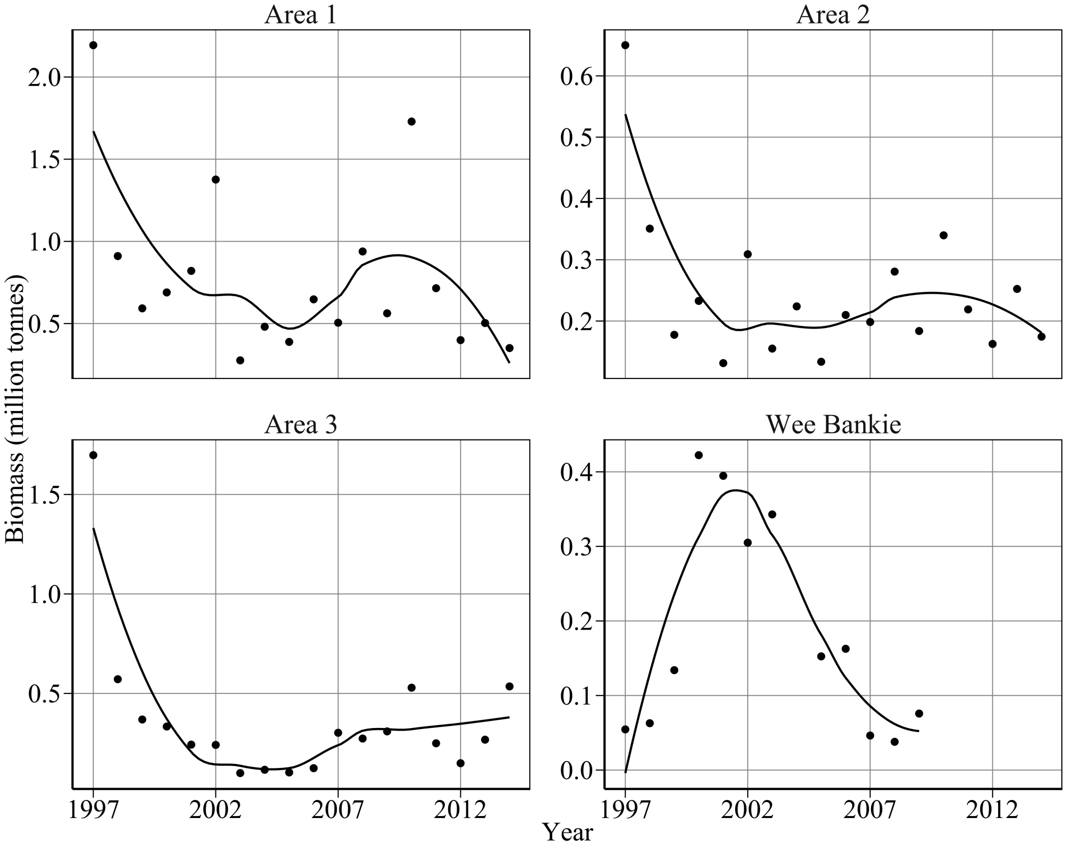


Figure 1.3: Spatio-temporal trends in sandeel stock biomass (TSB) between 1997 and 2014. Trends in stock biomass off the Scottish east coast contrasted with trends elsewhere. Stock biomass in areas 1 (Dogger Bank), 2 (Southeastern North Sea) and 3 (Central Eastern North Sea) plummeted in the late 1990s, corresponding to a North Sea regime shift in sandeels (Christensen et al., 2013). Data for areas 1, 2, 3 is taken from (ICES, 2014). Wee Bankie biomass represents the combined biomass of age 0 and age 1+ sandeels present in the sediment and water column, measured during May/June by scientific monitoring surveys (data digitised from Greenstreet et al. (2006) and Greenstreet et al. (2010)). See figure 1.6 for locations of the 4 stocks.

et al., 1979; Kirjasniemi and Valtonen, 1997; Biro et al., 2004). Hence, sandeels entering their first winter are most vulnerable to overwintering mortality. 0-group individuals require more time to accumulate the necessary energy reserves to overwinter than older individuals. This is supported by the fact that 0-group sandeels require at least one month extra feeding time than older sandeels (Macer, 1966; Reeves, 1994; Kvist et al., 2001). Due to differences in metabolism, starvation risk declines with increasing size (Shuter and Post, 1990; Schultz and Conover, 1999; Post and Parkinson, 2001). Hence, a trend towards smaller overwintering size can increase mortality (van Deurs et al., 2011). Indeed, there has been a long-term decline in 0-group length. Data from chick-feeding Atlantic puffins *Fratercula arctica* and Continuous Plankton Recorder samples

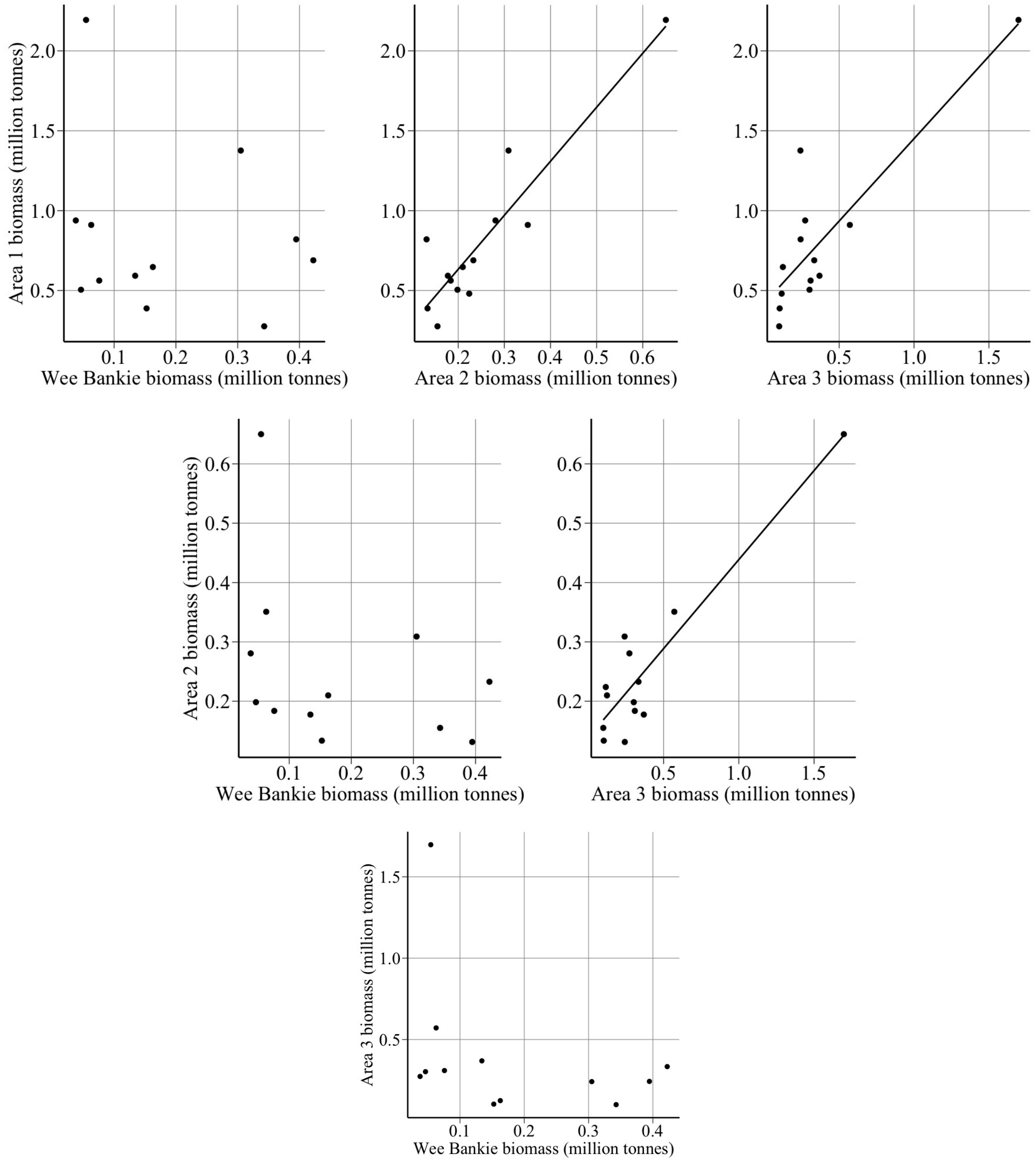


FIGURE 1.4: Relationships between biomass in different regions between 1997 and 2009. Wee Bankie TSB was not correlated with TSB in areas 1 (p = 0.55, R^2 = -0.06), area 2 (p = 0.24, R^2 = 0.047), or area 3 (p = 0.25, R^2 = 0.042). Significant correlations were observed between TSB in areas 1 and 2 (p <0.0001, R^2 = 0.83), areas 1 and 3 (p < 0.001, R^2 = 0.71) and areas 2 and 3 (p < 0.00001, R^2 = 0.83).

indicate that the size-at-date of 0-group sandeels has declined substantially since 1973 (Wanless et al., 2004).

It is unclear what the exact cause of a long term decline in sandeel length decline is (Wanless et al., 2004). A decline in 0-group size-at-date is presumably due to a mismatch between larval emergence and prey availability or decrease in growth rate (Frederiksen et al., 2011). The former is dependent on sandeel spawning and hatch dates. Changes

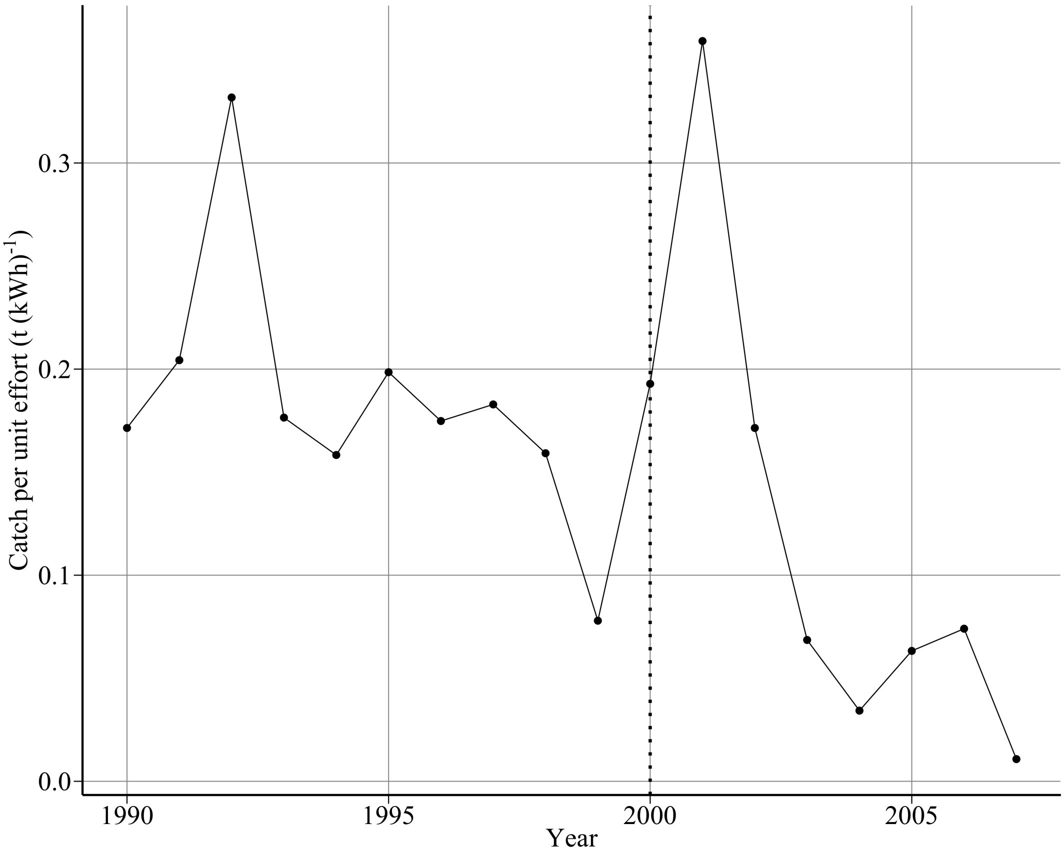


FIGURE 1.5: Catch per unit effort (CPUE) of sandeel larvae off the Firth of Forth. CPUE data from 1990 to 2000 were derived from analysis of vessel logbooks from the Danish sandeel fishery. CPUE data from 2000 onwards were taken from a supervised monitoring fishery. CPUE data for 2006 and 2007 were taken from H. Jensen, Danish Institute for Fisheries Research. The dotted line delineates the fishery closure.

in spawning and hatch dates can lead to a mismatch between larvae and zooplankton prey resulting in reduced growth (Wright and Bailey, 1996). However, the drivers of spawning and hatching are unclear. We do not know how sensitive hatch dates are to environment change.

Overwintering mortality may also have played a role in declining sandeel abundances around the Shetland Isles because sandeel growth rates are much lower there than elsewhere in UK waters (Wright and Bailey, 1991; Bergstad et al., 2002). Alternative explanations for the decline in this region are recruitment failure and increased predation by fish that consume sandeel larvae (Frederiksen et al., 2007).

1.2.2 Has predation mortality increased?

Herring *Clupea harengus* feed on larval sandeels (Hardy, 1924; Last, 1989), and stocks of herring have increased from 100,000 tonnes in the late 1970s to 2 million tonnes in 2004 (ICES Advice, 2004), an approximately inverse relationship with sandeel abundance around Shetland. Such a mirror-image pattern may indicate a top-down effect of herring predation on sandeel in the northern North Sea. There are precedents for such a phenomenon elsewhere; for example, herring predation has been implicated in the recruitment variability of Barents Sea capelin *Mallotus villosus* (Gjosaeter and Bogstad, 1998). However, counterevidence is that although adult herring biomass has been high since 2000, the survival and growth rate of herring larvae have declined (Payne et al., 2009, 2013), which might suggest a common environmental factor affecting both sandeels and herring.

1.2.3 Has there been a change in larval drift patterns?

Other possible reasons for recruitment failures of the northern sandeel populations are changes in the dispersal patterns of larvae from spawning to settlement sites (Proctor et al., 1998; Christensen et al., 2009). Recruitment in some populations may be highly dependent on larval import from regions afar (Proctor et al., 1998). In addition, changes in larval drift patterns may increase mortality because of transport to areas of unsuitable habitat.

Although changes in larval dispersal could have contributed to the decline in abundance in the Firth of Forth, this is unlikely. Hydrodynamic modelling suggests recent climate change impacts on sandeel transport are negligible (Christensen et al., 2008). Moreover, these studies predict limited export of larvae from Wee Bankie, and little import from regions afar (Christensen et al., 2008; Gallego et al., 2004; Magen, 2000; Proctor et al., 1998).

Data from other regions support the idea that a variety of factors may be causing the climate-related changes in sandeel abundances. Recruitment is strongly inversely related to winter temperatures for the sandeel stocks in the central North Sea, especially around Dogger Bank (Arnott and Ruxton, 2002), although the causal mechanism is not known (ICES, 2013).

The hypotheses discussed above mostly relate to direct climate impacts on sandeels. However, climate warming may be more likely to impact sandeels through changes on their main prey, zooplankton. Changes in growth rates in the southern North Sea have been linked to fluctuations in zooplankton abundance (van Deurs et al., 2014). Changes in the phenology of the spring plankton bloom in relation to burial and spawning times of the sandeels (Greenstreet et al., 2006; Scott et al., 2006).

1.3 Taxonomy

Sandeels are small lipid rich shoaling fish found in waters all across the globe. There are 6 species of sandeel in the North Sea - *Ammodytes marinus*, *Hyperoplus lanceolatus*, *Gymnammodytes semisquamatus*, *Ammodytes tobianus*, *Ammodytes dubius* and *Hyperoplus immaculatus*. Together, these species account for approximately 25% of North Sea fish biomass (Christensen et al., 2013). However, *A. marinus* is by far the most abundant sandeel, comprising >90% of the sandeel fishery catch (Macer, 1966; Goodlad and Napier, 1997). This thesis is concerned only with *A. marinus*, and to reflect their dominance of the sandeel community I use the term 'sandeels' to refer exclusively to *A. marinus*.

Age groups are classified as "Age in years - group" so 1-group denotes fish of age 1. Grouping of several age classes is common and 1+ group is taken as all fish which are age 1 and older. While inaccurate, it is the convention for fish to be given a birth date of 1st January. This is primarily for convenience in terms of the calendar.

1.4 Life Cycle

The life of a sandeel begins with the spawning of demersal eggs in winter (Reay, 1970; Bergstad et al., 2001). A few months later, eggs become larvae. These sandeels drift with currents for a few months before changing to juveniles, marked by the end of the drift phase (Wright and Bailey, 1996). Sandeels then settle at a location and remain there for life. During the day, individuals feed on zooplankton in surface waters, and spend the rest of the time buried in the sediment.

The sandeel lifecycle is highly unusual for teleosts; individuals overwinter in the sediment for up to 8 months without feeding (Reeves, 1994; Winslade, 1974). Many fish 'shutdown' in winter, feeding very infrequently and expending little energy. Overwintering is an adaptation to low food availability. The overwintering phase of sandeels, however, is more likely an adaptation to something else. The long overwintering period of the sandeel is exceptional, and appears to be the result of a trade-off between growth and mortality (Van Deurs et al., 2010). Sandeels are prey for a huge number of predators (Reay, 1970) and being outside the sediment carries a significant predation risk. Consequently, sandeels minimise the time they spend feeding. Individuals overwinter once they have accumulated the minimum energy to survive winter and reproduce.

Sandeels are an R-strategist which makes their long overwintering period unusual. However, predation mortality may be so great that the reproductive potential of the population is maximized when sandeels reduce the feeding season. Indeed, the time spent in the water column is only a few months (Reeves, 1994; Winslade, 1974). High mortality is compensated for by growing rapidly in order to mature at an early age and produce many eggs. *A. marinus* mature in July and lay a single batch of eggs in winter (Bergstad et al., 2001; Boulcott et al., 2007).

The natural mortality of sandeels is high with the result that the stock is usually dominated by fish < 2 years old. Separate studies indicate an instantaneous annual mortality coefficient between 1.2-1.3, which equates to a removal of approximately 70% of the population per year (Macer, 1966; Reay, 1973). This, however, ignores the age effect on mortality, which is considerable. In fact, 0-group mortality may be as high as 90%, twice as high than older fish (Reay, 1973; Cook, 2004).

1.5 Distribution and habitat

The geographic range of *A. marinus* extends from 49°N (Channel Islands, western English Channel) to 73°N (Novaya Zemlya and Bear Islands) (Reay, 1970). Many fish have a thermal niche, a range of temperature where survival and development is possible. Hence, fish distributions usually reflect a thermal niche. This does not appear to be the case for sandeels, whose distribution more likely reflects the availability of suitable habitat. Sandeels require well-oxygenated sand, since most of their lives are spent buried

(Wright et al., 2000). The most oxygen-retentive sand is coarse sandy sediment, which primarily occurs in shallow coastal sandbanks. Hence, high abundances of sandeels are rarely found outside sandbanks (Figure 1.6). Patchy availability of suitable habitat means that, within the North Sea, sandeels do not form a homogeneous unit. Instead, they exist as 7 separate distinct sub-populations (Figure 1.6).

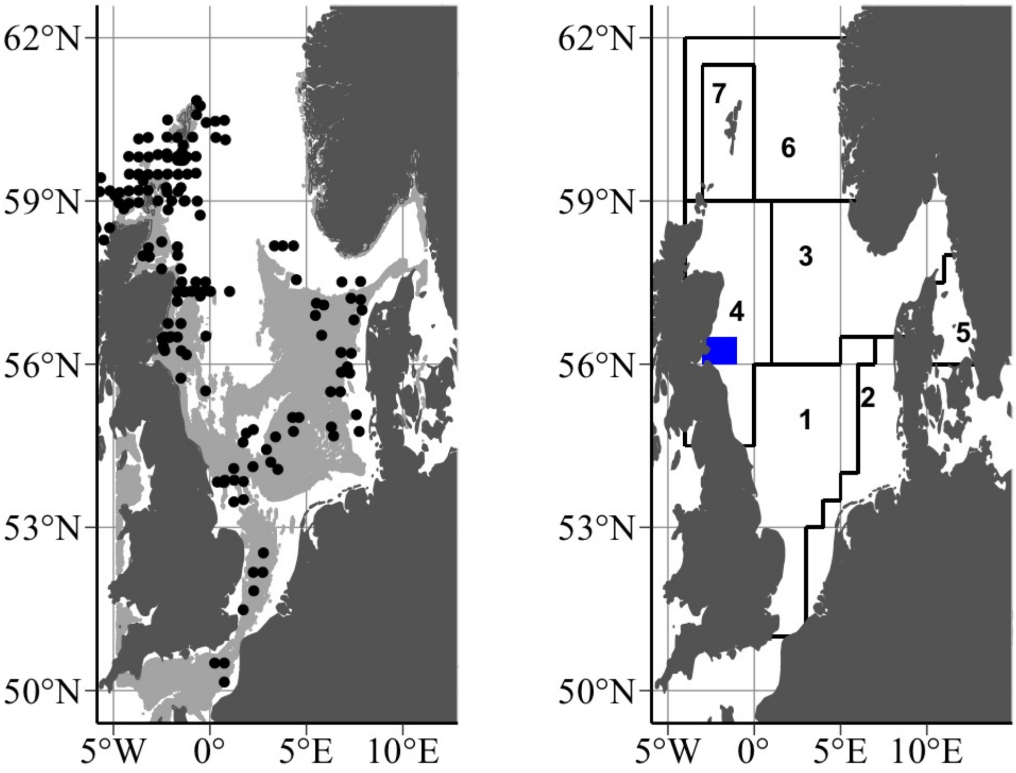


Figure 1.6: North Sea sandeel spawning areas (left panel) and ICES sandeel divisions (right panel). Shown in the left panel are sandeel spawning areas (black circles) in relation to shallow sandbanks. These areas are where yolk sac larvae were caught (data taken from ICES and unpublished larval survey data in 1992, 1993), and digitised data from Proctor et al. (1998). The pale grey shaded area indicates water depths between 30 and 70m, the range of depth sandeels are most commonly found (Wright et al., 2000). The majority of North Sea spawning areas overlap with shallow sandbanks, with the exception of habitat in Shetland waters. Bathymetry data came from the General Bathymetric Chart of the Oceans (GEBCO; www.bodc.ac.uk/projects/international/gebco) database. Shown in the right panel are the seven North Sea sandeel populations, as defined by ICES (ICES, 2014). 1: Dogger Bank, 2: Southeastern North Sea, 3: Central Eastern North Sea, 4: Central Western North Sea, 5: Viking and Bergen Bank areas, 6: Kattegat, 7: Shetland area. The Wee Bankie population, also referred to as the Firth of Forth population, is highlighted in blue.

1.6 Software used

All statistical analysis was carried out in R (Team, 2015). Figures were created using ggplot2 (Wickham, 2009). The dynamic energy budget model was coded up in C and model parameterisation was performed in R.

Chapter 2

Comparing sandeel sampling methods: implications for models

2.1 Survey methods used to sample sandeels

Here I give a brief description of the survey methods used to sample sandeels in this thesis. I then compare the suitability of these methods in estimating sandeel abundance.

Sampling of post-larval sandeels has taken place annually off the Firth of Forth between 1997-2003 and 2005-2009 (56^o 00N and 56^o 30N and longitudes 003^o 00W and 001^o 00W, Top three panels in Figure 2.1). Individuals were caught using dredge, grab and trawl surveys at various times of the year. This covered the main sandbanks off the Firth of Forth, the Wee Bankie, Marr Bank, and Berwicks Bank, which are prime habitat for sandeels in this area (Proctor et al., 1998; Pedersen et al., 1999). Sampling was undertaken by the FRV *Clupea* for the majority of the study period (1997-2007), before it was replaced by the FRV *Alba na Mara* (2008-2009). In each year, trawling was carried out between 0400h and 1800h GMT between late May and early July.

Sandeel larval sampling was conducted off the east coast by pelagic trawl between 2000 and 2009 (Bottom two panels in Figure 2.1). Small scale larval sampling took place at Stonehaven off the northeast coast of Scotland between 2000 and 2009 (56° 57.83N, 002° 06.74′W, water depth = 45m) between 2000 and 2009. Larvae were sampled with a 100 cm mouth diameter net of 350 μm mesh. The net was towed obliquely at a speed of 1 m s^{-1} to within ∼3 m of the seabed depth (45 m). Upon recovery of the net, the whole catch was washed into the cod-end. All sandeel larvae were removed from the catch and identified to species. *A. marinus* was distinguished from the other sandeel species present in the samples (*H. lanceolatus* the Greater Sandeel, and *A. tobianus*) by the absence of dorsal melanophores.

Large scale sampling of sandeel larvae was undertaken in 2002 across the northwestern North Sea by the FRV Scotia between 9-23 April. An ARIES high-speed sampler (Dunn et al., 1993; mouth area 0.1 m^2, mesh size 200 μm) and opening-closing Methot trawl (mouth area 2.25 m^2, mesh size 2 mm) were used to sample small and large sandeel larvae, respectively. All sandeel larvae were extracted from the samples and preserved in 4% formaldehyde and a subset of fish was selected for otolith analysis.

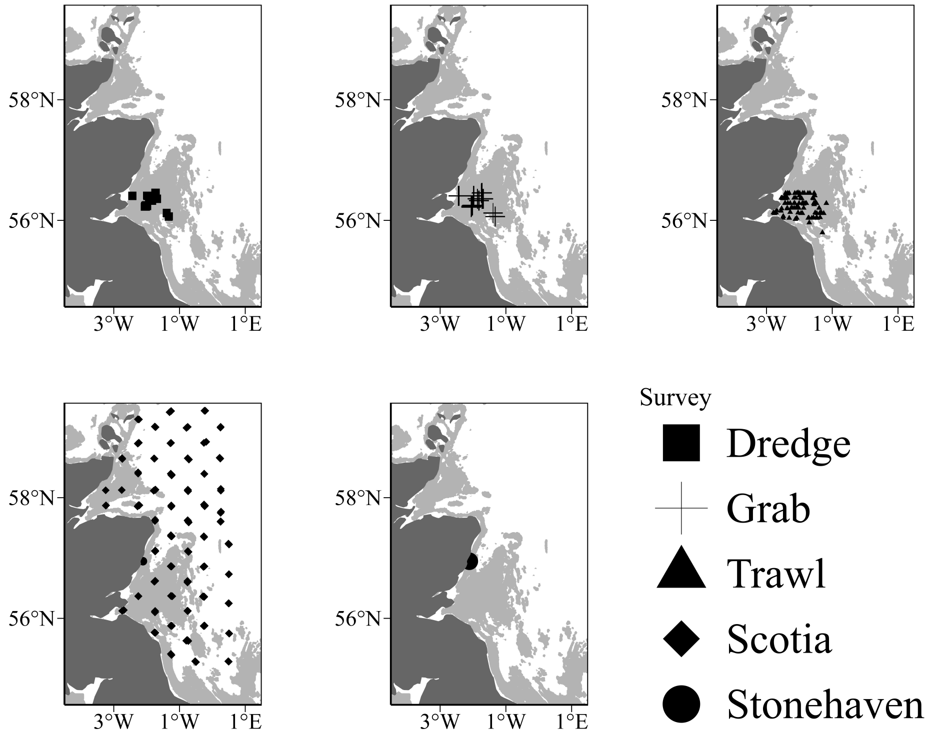


Figure 2.1: Locations of different survey methods in the thesis used to sample sandeels. The top three panels show locations of dredge, grab and trawl surveys conducted between 1997 and 2009 (all seasons) on the sandbanks off the Firth of Forth. These survey methods are used to sample sandeel juveniles and adults. The bottom panels shows locations of large and small scale trawl surveys used to sample sandeel larvae only. The bottom left panel shows locations of trawl surveys carried out by in Spring 2002. The bottom right panel shows locations of a small scale trawl survey at Stonehaven between 2000 and 2009.

Table 2.1: Temporal description of different survey methods in the thesis used to sample sandeels.

Cruise	Sandeels caught	Year	Season	Month & Day
Dredge	Post-metamorphic	2000	Summer	July 1-2
		2001	Spring	March 9,11
			Summer	May 27-28
			Autumn	October 16-17
		2002	Spring	March 26,28-30
			Summer	June 6-8
			Autumn	September 25-26,28, October 1
		2003	Spring	March 23-24,26-29
			Summer	June 19-21
			Autumn	September 28-30, October 1-2,4
		2004	Spring	March 21-24,26-27
			Autumn	September 29-30, October 1-2
		2010	Autumn	November 25-26
		2011	Spring	March 16-18
			Autumn	November 27-29
		2012	Spring	March 16-17
Grab	Post-metamorphic	2004	Spring	March 21-27
			Autumn	September 29-30, October 1-3
		2010	Autumn	November 25,27
		2011	Spring	March 17-18
			Autumn	November 28-29
		2012	Spring	March 17-18
Pelagic trawl	Post-metamorphic	1997	Spring	April 22-28
			Summer	June 18-19,21-25
			Autumn	September 11,13
		1998	Spring	March 20-21
			Summer	June 13-14
			Autumn	October 13-14
		1999	Summer	July 2-5
		2000	Summer	June 15-16,18-19
		2001	Summer	June 5-9
		2002	Summer	June 15-20
		2003	Summer	June 14-17
		2005	Summer	May 25-27
		2006	Summer	June 17-19
		2007	Summer	June 2-5
		2008	Summer	June 13,16
		2009	Summer	June 13-15
		2010	Summer	June 3-5
			Autumn	November 23-24
		2011	Spring	March 14
		2012	Summer	August 14
		2013	Spring	May 1
			Summer	June 14,16
Scotia	Larvae	2002	Spring	April 10,13,19
Stonehaven	Larvae	2000,2001	Weekly	—

2.2 The difficulty in estimating sandeel abundance

Estimating sandeel abundance is extremely challenging. Gaining accurate estimates of abundance over any time frame requires the entire population to be surveyed. This is impossible, primarily due to population patchiness, the difficult task of achieving adequate temporal and spatial coverage, and sandeels constantly moving in and out of the sediment. However, increasing the amount of surveys or expanding the area surveyed can nullify this effect. Indeed, because of these difficulties, it is not uncommon to record an increase of abundance with age (ICES, 2014).

Credible abundance estimates can be achieved, though this requires two conditions to be satisfied. First, surveys must not be prone to bias. For example, length-dependent catchabililty is a common problem in stock assessments, and this complicates efforts to measure abundance. Second, knowledge of fish biology is crucial to know when and where surveys should be undertaken, and if the whole population can be sampled.

2.3 Comparison of different survey methods to estimate abundance

In this section I briefly review the various survey methods currently used for sandeel stock assessment, with the aim of selecting a survey method that produces the most accurate estimates of stock abundance.

Four different survey methods are commonly employed to measure sandeel abundance - acoustic, dredge, trawl and grab surveys (Greenstreet et al., 2010, 2006, 2010). However, it is unclear which method is most efficient. For example, grab catchability may be close to 100%, but the area sample is extremely small, (∼0.0961 m^2 , Greenstreet et al., 2010). This is problematic because animals display extreme habitat patchiness, making it difficult to obtain accurate abundance estimates unless the number of grab stations is high. Sampling efficiency of the grab can be increased by only surveying areas deemed to be suitable habitat (Holland et al., 2005; Greenstreet et al., 2010; Wright et al., 2000). However, even in prime habitat, the grab will occasionally catch no sandeels, even though individuals may be present in great numbers nearby (S. Greenstreet, pers. comm.).

Some survey methods are prone to length dependent catchabililty, the dredge being a prime example. Figure 2.2 shows variation in abundance for several cohorts, as calculated from dredge survey data. There is a pattern of increasing abundance between age 0 and age 2/age 3 whenever younger age classes are present, which is clearly a signature of length-dependent catchability. Furthermore, comparison of length distributions between pelagic trawl and dredge surveys indicate a disparity in capture rates of smaller fish (Figure 2.3). For example, in 2001 and 2002, 0-group fish were poorly sampled by the dredge, however the dredge performed better at capturing larger sandeels in 2002 and 2003 (Figure 2.3). The pelagic trawl will sometimes fail to capture the largest sandeels because these fish may begin overwintering in the sediment before the survey takes place (Greenstreet et al., 2006). However, the overall degree of length-dependent catchability is considerably weaker in the pelagic trawl than it is in the dredge (Figure 2.3).

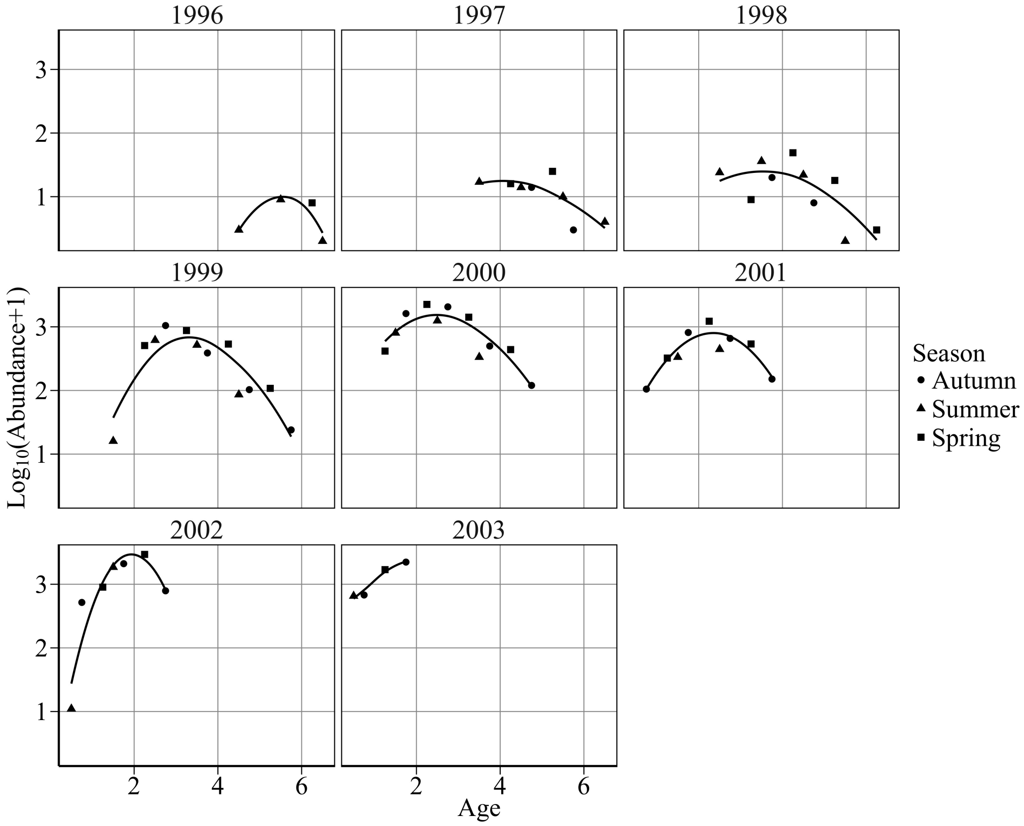


FIGURE 2.2: Changes in abundance at age from the dredge survey. Shown are sandeels born between 1996 and 2003. A consistent rise and fall in abundance for each cohort suggests catchabililty is strongly length-dependent. A loess smooth with span = 2 is fitted to abundance estimates (points) for each cohort.

There are several reasons why the dredge may under sample small individuals. First, in order to prevent the net becoming clogged with sediment, a large mesh size is required (∼ 10 mm) which smaller fish may escape through (Camphuijsen, 2005). Second, vibration of demersal gear along the seabed might provoke an escape response (P.J.Wright, unpublished data). These results contradict the conclusion made by Johnsen and Harbitz (2013), who argue that close similarity in length distributions of individuals caught in grab and dredge surveys do not support length-dependent catchability. However, this

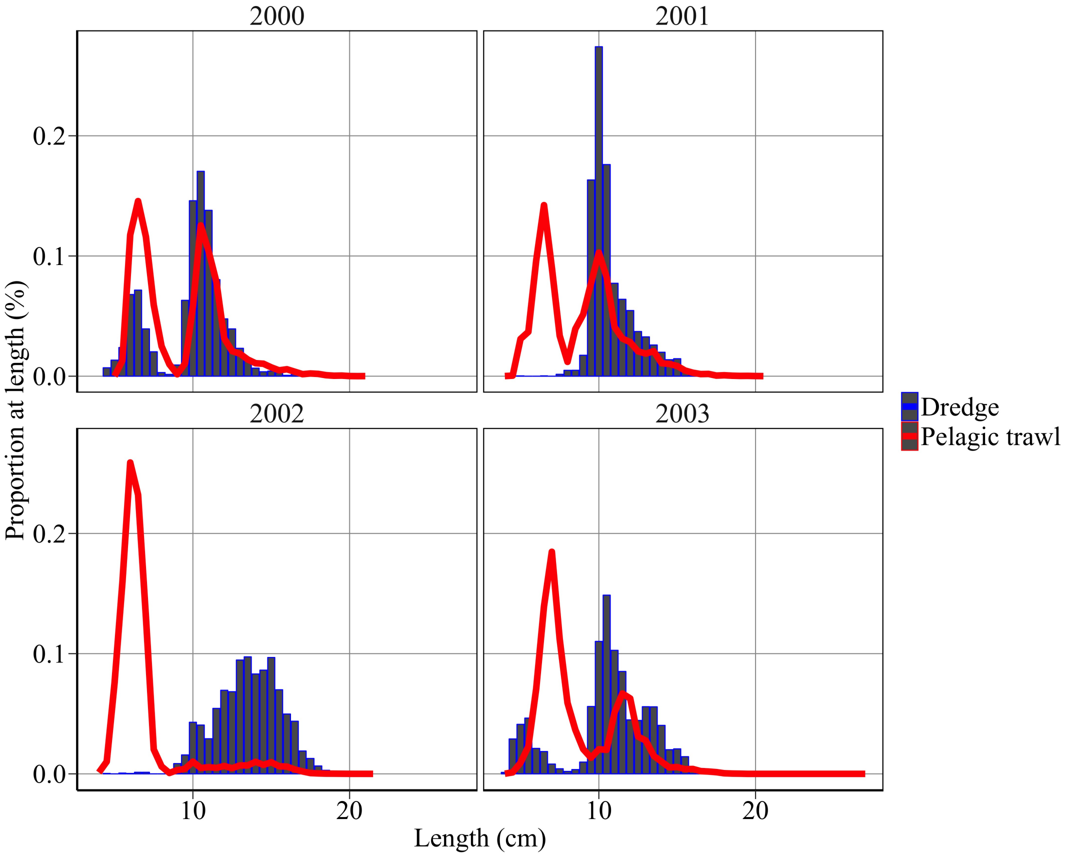


FIGURE 2.3: Comparison of length distributions from pelagic trawl (red line) and dredge surveys (blue bars). The dredge appears to under sample small sandeels, but is more efficient at capturing larger sandeels than the pelagic trawl.

is only valid if grab estimates are reliable. Another drawback of using dredge to measure abundance is that catchability is density dependent. That is, as the number of sandeels increase, so does the probability of being caught (Johnsen and Harbitz, 2013). It is unclear whether this is also true for the trawl and grab surveys.

While the pelagic trawl appears to provide a reasonable account of length composition, it does not provide estimates of abundance. This is because fish are constantly in motion between the sediment and pelagic, and the relative amount in each part is highly variable (Greenstreet et al., 2006, 2010). The demersal trawl and acoustic surveys do provide estimates of sandeel biomass in the sediment and water column, respectively (Greenstreet et al., 2006). However, they are inferior methods if one wishes to estimate sandeel length and weight composition. Therefore, the estimation of sandeel abundance at a given length, weight and age requires the use of demersal, trawl and acoustic data. Abundance is estimated by first estimating sandeel length composition from pelagic trawl data to estimate abundance at length, weight and age, then applying correction factors to bring the pelagic trawl biomass-at-age in line with the combined dredge and acoustic biomass-at-age.

Sandeel abundance was determined using the following method. First, a biomass at length distribution was estimated by applying a year-specific weight at length relationship to the length frequency of sandeels caught in all trawls. Probability distributions of ages for each 5 mm length class were determined using the continuation-ratio logit method for each survey (Kvist et al., 2000; Rindorf and Lewy, 2001; Stari et al., 2010). Then, changes in distribution of age at a given length, as a function of length, were estimated using Generalised Linear Modeling. Fitting was performed using Maximum Likelihood code (Stari et al., 2010). The resultant probability matrices of age-given-length were multiplied by biomass-at-length to give matrices of biomass-at-age-and-length. While these biomass-at-age-and-length matrices give accounts of biomass caught by trawling, they are not a measure of biomass at the scale of the Firth of Forth sandbanks (Figure 5.1). To obtain the true biomass of sandeels in the study area, correction factors must be applied to biomass-at-age-and-length matrices. Greenstreet et al. (2010) measured the biomass of Firth of Forth 0-group and 1+ group sandeels between 1997 and 2009. Correction factors are derived using these estimates and are estimated in the following way:

0-group biomass at year in the pelagic trawl y ($B_{0,\mathrm{PT},y}$) is related to 0-group biomass at year y in the study area ($B_{0,\mathrm{GREEN},y}$) using a correction factor ($CF_{0,y}$),

$$CF_{0,y} = \frac{B_{0,\mathrm{GREEN},y}}{B_{0,\mathrm{PT},y}} \tag{2.1}$$

The biomass of 1+ group sandeels in the study area is found in a similar way, using a correction factor for 1+ group sandeels ($CF_{1+,y}$).

Hence,

$$CF_{1+,y} = \frac{B_{1+,\mathrm{GREEN},y}}{B_{1+,\mathrm{PT},y}} \tag{2.2}$$

Next, abundance-at-age-and-length was estimated by multipling probability matrices of age-given-length by abundance-at-length. This produced abundance-at-age-and-length matrices of sandeels caught by trawling. These matrices were then multiplied by the appropriate correction factors defined above to give abundance-at-age-and-length of sandeels in the study area.

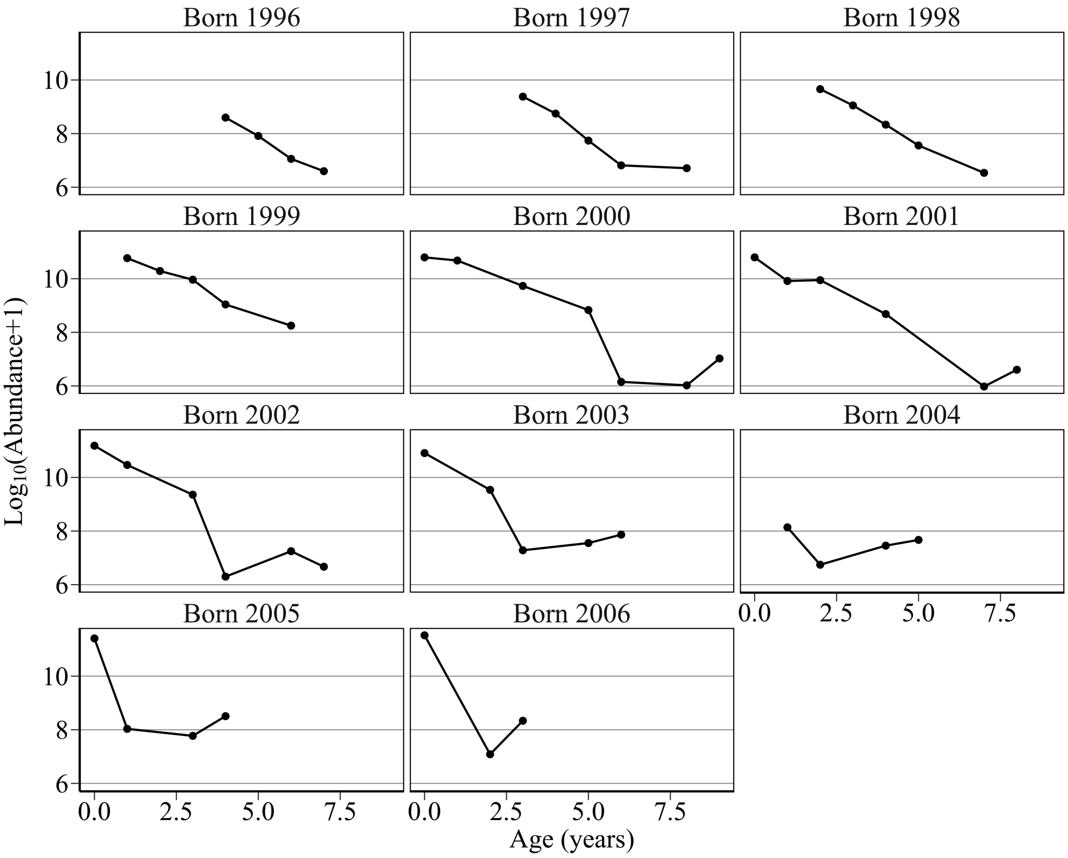


Figure 2.4: Estimated changes in total cohort abundance of sandeels in Wee Bankie. Total cohort abundance was estimated by applying correction factors to pelagic trawl abundance data (see text).

Figure 2.4 shows the absolute abundance of animals in the Firth of Forth, after correction factors have been applied. On average, 0-group were $\sim$ 8 times more numerous than age 1 fish between 2000—2003, 2005—2006, with 1-group fish being over 3 times more abundant than 2-group sandeels. Individuals older than age 2 constituted an average of less than 2% of the stock emphasising the importance of young age classes. There appears to be marked year-to-year and age-specific variation in survival. For example, between summer 2000 and summer 2001, 0-group and 1-group sandeels suffered annual mortality rates of 24% and 67%, respectively. However, between summer 2005 and the following summer, 0-group and 1-group sandeels suffered much higher annual mortality rates of ~100% and 96%, respectively. Survival rates for 1-group fish were almost 2 orders of magnitude higher than 0-group in this year.

Chapter 3

Links to higher trophic levels

Here, I synthesize the literature on climate effects on all trophic levels, and discuss how these effects propagate onto seabirds. It is important to note that this review is based on ‘A view from above: changing seas, seabirds and food sources’, a report commissioned by the United Kingdom Marine Climate Change Impacts Partnership (MCCIP) to review the evidence for climate effects on UK seabirds. Some of the original content from the report appears in the following review. Therefore, my realised contribution is 75%, instead of 100%.

3.1 Importance of sandeels to predators

Sandeels are the dominant forage fish in the North Sea. Constituting approximately 25% of the total fish biomass here, they exert a huge influence on zooplankton and piscivorous fish (Christensen et al., 2013). Further sandeel declines have the potential to profoundly alter the ecosystem, since few species are capable of replacing sandeels role of transferring zooplankton energy onto higher trophic levels. Sandeels constitute a significant proportion of the diet of seabirds, fish and marine mammals (Table 3.1).

Table 3.1: Proportion of sandeel in diet (by weight) of various predator species off the Scottish east coast. *95% confidence interval derived from Table 8. **95% confidence interval derived from Table 1. Sources: [1] Camphuysen, 2006 ; [2] Newell et al., 2013 ; [3] Engelhard et al., 2014 ; [4] MacLeod et al., 2007

Predator group	Species	Predator length (PL,cm)	% sandeel in diet	Source
Fish	Cod *Gadus morhua*	$PL < 30$	50	[1]
	Haddock*Melanogrammus aeglefinu*	$15 < PL < 45$	$40 - 70$	[1]
	Whiting *Merlangius merlangus*	$PL < 30$	> 75	[1]
	Saithe *Pollachius virens*	NA	5	[3]
	Horse-mackerel *Trachurus trachurus*	NA	17	[3]
	Starry ray *Amblyraja radiata*	NA	18	[3]
	Grey gurnard *Eutrigla gurnardus*	NA	12	[3]
	Mackerel *Scomber scombrus*	NA	10	[3]
Birds	Atlantic puffin *Fratercula arctica*	NA	$66 - 80$	[2]*
	Black-legged kittiwake *Rissa tridactyla*	NA	$65 - 81$	[2]*
	European shag *Phalacrocorax aristotelis*	NA	$69 - 90$	[2]*
	Common guillemot *Uria aalge*	NA	$16 - 37$	[2]*
	Great skua *Catharacta skua*	NA	$10 - 95$	[3]
	Razorbill *Alca torda*	NA	37	[3]
	Gannet *Morus bassanus*	NA	18	[3]
	Northern fulmar *Fulmarus glacialis*	NA	11	[3]
Mammals	Harbour porpoise *Phocoena phocoena*	NA	$61 - 100$	[4]**
	Minke whale *Balaenoptera acutorostrata*	NA	56	[3]
	Harbour seal *Phoca vitulina*	NA	37	[3]
	Grey seal *Halichoerus grypus*	NA	41	[3]
	Striped dolphin *Stenella coeruleoalba*	NA	3	[3]

Seabirds consume a considerable amount of sandeels during the breeding season (Wanless et al., 1998; Furness and Tasker, 2000; Furness, 2002; Frederiksen et al., 2004; Sandvik et al., 2005; Lahoz-Monfort et al., 2011). Between 1991 and 2011 on the Isle of May, sandeels comprised approximately 75% of the diet of European shag, kittiwake, and Atlantic puffins (Newell et al. 2013). Some seabirds, such as kittiwakes and Arctic skuas *Stercorarius parasiticus*, are highly sensitive to fluctuations in sandeel abundance; others, such as the northern gannet *Morus bassanus*, appear less affected (Furness and Tasker, 2000). The most sensitive seabirds are those with high foraging costs, little ability to dive below the sea surface, little spare time in their daily activity budget, short foraging range from the breeding site, and little ability to switch diet (Furness and Tasker, 2000).

Here I summarize the importance of sandeels for seabirds and do not discuss their relevance to fish and marine mammals. There are two reasons for this. First, few studies have been carried out on the impact of sandeels on marine mammals (MacLeod et al., 2007), so little is known of the responses of these animals to changes in food abundance. Clearly more research is required in this area, especially since the indication is that a lack of sandeel availability is detrimental for this group (MacLeod et al., 2007). Implications of changes in sandeels to fish are also not discussed. This is because fish are insensitive to these changes (Reilly et al., 2014).

In contrast to fish, seabirds are strongly bottom-up limited by sandeel abundance (Frederiksen et al., 2007). Among the reasons for this are: 1. Seabirds may only feed on one or two pelagic fish species while piscivorous fish usually prey on multiple species. 2. Seabirds must provide for their young and can only carry a small number of fish back to nesting sites. However, there is marked variation in sensitivity to sandeel abundance across seabird species (Furness and Tasker, 2000). For example, some seabirds are able to switch to other prey and so are buffered against declines in key prey species (Smout et al., 2013). When sandeels declined, Common guillemot *Uria aalge* and European shag *Phalacrocorax aristotelis*, seabirds capable of switching prey easily, consumed significantly less sandeels. However, Black-legged kittiwake *Rissa tridactyla* and Atlantic puffin *Fratercula arctica*, both sandeel specialists, continued to consume the same amount of sandeel (Figure 3.1).

At the time of writing, sandeel stock abundance is still at low levels (ICES, 2014). The contrasting stock dynamics between northern and southern areas have mirrored declines in sandeel-dependent seabirds. From a conservationist's viewpoint, investigating the causes of decreasing sandeel abundance close to major seabird colonies, i.e. within seabird foraging range, is crucial. A large percentage of several UK seabirds reside on the Isle of May National Nature Reserve off the Scottish east coast in the vicinity of the northwestern stock. Since 2000, sandeels and seabirds have declined in this region.

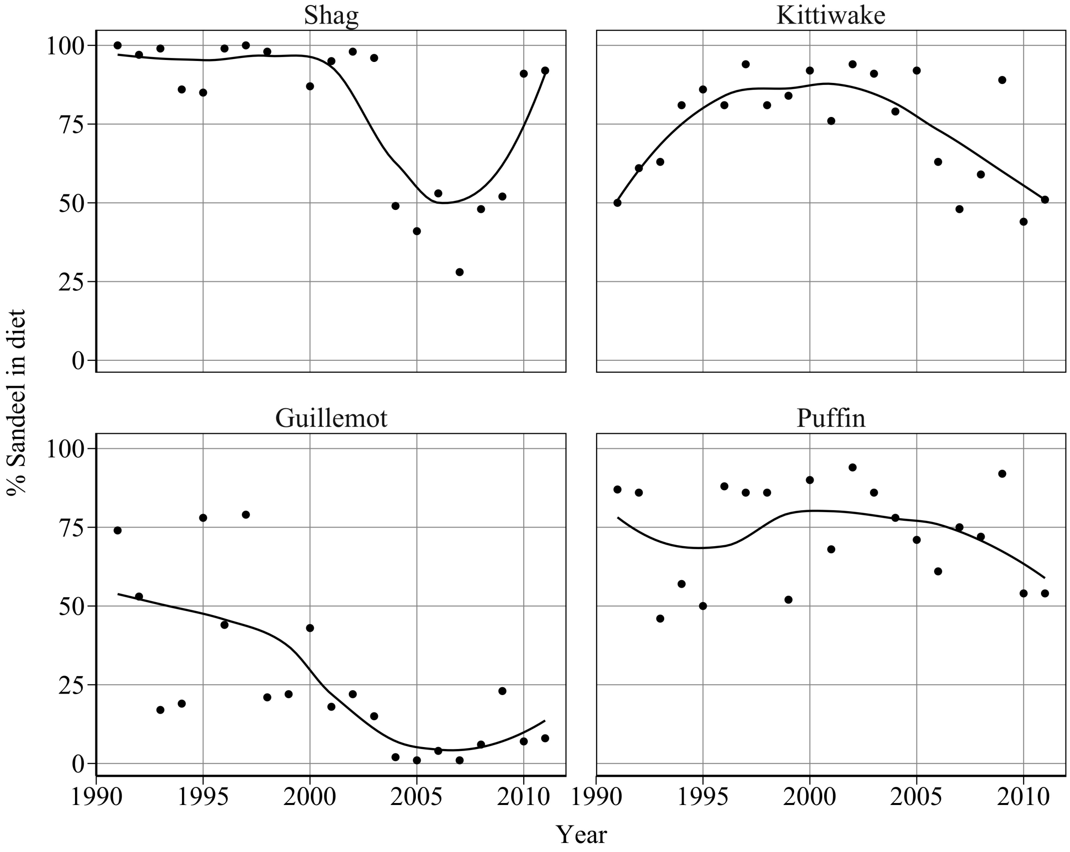


FIGURE 3.1: Percentage of sandeel (by weight) in the diet of young seabirds from the Isle of May between 1991 and 2011. Seabird diet data was taken from Table 8 in Newell et al. (2013). Black points and solid lines represent observations and loess smooths (span = 0.75) through the data, respectively. Sandeels made up significantly less of shag and guillemot diets between 2001 and 2011 than between 1991 and 2000 (t—test, $t = 2.96$ & $t = 4.39$, $p < 0.01$, $p < 0.001$, respectively). Sandeels made a similar contribution to the diet of puffins and kittiwake between 1991—2000 and 2001—2011 (t—test, $t = 0.054$ & $t = -0.79$, $p < 0.96$, $p < 0.44$, respectively).

3.2 Declines in sandeel dependent seabirds

North Sea surface temperature has risen dramatically since the 1970s (Rayner et al., 2003). As a consequence, there have been marked changes in the phenology, survival, growth and reproduction of marine organisms (Edwards and Richardson, 2004). There has been a shift towards earlier phenology in prey species leading to a mismatch between predator and prey (Edwards and Richardson, 2004). This is disrupting the flow of energy between the bottom of the food chain and marine top predators. Seabirds are a prime example of a marine top predator that appears to have been affected by climate change.

After flourishing during the second half of the twentieth century, many North Sea seabird populations are now in decline. Much evidence is accumulating that climate change is driving these negative trends in growth rate. Climate driven changes in the physical environment may affect seabirds both directly and indirectly. Direct impacts such as increasingly common extreme weather events will negatively affect seabird physiology. However, climate effects on seabirds are more likely to be indirect, and mediated by prey quality and availability. Mounting evidence suggests that climate impacts on lower trophic levels are altering the pathway of energy to seabirds. While the basis for changes in primary production are complex and uncertain, climate driven changes in sandeels, and *Calanus finmarchicus*, key prey species in adjacent trophic levels, appear to be causing a reduction in breeding success and growth rate in several British seabird species.

Numbers of many species of seabirds around the United Kingdom increased between 1970 and 2000 (Figure 3.2). However, since the Seabird 2000 census (Mitchell et al., 2004), populations of some of the species have started to decline, such as the Atlantic puffin *Fratercula arctica* (Harris and Wanless, 2011), northern fulmar *Fulmarus glacialis*, and great cormorant *Phalacrocorax carbo*. Others have continued to increase, for example, the common guillemot *Uria aalge*, razorbill *Alca torda*, and especially the northern gannet *Morus bassanus*. In Scotland, northern gannets are possibly the only species to increase in abundance in the past decade (Wanless and Harris, 2012) and are continuing to form new colonies (Murray et al., 2006).

Most surface-feeding seabird species in the northern North Sea have suffered breeding failure since 2003. In Shetland, similar declines in breeding success happened earlier, during the 1980s. Large pursuit-diving species have not been so affected (Heubeck, 1989; Okill, 1989). Consequences of such declines in breeding success only become apparent in the population numbers after a considerable time lag, as these year-classes of birds mature and join the breeding population (Frederiksen et al., 2004; Mavor et al., 2005, 2006, 2008; Reed et al., 2006).

The overall trends in numbers of breeding seabirds over recent decades mask some marked regional variations (Figure 3.3). Significant increases were observed in the breeding numbers of, for example, guillemots in England and Wales; however, the trend was the opposite for those breeding in Scotland. Within any one year, some species have bred successfully, and others have not. For a given species, some regions have produced successful breeding and others not. In some cases, a lack of consistency has even been found among species inhabiting the same region (Wanless and Harris, 2012).

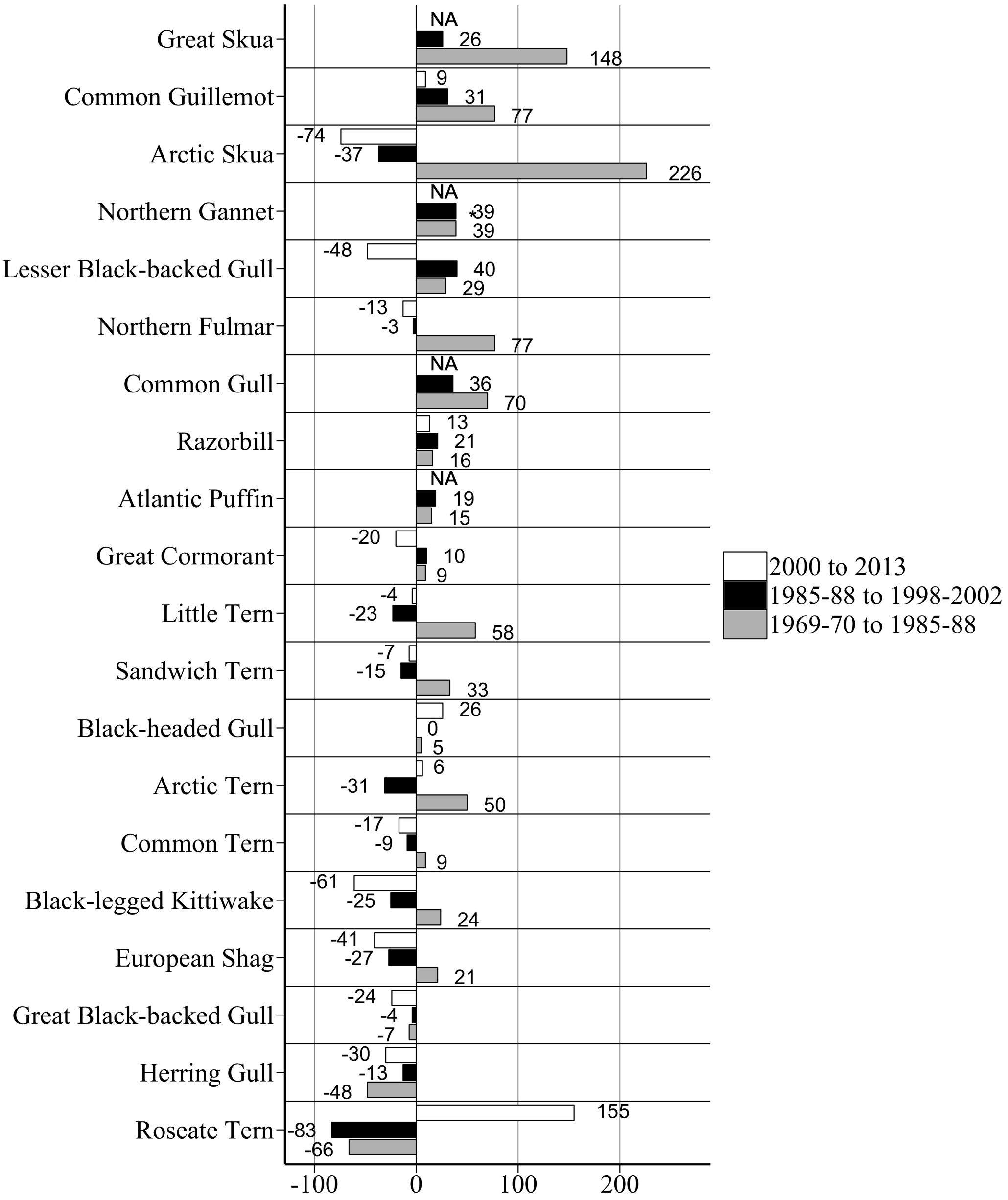


FIGURE 3.2: Changes in the numbers of breeding seabirds in the United Kingdom 1969—2002 (JNCC, 2013). Percentage changes refer to coastal-nesting seabirds only; inland colonies were not surveyed during the Operation Seafarer (1969 — 1970) (Cramp et al., 1974) and the Seabird Colony Register (SCR) censuses (1985 — 1988) (Lloyd et al., 1991) Manx shearwater, Leachs storm petrel, and European storm petrel are omitted as they were not surveyed during the Operation Seafarer (1969 — 1970) and the SCR censuses (1985 — 1988). Survey methods for black guillemots during Operation Seafarer (1969 — 1970) were not comparable with Seabird 2000 (1998 — 2002). Change from 2000 to 2012 (i.e., over the period since the last national census) was estimated from trends derived from the Seabirds Monitoring Programme sample of colonies; this analysis is only available for species with sufficient data to estimate trends accurately. *Change between censuses in 1984 — 1985 and 2004 — 2005.

Climate change is considered to be playing a significant role in the declines in seabird breeding numbers (Russell et al., 2015). In particular, sea-surface temperatures (SSTs)

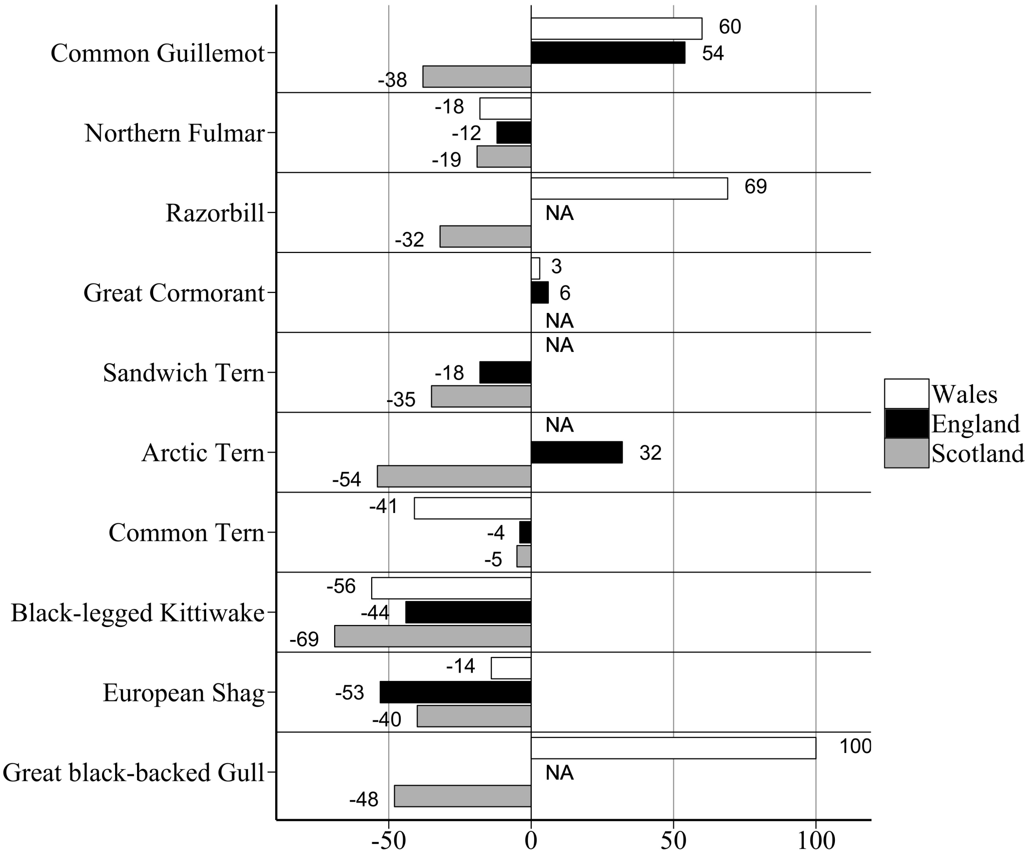


FIGURE 3.3: Changes in the numbers of breeding seabirds in Scotland, England, and Wales during the period 2000—2013 (JNCC, 2013). Change from 2000 to 2013 (i.e., over the period since the last national census) was estimated from trends derived from the Seabirds Monitoring Programme sample of colonies; this analysis is only available for species with sufficient data to estimate trends accurately (JNCC, 2013).

in UK coastal waters, which have been rising between 0.1°C and 0.5°C per decade for the past 30 years (Dye et al., 2013), have shown a strong negative relationship with the demographic rates of several seabird species. For example, the productivity of northern fulmar and black-legged kittiwake *Rissa tridactyla* on the Scottish eastern coast shows a negative relationship with SST (Burthe et al., 2014). Furthermore, survival rates of kittiwakes, European shags *Phalacrocorax aristotelis* (Burthe et al., 2014), Atlantic puffins, guillemots, and razorbills (Lahoz-Monfort et al., 2011) are also strongly negatively correlated with SST.

The physical environmental changes that accompany climate change may affect seabirds in a variety of direct and indirect ways. Direct effects include incidences of extreme weather events causing mass mortalities and damage to nests in breeding colonies (Frederiksen et al., 2008; Wanless and Harris, 2012).

In contrast, indirect effects may be mediated through prey quality and availability (Wanless et al., 2005; Burthe et al., 2012) affecting growth rates and breeding success. These are referred to as bottom-up cascading trophic effects (Carpenter et al., 1985; Pace et al., 1999; Polis et al., 2000; Heath et al., 2014). Here we review and synthesize the evidence for these climate-driven trophic cascade effects on seabirds in waters around the British Isles. We review evidence for the following hypothesis: Climate-driven changes in phytoplankton and zooplankton have led to a decline in sandeels, and hence declines in seabird breeding success, frequency of breeding, and survival (Figure 3.4). This is done by addressing the coupling between successive trophic levels in the food web. We begin with the connection between seabirds and sandeels and work towards lower levels.

3.3 Connections between seabirds and sandeels

The majority of open-sea bird species around Britain are essentially piscivorous. The prey items brought back to breeding sites by the 26 major seabird species were analysed during the Seabird 2000 survey (1998—2002) (Table 3.2) and found to consist mostly of sandeels (mainly *A. marinus*), small clupeoid fish, and zooplankton. Prey were either self-caught (i.e., taken alive from the sea) or stolen from other birds (Furness, 1987; Davis et al., 2005). Exceptions were scavenging species such as northern fulmars and gulls, which feed opportunistically and rely partly on discarded fish and offal from commercial fishing vessels (Camphuijsen and Garthe, 1997; Furness, 2003), and some of the diving species, whose diet includes a proportion of benthic organisms (Furness et al., 2012). There is overwhelming evidence that fish communities are being affected by climate change. Geographical shifts in the distribution of many shelf-sea fish communities around the British Isles have been well documented. Broadly speaking, these changes can be viewed as a response to warming sea temperatures to maintain individuals in a preferred temperature range (Hedger et al., 2004; Perry et al., 2005; Poulard and Blanchard, 2005; Désaunay et al., 2006; Heath, 2006; Dulvy et al., 2008). In some areas, this is manifested as a polewards shift in distribution or a move into deeper water. However, local topography and hydrography may limit the extent of such shifts.

Sandeels are currently at the southern edge of its latitudinal range around the British Isles (Fishbase, 2014), but unlike most other fish species, are not free to move into deeper waters in response to warming sea temperatures because of limited availability of suitable

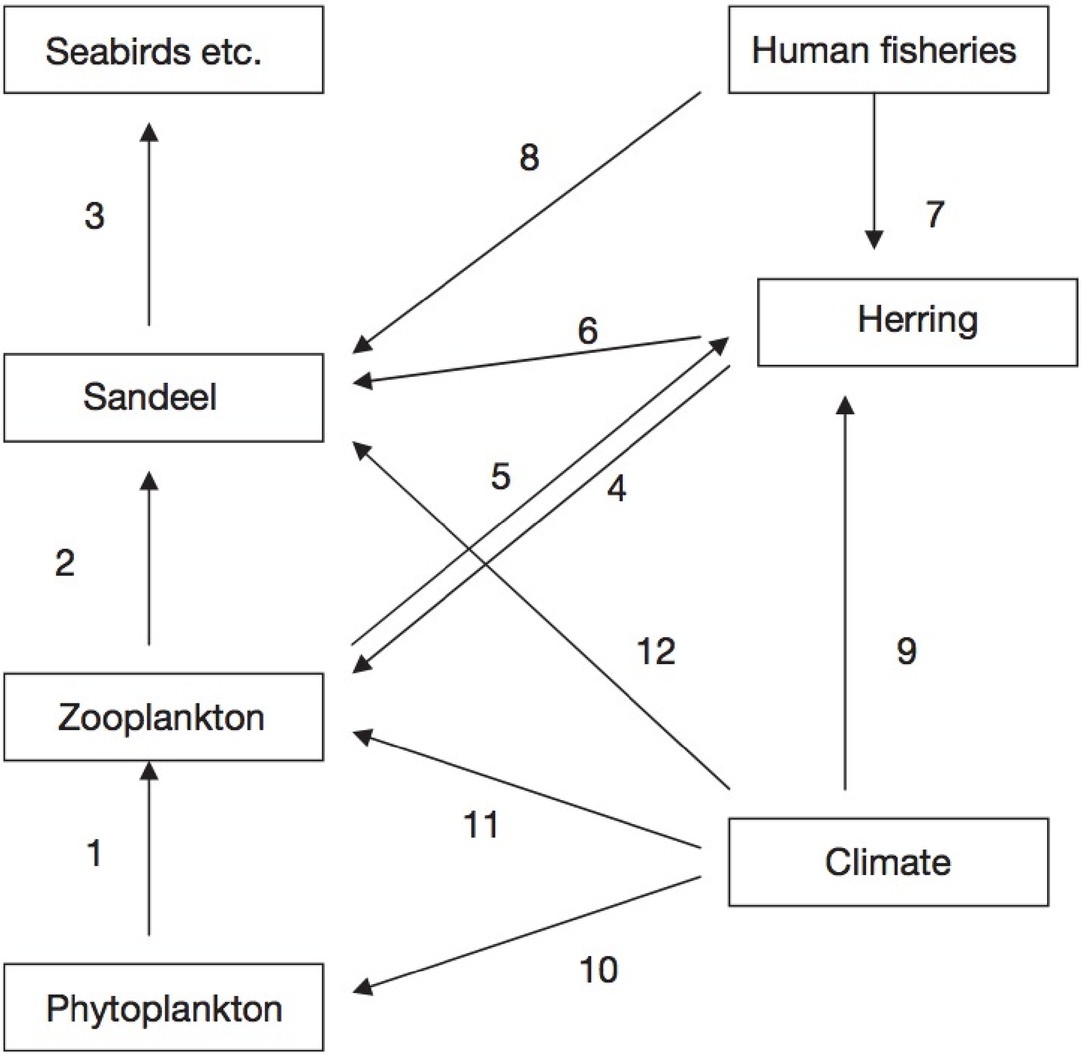


Figure 3.4: Simplified diagram of some documented and probable trophic and climatic controls in the North Sea pelagic ecosystem (after Frederiksen et al., 2007). 1, Bottom-up control of zooplankton by phytoplankton (Richardson and Schoeman, 2004); 2, bottom-up control of sandeel larvae by zooplankton (Frederiksen et al., 2006); 3, bottom-up control of seabird breeding success by sandeels (Hamer et al., 1993; Frederiksen et al., 2006); 4, top-down control of zooplankton by herring predation (Arrhenius, 1997); 5, bottom-up control of herring by zooplankton (Corten, 2001; Beaugrand, 2004); 6, top-down control of sandeels by herring predation (Frederiksen et al., 2007); 7, top-down control of herring by fisheries (Jennings et al., 2001); 8, local top-down control of sandeels by human fisheries (Rindorf et al., 2000); 9, climatic control of herring recruitment (Sætre et al., 2002); 10 and 11, climatic control of phytoplankton and zooplankton (Edwards and Richardson, 2004; Hays et al., 2005); 12, climatic control of sandeel recruitment (not known if direct) (Arnott and Ruxton, 2002).

habitat (Wright et al., 2000; Holland et al., 2005; Greenstreet et al., 2010). Sandeels' complex spatial population structure may further limit their capacity to adjust their distribution in response to warming. For example, the North Sea stock is composed of seven distinct populations, each exhibiting different population dynamics ((ICES), 2010,

Table 3.2: Names and life history characteristics of seabird species regularly breeding in the British Isles included in the JNCCs Seabird Monitoring Programme and the Seabird Colony Register.

Common name	Scientific name	General diet	Clutch size (no. eggs)	Age at first breeding (year)	Adult survival rate (year^1)	Lifespan (year)
Red-throated diver	*Gavia stellata*	Primarily fish, captured by seizing in bill; also frogs, large invertebrates	2	3 (Okill, 1994)	0.840 (Hemmingsson and Eriksson, 2002)	9
Northern fulmar	*Fulmarus glacialis*	Crustaceans, squid, fish, offal, carrion mostly from surface	1	9 (Dunnet and Ollason, 1978a)	0.972 (Dunnet and Ollason, 1978b)	44
Manx shearwater	*Puffinus puffinus*	Mostly small fish and squid, also small crustaceans and offal from surface or diving	1	5 (Thompson, 1987)	0.905 (Brooke, 1990)	15
European storm petrel	*Hydrobates pelagicus*	Mainly surface plankton, small fish; feeds from water surface without alighting	1	4—5 (Scott, 1970)	0.870 (Cramp, 1994)	11—12
Leachs storm petrel	*Oceanodroma leucorhoa*	Mainly surface plankton, small fish; feeds from water surface without alighting	1	4—5 (Huntington and Burtt, 1972)	0.880 (Furness, 1984)	12—13
Northern gannet	*Morus bassanus*	Fish (up to 30 cm), usually plunging from heights of 1040 m	1	5 (Alerstam, 1990)	0.919 (Wanless et al., 2006)	17
Great cormorant	*Phalacrocorax carbo*	Fish, mostly by diving from surface	3—4	2—4 (Cramp, 1977)	0.880 (Frederiksen and Bregnballe, 2000)	10—12
European shag	*Phalacrocorax aristotelis*	Fish, mostly by diving from surface	3	3 (Potts et al., 1980)	0.878 (Harris et al., 1994)	11
Arctic skua	*Stercorarius parasiticus*	Summer: mostly birds, small mammals, insects Winter: fish, mostly by piracy from other birds	2 (Furness, 1987)	4 (Lloyd et al., 1991)	0.886 (O'Donald, 1983)	12
Great skua	*Catharacta skua*	Mostly fish, obtained from sea, scavenging or by piracy	2 (Furness, 1987)	7 (Klomp and Furness, 1991)	0.888 (Ratcliffe et al., 2002)	15
Mediterranean gull	*Larus melanocephalus*	Summer: insects Winter: marine fish and molluscs	3	NA	NA	NA
Black-headed gull	*Larus ridibundus*	Opportunist, insects, earthworms, also plant material and scraps	2—3	2—5 (Clobert et al., 1994)	0.9 (Prévot- Julliard et al., 1998)	11—14
Mew gull	*Larus canus*	Invertebrates, some fish; preference for foraging on ground	3	3—4 (Cramp and Simmons, 1983)	0.860 (Bukacinski and Bukacinska, 2003)	10—11
Lesser black-backed gull	*Larus fuscus*	Omnivorous; often feeds at rubbish dumps or on shoals of fish	3	4—5 (Harris, 1970)	0.913 (Wanless et al., 1996)	15—16

2013; Boulcott and Wright, 2011).

The well-documented declines in breeding productivity of kittiwakes, shags, and Atlantic puffins (Lahoz-Monfort et al., 2013) are highly correlated with the availability of sandeels, especially the older age classes of sandeel (Pinaud and Weimerskirch, 2002; Frederiksen et al., 2006, 2013).

There are strong regional variations in the importance of sandeels in the seabird diet. In northern UK waters, sandeels are the only significant prey for seabirds. For example,

TABLE 2.2 continued. Names and life history characteristics of seabird species regularly breeding in the British Isles included in the JNCCs Seabird Monitoring Programme and the Seabird Colony Register.

Common name	Scientific name	General diet	Clutch size (no. eggs)	Age at first breeding (year)	Adult survival rate ($year^{-1}$)	Lifespan (year)
Herring gull	*Larus argentatus*	Omnivorous, but mostly animal material; also scavenges and kleptoparasitizes	3	4—5 (Chabrzyk and Coulson, 1976)	0.880 (Wanless et al., 1996)	12—13
Great black-backed gull	*Larus marinus*	Omnivorous, but mostly animals, including other seabirds; also scavenges and kleptoparasitizes	2—3	4—5 (Cramp and Simmons, 1983)	NA	NA
Black-legged kittiwake	*Rissa tridactyla*	Mainly marine invertebrates and Mainly marine invertebrates and fish	2	3—4 (Coulson and White, 1959)	0.882 (Harris et al., 2000)	11—12
Sandwich tern	*Sterna sandvicensis*	Fish; mostly plunge-diving	1—2	3 (Snow and Perrins, 1998)	0.898 (Robinson, 2010)	12
Roseate tern	*Sterna dougallii*	Fish; mostly plunge-diving	1—2	3—4 (Spendelow, 1991)	0.855 (Ratcliffe et al., 2008)	9—10
Common tern	*Sterna hirundo*	Mostly fish, also crustaceans in some areas, mostly by plunge-diving	2—3	3—4 (Nisbet et al., 1984)	0.900 (Becker and Ludwigs, 2004)	12—13
Arctic tern	*Sterna paradisaea*	Fish, crustaceans, and insects	1—2	4 (Coulson and Horobin, 1976)	0.900 (Balmer and Peach, 1997)	13
Little tern	*Sterna albifrons*	Small fish and invertebrates; often hovers before plunge-diving	2—3	3 (Massey et al., 1992)	0.899 (Tavecchia et al., 2006)	12
Common guillemot	*Uria aalge*	Mostly fish, usually taken from depths up to 60 m	1	5 (Olsson et al., 2000)	0.946 (Harris et al., 2000)	23
Razorbill	*Alca torda*	Fish, some invertebrates	1	4—5 (Lloyd, 1976)	0.900 (Chapdelaine, 1997)	13—14
Black guillemot	*Cepphus grylle*	Mostly fish, also crustaceans, especially in the Arctic	1—2	3—4 (Ewins, 1988)	0.870 (Frederiksen and Petersen, 1999)	10—11
Atlantic puffin	*Fratercula arctica*	Mostly fish, also crustaceans, especially in the Arctic	1	4—6 (Harris, 1983; Johnsgard, 1987)	0.924 (Harris et al., 1997)	17—19

sandeels have been the only common high-lipid schooling fish around Shetland in recent decades. Breeding success of most seabirds is therefore strongly related to sandeel abundance in that region (Hamer et al., 1993; Davis et al., 2005). Seabirds off south-eastern Scotland have access to other fish prey (e.g., young herring and sprat; Bull et al., 2004; Harris et al., 2004; Wilson et al., 2004), but sandeels are still the main prey (Wanless et al., 1998). However, in south-western British waters there are higher abundances of alternative prey such as sprat and juvenile herring, so the linkage to sandeel availability is correspondingly weaker.

It cannot be ruled out that climate change could result in the growth of sprat or juvenile herring populations in northern waters. Abundance of European sprat in the North Sea increased markedly between 2000 and 2005, changes ascribed to increases in temperature (Lenoir et al., 2011). During this time, guillemots at Fair Isle, between Orkney and Shetland, underwent a dietary shift (Heubeck, 2009), consuming more gadoids and sprat and fewer sandeels, than previously. Records on guillemot chick diet composition from the Isle of May in the Firth of Forth indicate that sprat have accounted for the majority of chick diet since 2000 (Anderson et al., 2014). While this is probably a response to lack of sandeels, it is possible that guillemot diet partially reflects their preference for sprat. Indeed, sprat might actually represent a higher-quality prey resource than sandeels (Smout et al., 2013). This may be why guillemots have been known to switch to sprat even when sandeels are orders of magnitude more abundant (Greenstreet et al., 2010).

In the north-western North Sea, other potential effects on seabirds arise from the apparent changes in growth rates of sandeels since the 1970s. The decline in size-at-date of post-metamorphic 0-group sandeels leads to a mismatch between the timing of seabird breeding and availability of adequate prey. The weight-specific energy content of sandeel is related to their body size, so slower growth rates mean declining calorific content of prey fed to chicks on a given day of the year (Wanless et al., 2004; Burthe et al., 2012). Prey energy value is critical for seabird breeding success (Wanless et al., 2005). This was most apparent in 2004, when the Isle of May was the site of unprecedented catastrophic breeding failures. Subsequent analysis revealed that sandeel energy content was much lower than expected (Wanless et al., 2005). Figure 3.5 shows the differences in energy content at length between 2004 and 4 other years,1976, 1986, 1987 and 1988. Interestingly, there has been a trend towards later breeding in several species (Burthe et al., 2012), almost as if seabirds are attempting to mitigate the negative trend in sandeel energy content. However, chicks of guillemot, shag, kittiwake, Atlantic puffin, and razorbill have all suffered net reductions in energy value because of this decline in sandeel energy content (Burthe et al., 2012).

In addition to effects on seabird chicks, a lack of 0-group sandeel availability and quality can affect adult seabirds. Adult mortality is particularly sensitive to prey availability during the breeding season. This is because seabirds must attain a sufficient level of body energy to meet breeding costs (Oro and Furness, 2014; Ratcliffe et al., 2002). In Shetland, sandeel abundance is related to adult survival of various species, in particular kittiwake and great skua *Catharacta skua* (Oro and Furness, 2014; Ratcliffe et al., 2002).

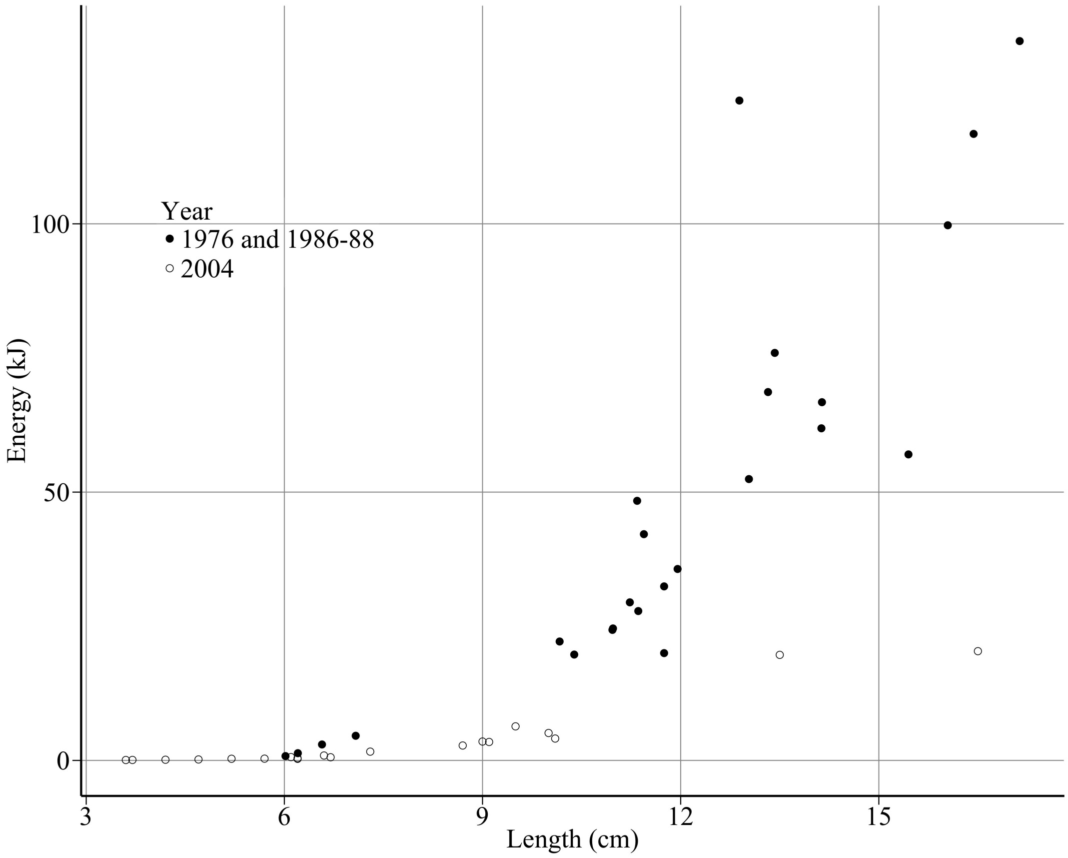


FIGURE 3.5: An example of marked annual variation in sandeel energy content. Shown is the energy content of sandeels taken by seabirds in 1976 and 1986-88 (black points) and 2004, the year of catastrophic seabird breeding failures on the Scottish east coast (clear points). Data from 1976 and 1986—88 was digitised from Figure 1 in Hislop et al. (1991). Data from 2004 was taken from Table 2 in Wanless et al. (2005).

3.4 Connections between sandeels and zooplankton

Zooplankton carry out the role of transferring primary production to fish. Sandeels are likely to be bottom-up limited by zooplankton abundance (Frederiksen et al., 2006; Pitois et al., 2012).

During the 1980s, the North Sea ecosystem underwent a regime shift that resulted in pronounced changes to the composition of the fish and plankton community (Beaugrand, 2004). These changes have been ascribed to increased sea temperature (Beaugrand et al., 2002; Perry et al., 2005). Recent decades have seen pronounced northwards shifts in the range of calanoid copepods (Reid et al., 1998, 2001; Beaugrand et al., 2002; Drinkwater et al., 2003; Reygondeau and Beaugrand, 2011). The mean rate of northwards movement for some north-eastern North Atlantic species assemblages between 1958 and 2005 has been estimated at roughly 23 km $year^{-1}$ (Beaugrand et al., 2009). During this time, the critical threshold separating boreal and temperate zooplankton systems has moved northwards by 22 km $year^{-1}$ (Beaugrand et al., 2008).

Changes in zooplankton composition could be damaging to sandeels. There are 2 main reasons for this, the ongoing decline in the calanoid copepod *C. finmarchicus*, and decreasing zooplankton size. *C. finmarchicus* are currently vital for sandeels, since larval survival depends specifically on *C. finmarchicus* abundance, and not the abundance of any other copepod group. Despite being previously dominant in the North Sea, *C. finmarchicus*, has declined in biomass by 70% since the 1960s. Species with warmer-water affinities are moving northwards to replace *C. finmarchicus*, but are not as numerically abundant or nutritionally beneficial to higher trophic levels.

Recent temperature increases have reduced the size of zooplankton (Beaugrand et al., 2003), which could decrease sandeel growth and survival. Declines in sandeel length could be linked to decreases in zooplankton size (van Deurs et al., 2014). A time series of sandeel length at age in the southern North Sea shows a decrease in the late 1980s, around the time when the mean size of calanoid copepods decreased by a factor of two (Beaugrand et al., 2003). This decrease in copepod size was an effect of the regime shift that took place in the North Sea in the late 1980s, associated with a switch in the NAO (North Atlantic Oscillation) index from a negative to a positive phase (Reid et al., 2001; Beaugrand et al., 2002, 2003; Beaugrand and Reid, 2003; Beaugrand, 2004).

Despite the documentation of changes in species distribution, there is little clear evidence of changes in overall zooplankton production in the North Sea. Trends in zooplankton production off the Scottish eastern coast do not reflect the pattern of decline in sandeels (Heath et al., 2012; OBrien et al., 2013). Changes in seasonality (van Deurs et al., 2009), size (Beaugrand et al., 2003), and lipid content of zooplankton (Wanless et al., 2005; Beaugrand et al., 2009) could all affect sandeel populations. However, we cannot definitively rule out the hypothesis that changes in zooplankton production contributed to the sandeel decline. Zooplankton community production is exceptionally difficult to estimate, even by direct experimental measurements.

Northward shifts of plankton species are expected to continue with increasing sea temperatures (Reygondeau and Beaugrand, 2011). How these changes will affect higher trophic levels remains unclear. However, it is thought that the retreat of *C. finmarchicus* will be damaging to sandeel populations (van Deurs et al., 2009) and, ultimately, seabirds (Frederiksen et al., 2013). A recent niche model study (Frederiksen et al., 2013) showed that the breeding success of kittiwakes and Atlantic puffins on the Isle of May is significantly related to environmental suitability for *C. finmarchicus* (van Deurs et al., 2009). Therefore, it may become increasingly difficult for several boreal seabird species to maintain adequate breeding success as this *Calanus* species continues its retreat.

The future of sandeels in the North Sea will rest on whether a suitable replacement prey can be found, with the most viable candidate being *Calanus helgolandicus.* However, *C. finmarchicus* abundance peaks in spring (Bonnet et al., 2005) concurrently with mean larval hatch date (Heath et al., 2012), whereas *C. helgolandicus* abundance peaks in autumn (Bonnet et al., 2005). Therefore, a mismatch between larval emergence and prey availability may occur if *C. helgolandicus* becomes the dominant prey species for sandeels.

Geographical shifts in plankton species can be related to environmental changes (Beaugrand and Helaouët, 2008). There can be reasonable confidence in predictions of shifts in geographical distributions for different climate-change scenarios, subject to the assumption that the underlying processes governing species environmental preferences and tolerances (their environmental envelope) will remain constant in the future (Davis et al., 1998; Pearson and Dawson, 2003). In addition, it seems reasonably certain that the zooplankton diversity in waters around the British Isles will increase with continued warming (Beaugrand et al., 2008), with a progressive shift towards smaller plankton. A shift towards smaller zooplankton may lead to reductions in trophic transfer efficiency due to increased food-chain length.

Ocean modelling predicts a reduction in zooplankton biomass in the North Sea over the next century (Chust et al., 2014). These changes are thought to arise via bottom-up amplification of climate-driven impacts on phytoplankton (Chust et al., 2014). Understanding how climate change may affect zooplankton indirectly through changes in primary production is, therefore, essential.

3.5 Connections between zooplankton and phytoplankton

The production of zooplankton, fish, and higher trophic levels in the marine ecosystem is ultimately be related to primary production and the efficiency of transfer between trophic levels (Aebischer et al., 1990; Schwartzlose et al., 1999; Chavez et al., 2003). Hence, comparing across ecosystems in the north-western Atlantic, there is a positive correlation between long-term average chlorophyll concentration and fishery yield (Frank et al., 2005). It is clear that primary production drives sandeel stock biomass in some ecosystems (Eliasen et al., 2011). However, within individual ecosystems, the relationship between primary production and fisheries yield varies over time. This is due to a range of factors affecting the transfer of energy up the food web, and the intensity of exploitation of the fish stocks.

Over several decades, changes in phytoplankton species and communities in the North Atlantic have been associated with temperature trends and variations in the NAO index (Beaugrand and Reid, 2003). These changes have included the occurrence of subtropical species in temperate waters, changes in overall phytoplankton biomass and seasonality, and changes in the ecosystem functioning and productivity of the North Atlantic (Edwards et al., 2001; Beaugrand, 2004). North Sea phytoplankton biomass has increased in recent decades (Edwards et al., 2001), and there has been a concurrent increase in smaller flagellates, which are promoted by warmer and more stratified conditions (Edwards & Richardson 2004). Over the whole north-eastern Atlantic, there has been an increase in phytoplankton biomass with increasing temperatures in cooler regions, but a decrease in phytoplankton biomass in warmer regions (Barton et al., 2003). However, nutrient concentrations are likely to limit any sustained positive response to warming (OBrien et al., 2013).

Unfortunately, it is only possible to speculate on how climate change may indirectly impact zooplankton through changes in phytoplankton. It is possible that climate-driven changes in phytoplankton and zooplankton phenology (Edwards and Richardson, 2004) may reduce prey availability for zooplankton. However, clear evidence that changes in climate have already impacted phytoplankton, resulting in zooplankton changes, remains thin.

3.6 Discussion of climate-driven trophic cascades

Climate-driven trophic cascades may already be affecting UK seabirds. Whilst the basis for changes being driven by primary production are complex and uncertain, there is string evidence of direct climate impacts on zooplankton (Beaugrand et al., 2002; Hays et al., 2005; Beaugrand et al., 2009; Reygondeau and Beaugrand, 2011) and indirect climate impacts on sandeels (van Deurs et al., 2014). This appears to be distrupting the transfer of energy to seabirds, causing declines in their breeding success and survival, primarily those off the Scottish east coast.

It is likely the recent succession of poor breeding years will propagate through seabird populations to cause a decline in breeding numbers in the short term. Beyond this, changes will depend on the balance between breeding success and adult survival, and both depend critically on the scope for feeding on alternative prey if sandeel stocks do not recover over time. However, UK seabirds will vary in their response to declines in sandeel abundance, and indeed to changes in the forage fish community. Certainly, the strength of resilience to food shortages appears to differ among species. For example, kittiwakes are sensitive to reductions in sandeel availability (Furness and Tasker, 2000), while adult guillemots seem able to maintain provisioning of their chicks despite fluctuating abundances of key prey (Smout et al., 2013).

Interspecific variation in sensitivity to reductions in sandeel abundance may explain why climate effects appear to be species specific (Lahoz-Monfort et al., 2011). This is true if sandeel abundance is negatively correlated with climate indices. Winter NAO and SST are contributing to synchrony, as well as desynchrony, in survival rates of auks (Alcidae) off the Scottish eastern coast (Lahoz-Monfort et al., 2011).

Continued decline in sandeel quality and abundance can cause the North Sea seabird community to become increasingly dominated by species least reliant on sandeels (Furness and Tasker, 2000). The recent increase in northern gannet populations may be an example of this (Wanless et al., 2005; Murray et al., 2014). These birds are insensitive to reductions in sandeel availability, owing in part to their high ability to switch diet (Furness and Tasker, 2000). Northern gannets are also the largest seabirds in the North Atlantic. Therefore, a trend towards a seabird community dominated by larger seabirds contrasts strongly with observed trends in prey length in lower trophic levels.

The regional pattern of decline in seabird numbers is strikingly similar to the decline in sandeel populations. Regional differences in the strength of bottom-up regulation may provide an explanation. In the Irish Sea, Celtic Sea, and the English Channel, there appears to be little evidence of bottom-up regulation (Lauria et al., 2013). However, bottom-up effects have been found in the north-western North Sea (Frederiksen et al., 2006), which could be indicative of different oceanographic conditions (Lauria et al., 2013). Climate change impacts on lower trophic levels may therefore affect seabird numbers in the northern North Sea but have little effect on seabirds in southern areas.

It is unclear if other forage fish can adequately replace sandeels in the seabird diet. The predicted temperature-related increase in sprat around Britain (Lenoir et al., 2011) may mitigate a shortage of sandeels. However, sprat are predicted to dissappear from British waters by the end of the twenty-first century (Lenoir et al., 2011), and so do not represent a long-term solution for seabirds. The ecosystem role vacated by sandeels and sprat will likely be filled by warm-water midtrophic fishes such as anchovies (Lenoir et al., 2011). Although these fishes may fill the void left by sprat and sandeels in seabird diets, whether or not there will be a smooth transition in prey is unknown. Consistent recruitment failure of herring (Payne et al., 2013, 2009) places in doubt the viability of this species as alternative prey for seabirds. Many seabirds are able to prey on piscivorous demersal fish like whiting (*Merlangius merlangus*), but these have a low energy density, and the body condition of chicks is much poorer in years when whiting are the main prey (Harris, 1980).

Anthropogenic impacts may exacerbate climate impacts on seabirds (Frederiksen et al., 2004; Votier et al., 2005). On the Scottish eastern coast, the species most vulnerable to these combined threats are northern fulmars, kittiwakes, and shags (Burthe et al., 2014). Their growth and survival has been decreasing with rising temperature, most likely through changes in prey such as sandeels. To ameliorate any declines in these demographic parameters, efforts to safeguard vital seabird prey around important colonies, such as the Isle of May, could be put in place.

The most notable example of a measure to protect seabird prey has been the sandeel fishery closure off the eastern coast of Scotland. Established in 2000 with the aim of avoiding depletion of the sandeel stock, an area covering approximately 21,000 km^2 was closed to sandeel fishing (Frederiksen et al., 2008; Greenstreet et al., 2010). However, closing the area to fishing has not been sufficient to ensure high sandeel abundance (Figure 1.5).

Recent measures have been implemented to protect marine habitats adjacent to seabird colonies. In 2009, the boundaries of 31 of the Special Protection Areas (SPAs) designated for seabird breeding colonies in Scotland were extended seawards (Scottish Natural Heritage 2009); however, these expanded areas are extremely small (extending to <5 km off shore) and therefore may not effectively safeguard seabird prey. This is especially true for sandeel-feeding seabirds because of the patchiness of sandeel habitat. Moreover, many seabirds have foraging ranges that span many tens of kilometres (Thaxter et al., 2012).

Measures to protect sources of sandeel larvae that are exported to seabird colonies can also be put in place. Recently, two marine protected areas (MPAs), to the north-west of the Orkney Islands (59°31′N 3°14′W) and around Turbot Bank (off the north-eastern coast of Scotland, 57°23′N 0°56′W), have been established with the aim of protecting the supply of sandeel larvae (Joint Nature Conservation Committee [JNCC] 2014a,b). These locations are considered to be important sources of newly hatched sandeel larvae (Wright & Bailey 1996), which, through dispersal, support sandeel stocks afar. MPAs may lead to increased abundance outside the MPA through larval spillover (Christensen et al. 2009); however, the extent of effective spillover will obviously depend on availability of suitable habitat elsewhere.

Part II

Modelling spawning and hatch dates and growth rates

Chapter 4

A long term decline in sandeel juvenile size is not caused by changes in spawning or hatch dates

Here I analyse spawning or hatch dates, a possible contributor to the long-term negative trend in 0-group size. A 10-year time series (2000-2009) of sandeel catches is used to calculate the timing of spawning and hatching. Results indicate that spawning and hatch dates do not explain a negative trend in 0-group size. Instead, the timing of both life cycle events is relatively fixed and is governed by predictable environmental cues. Spawning is synchronous and cued by the neap tide, while hatch dates relate significantly to the date of annual minimum temperature. Moreover, given the weak temperature effect on spawning and hatching, future temperature changes appear unlikely to significantly affect hatch date. The causes of declining 0-group size can be narrowed down to indirect changes e.g. changes in prey availability or predation.

4.1 Potential drivers of a long-term decline in sandeel length

Ongoing climate change is causing significant changes in the phenology of marine organisms (Thackeray et al., 2010 and Edwards and Richardson, 2004). These changes have a number of effects at the level of interactions between species, with mismatches between the timing of life cycle events being suggested as a major driver of recruitment in some species (Beaugrand et al., 2003; Platt et al., 2003). Significant oceanic warming is likely unavoidable this century (Intergovernmental Panel on Climate Change, 2007). Therefore, understanding the environmental drivers of the timing of life cycle events is a key challenge of current marine biology and ecology. Phenological changes in prey that trigger changes in predator abundance are referred to as bottom-up trophic cascades (Carpenter et al., 1985; Pace et al., 1999; Polis et al., 2000; Heath et al., 2014). In the North Sea, the connection between seabirds and sandeels provides an illustrative example of a trophic cascade. Here a reduction in sandeel quality and availability has likely contributed to the decline in seabird breeding numbers (MacDonald et al., 2015).

Off the Scottish east coast, sandeel juveniles play a key role in the diet of seabird chicks during the breeding season (Wanless et al., 1998; Lewis et al., 2001; Wanless et al., 2004; Lahoz-Monfort et al., 2011). In some years, several seabird species feed their chicks a diet comprised almost exclusively of sandeel juveniles (Lewis et al., 2001). Seabirds are influenced by a number of factors, including total abundance and timing of seasonal abundance peaks in 0-group sandeels (Pinaud and Weimerskirch, 2002; Frederiksen et al., 2006, 2007; Wright 1996). In addition, seabirds are sensitive to 0-group energy value (Wanless et al., 2004; Wilson et al., 2004; Burthe et al., 2012). This energy value is mostly determined by sandeel length, which is why poor breeding success has often occurred in years when length is smaller than average (Wright 1996, Lewis et al., 2001). Hence, it is a concern that juvenile length has been declining for the past few decades (Wanless et al., 2004; Frederiksen et al., 2011).

Several mechanisms could drive a long-term decline in 0-group length. Changes in larval mortality with respect to hatch date could explain this decline if mortality of early hatching larvae gradually increased. Other mechanisms which could drive this decline are changes in spawning and hatching dates, and larval growth rate. Only Frederiksen et al. (2011) has attempted to address which mechanisms have caused this decline in 0-group size. This study used Continuous Plankton Recorder Data to reconstruct changes in hatch date and growth rates between 1975 and 2006 across the northwestern North Sea. It was concluded that the principal driver of a reduction in juvenile size between 1975 and 1995 was later hatching. This would result in sandeels being younger, and therefore smaller during seabird breeding season. Further, despite a trend towards earlier hatching a decrease in growth rate was proposed as the cause of declining size between 1996 and 2006. The difficulty in using CPR data to estimate sandeel hatch dates is that catches by the CPR sampler are low and are conducted at 1-month nominal intervals. To correct for this, catch data has to be aggregated over a large area. However, this is problematic if there is large spatio-temporal variation in hatching which may be the case in sandeels (Lynam et al., 2013). If large spatial variation in hatch timing exists, then aggregating CPR data over a large area to correct for small catches of sandeel larvae might result in a skewed estimation of hatch date. In this case, it is wise to derive hatch dates from a single location, so long as there is high temporal resolution.

The mechanisms underpinning spawning and hatching are poorly understood. This is largely due to a lack of long-term data, which makes it difficult to analyse correlations with environmental variables such as temperature. Spawning occurs in December and January (Winslade, 1974; Bergstad et al., 2001). Temperature can be a major driver of spawning time (Carscadden et al., 1997) or not at all (Gordoa and Carreras, 2014). The little we do know about spawning mechanisms is gathered from the Pacific sandeel (*A. Hexapterus*). This species occasionally spawns en masse during the high tide period (Penttila, 1995).

Hatching in *A. marinus* occurs well in advance of the spring bloom, around the date of annual temperature minimum (Coombs, 1980; Wright and Bailey, 1996). There are two main drivers of hatch date, a temperature-dependent incubation period and spawning date (Winslade, 1971). One of the few studies on hatch date variability showed that large inter-annual changes in hatching were not driven by temperature during the incubation period. Instead, changes in spawning dates or oxygen concentration were proposed as potential hatch date drivers (Winslade, 1971). Recent laboratory work shows that the effect of temperature on the duration of ovarian development, and therefore spawning date, may be much greater than the effect on the duration of embryonic development (Wright et al., 2017).

Here I examined possible environmental drivers of sandeel spawning and hatching. Using weekly catches of sandeel larvae between 2000 and 2009 on the Scottish east coast, the most detailed account of inter-annual variation in sandeel hatching to date is presented. Temperature data is then used to hindcast the likely spawning dates. I show that spawning and hatch dates are relatively fixed in time and are cued by predictable environmental changes.

4.2 Materials and methods

4.2.1 Year-to-year changes in juvenile length

Between 2000 and 2009 Scientific monitoring of sandeels was conducted in the sandbanks off the Firth of Forth (between 56° 00′N and 56° 30′N and 003° 00′W and 001° 00′W) (Table 4.1). Changes in summer 0-group length were estimated from pelagic trawl catch data (Table 4.1). The total catch in each trawl sample was quantified (number caught per 0.5-cm size class). Length-stratified subsamples were taken and otoliths were extracted to determine age length keys for each cruise. Age was determined from otolith macrostructure using counts of annuli (ICES, 1995).

Table 4.1: The number of sandeels caught and aged from pelagic trawls. Juveniles were captured in 2000—2003, 2005—2006 and 2009. No survey took place in 2004, and only 6 sandeels were measured for length in 2007. In addition, pelagic trawling in 2008 caught no 0-group.

Year	Date	Number of individuals caught	Number of otoliths measured
2000	15th —19th June	2626	842
2001	5th —9th June	5362	1265
2002	15th —20th June	5584	416
2003	14th —17th June	5877	1305
2005	25th —27th May	4759	906
2006	17th —19th June	231	203
2009	13th —15th June	1358	295

To generate probability distributions of age-given-length for each 1 mm length class in the sample, the continuation-ratio logit method was applied to otolith data to produce smooth age length keys (Kvist et al., 2000; Rindorf and Lewy, 2001; Stari et al., 2010). Changes in distribution of age at a given length, as a function of length, were estimated using Generalized Linear Modelling. Fitting was performed using Maximum Likelihood Estimation. For each sample, abundance-at-age-and-length was given by the product of abundance-at-length and probability of age given length. This produced a matrix of abundance at age (columns) and length (rows). Mean length at age a (M_L) was given by

$$M_L = \frac{\sum_i L_i f_{i,a}}{\sum_i f_{i,a}} \tag{4.1}$$

where L_i is length i (cm) and $f_{i,a}$ is the abundance of sandeels at age a (years) and length i.

4.2.2 Year-to-year changes in larval abundance

Weekly sampling of plankton and fish larvae took place on the northeast coast of Scotland (56° 57.83N, 002° 06.74′W, water depth = 45m; Figure 4.1) between 2000 and 2009. Plankton were sampled with a 100 cm mouth diameter net of 350 μm mesh. The net was towed obliquely at a speed of 1 m s^{-1} to within ~3 m of the seabed depth (45 m). Upon recovery of the net, the whole catch was washed into the cod-end. Temperature data was recorded during each survey at 1 m and 45 m depths, respectively, using reversing thermometers and conductivity, temperature and depth probes. All sandeel larvae were removed from the catch and identified to species. *A. marinus* was distinguished from the other sandeel species present in the samples (*H. lanceolatus*, the Greater Sandeel, and *A. tobianus*) by the absence of dorsal melanophores.

The majority of the larval catch between 2000 and 2009 was *A. marinus*, with *H. lanceolatus* forming a much smaller proportion (Figure 4.2). In February and March the catch was composed exclusively of *A. marinus*. However, *H. lanceolatus* formed an increasing proportion of the catch after March, comprising 20%, 39% and 81% of the catch in April, May and June, respectively (Figure 4.2).

A. marinus larvae were measured to the nearest 0.1 mm in standard (notochord) length using a binocular microscope and calibrated digitising pad connected to a PC. On each sampling occasion, the depth-averaged concentration (m^{-3}) of sandeel larvae was estimated by dividing the total catch by the volume of water filtered. Larval concentration was then binned to 1 mm length groups by applying the proportions of measured larvae in each length class. Sea surface area specific abundances (m^{-2}) were estimated by multiplying the depth average concentration and seabed depth.

Volume filtered was estimated preferentially from the flowmeter data by applying an instrument-specific calibration factor (c, revs m^{-1}) and the net mouth area, to the total

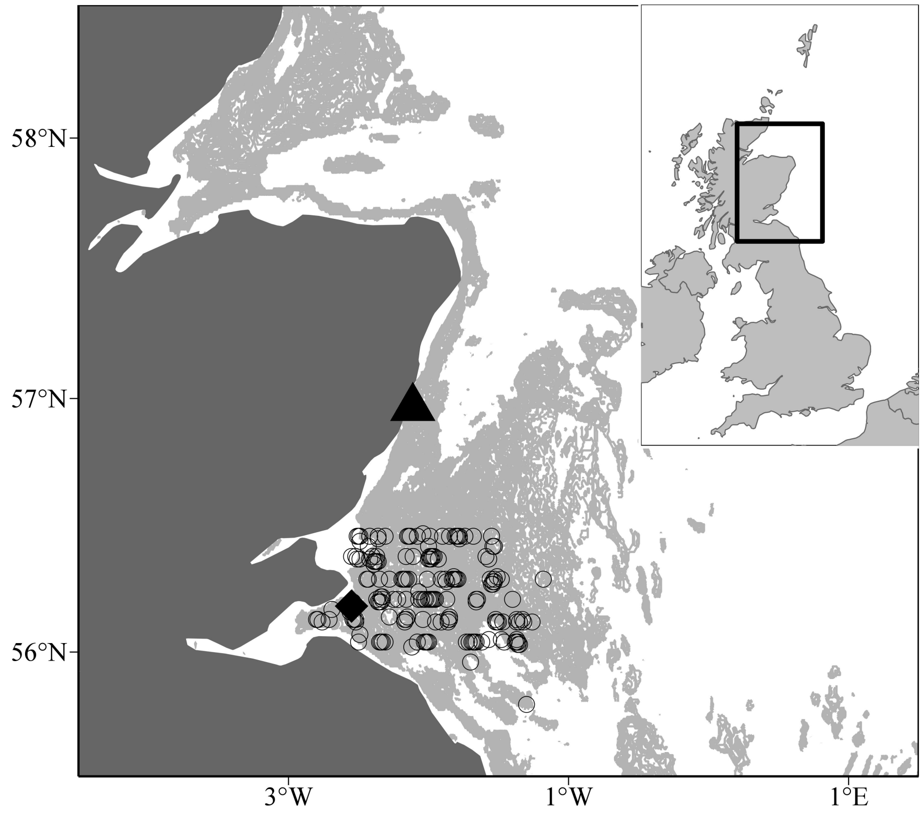


FIGURE 4.1: Location of the monitoring site off the Scottish east coast (black traingle, 56° 57.83′N, 002° 06.74′W) and pelagic trawl locations (open circles). The black diamond denotes the Isle of May seabird colony. The pale grey shaded area indicates water depths between 30 and 70m, the range of depth sandeels are most commonly found (Wright et al., 2000), and marks out the 3 main sandbanks, Wee Bankie, Marr Bank and Berwicks Bank.

flowmeter revs during each tow (area × revs × $1/c$). In cases where flowmeter data were missing, volume was estimated from the product of tow duration, speed of the boat through the water, mouth area of the net, and a flow-resistance factor (f). The flow-resistance factor (f=0.46) was estimated from the coefficient of a linear regression between y= revs × $1/c$ and x=duration × speed based on tows with valid flowmeter data (r=0.86, n=191).

4.2.3 Hatch date estimation

Daily increments on larval sagitta otoliths were used to calculate sandeel age (Wright, 1993). Otolith ages were determined for 307 individual larvae collected at the monitoring site during 2000-2001 (141 in 2000, and 166 in 2001). Next, the methodology

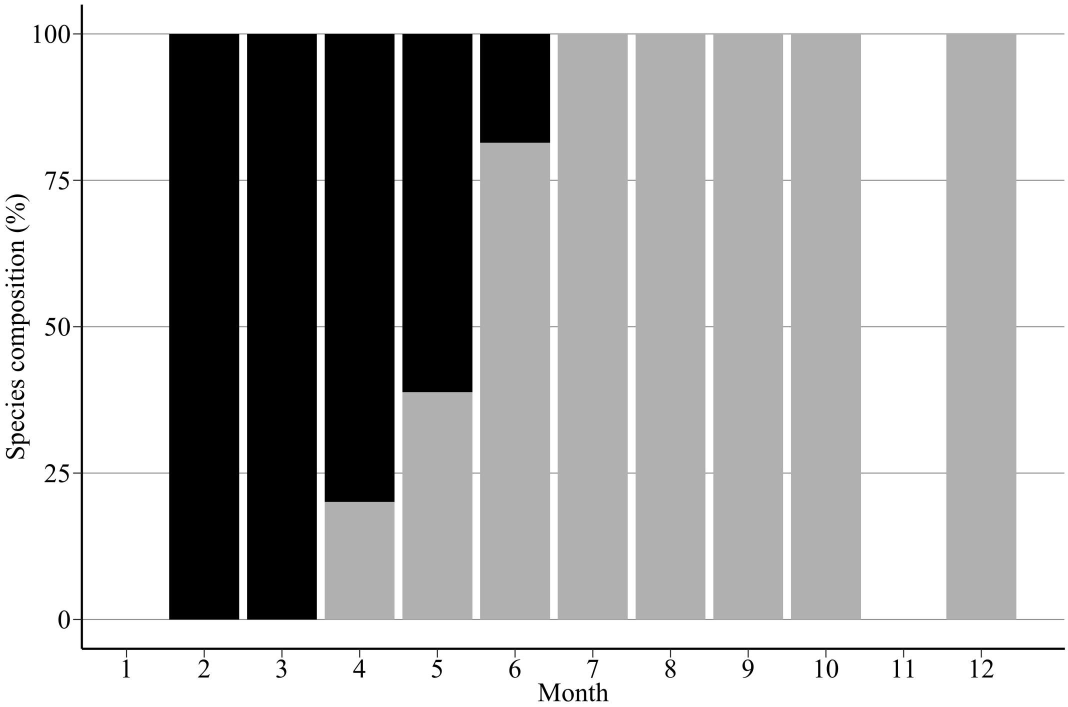


FIGURE 4.2: Mean seasonal distributions of *A. marinus* and *H. lanceolatus* larvae. Bars show the mean proportion by numbers averaged over calendar months for all 10 years of sampling.

used to estimate 0-group abundance-at-age at each survey, explained previously to estimate larval abundance-at-age at each survey, was employed. Note that otolith data for 2000 and 2001 was combined because too few otoliths were analysed to conduct the continuation-ratio logits analysis separately for each year.

Abundance-at-age was then transformed into abundance-at-hatch-date (hatch date = catch date − age). This produced a matrix of abundance at age and hatch date. For each year, the matrix was aggregated by averaging each daily age class over 8 x 14 Julian day intervals of hatch date, equivalent to 8 cohorts of larvae per year (days 29—42, 43—56, 57—70, 71—84, 85—98, 99—112, 113—126, and 127—140). This was done because some ages and hatch dates were, by chance, not sampled by the weekly sampling scheme.

Only larvae younger than 7 days old are considered in the estimation of hatch dates. This is because, unlike older larvae, that may have been imported from spawning grounds afar, these newly hatched larvae are likely to have originated exclusively from local spawning sites (Figure 4.3). The 10^{th}, 50^{th} and 90^{th} percentiles of the cumulative abundance of newly hatched larvae were used as proxies for hatch start D_{Hs}, hatch median D_{Hm}, and hatch end D_{He}, for each year.

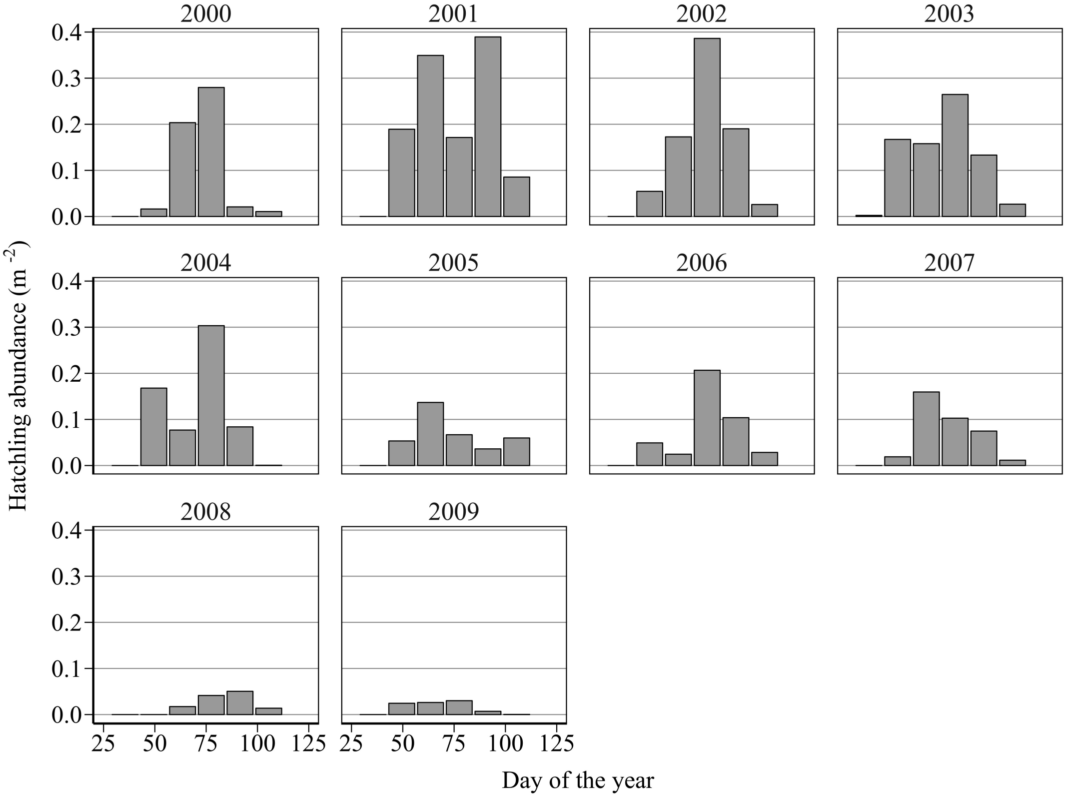


FIGURE 4.3: Mean abundance (m^{-2}) of newly hatched larvae (age 3—7 days old when caught) at successive hatch intervals of (days 29—42, 43—56, 57—70, 71—84, 85—98, 99—112, 113—126, and 127—140).

4.2.4 Hindcasting spawning dates between 2000 and 2009

Given hatch date, spawning dates were estimated by assuming a temperature dependent egg development time. To achieve this, a smooth (LOESS, span = 0.065) was fitted to the weekly resolution time series of 45 m temperature measurements, and interpolated to daily intervals. Then, with egg incubation time as a function of temperature ($f(T)$, days), the estimated spawning day t_{spawn}, is described by the equation

$$\int_{t_{\text{hatch}}}^{t_{\text{spawn}}} \frac{dT}{f(T)} = 1 \qquad (4.2)$$

where t_{hatch} is D_{Hs} ,D_{Hm}, or D_{He}.

$f(T)$ was derived using laboratory data on sandeel egg incubation data. Egg incubation data for *A. marinus* are scarce. Therefore, data from two similar species, *Ammodytes americanus* (Smigielski et al., 1984) and *Ammodytes personatus* (Yamashita and Aoyama, 1985) were combined. Although this introduces uncertainty into the calculations, these species are similar in biology (Reay, 1970) and development times in congeneric species have been shown to be similar (Wilson et al., 2015). Using nonlinear regression, exponential functions were fitted to the data to give the incubation time from spawning to hatch start date (D_{Hs}), hatch median date (D_{Hm}), and hatch end date (D_{He}), as a function of temperature.

$$f(T) = Ae^{-kT} \tag{4.3}$$

where $f(T)$ is either the time to hatch onset (D_{s_T}), the median incubation time (D_{m_T}), or the time to hatch cessation (D_{e_T}). A is the incubation time constant (days) and k is the incubation time slope (^{o}C^{-1}). Values for A and k, and model fits are provided in Table 4.2 and Figure 4.4, respectively.

TABLE 4.2: Parameters for incubation times to hatch start, median and end dates, estimated using egg incubation data for related species (Smigielski et al., 1984; Yamashita and Aoyama, 1985). The coefficient of determination is listed for each regression.

	D_{s_T}	D_{m_T}	D_{e_T}
A (days)	78.867	105.917	177.0417
k (^{o}C^{-1})	0.119	0.119	0.115
R^2	0.964	0.982	0.981

4.2.5 Hindcasting historical hatch dates between 1973 and 1999

The hypothesis that increases in temperature during the egg incubation period could have significantly influenced hatch dates in the past given a fixed synchronous spawning date was considered. Temperature data for the Scottish east coast (54 to 59°N, 2°W to 2°E) between 1973 and 2009 was extracted from the global ocean surface temperature (HadlSST 1.1) databank of the UK Meteorological Office Hadley Centre (http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html). This data is comprised of monthly mean temperature gridded by 1 latitude and longitude units. Mean temperature between February and April in each year was calculated (T'), since this is the approximate time of egg incubation. Then, assuming a fixed spawning date and temperature T', median hatch dates were estimated using the development time equation for median incubation time D_{m_T} (equation 4.2).

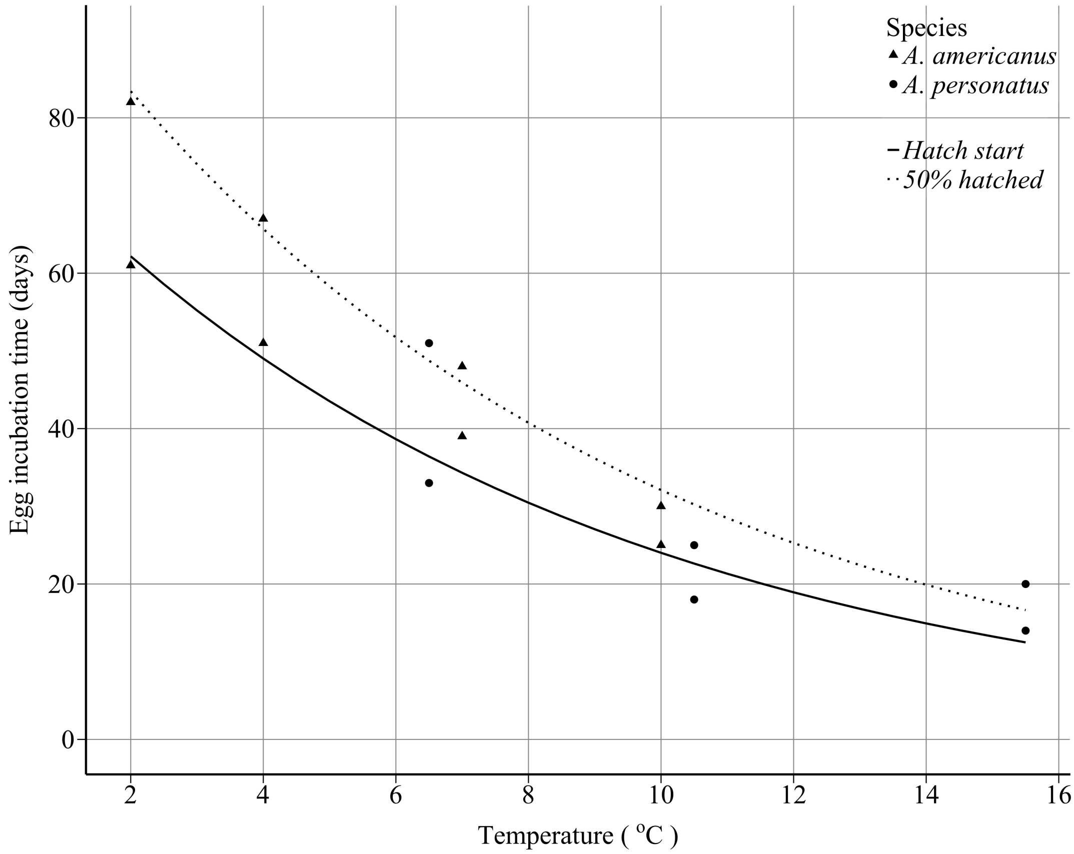


FIGURE 4.4: Effect of temperature on the incubation time of two sandeel species,*A. americanus* and *A. personatus*. Triangles and circles represent experimental data on *A. americanus* and *A. personatus* incubation times (Table 2 in Smigielski et al. (1984) and Yamashita and Aoyama (1985), respectively.) Solid and dotted lines indicate model fits to the experimental data on time to hatch start and 50% hatching. Model parameters are given in Table 4.2.

4.2.6 Environmental cues for spawning and hatching

Various environmental cues for spawning and hatching were considered. First, I tested whether hatch percentiles and mean spawning date were related to absolute temperature. Then, the existence of lunar and tidal cues was investigated.

Dates of new and full moon and tidal height at Aberdeen (15 km north of the monitoring site) each year was obtained from the Xtide Prediction Server (Flater, 2014).

The hypothesis of lunar and tidal cued hatching/spawning was tested using the following procedure:

The length of the lunar cycle is approximately 29.53 days. lc, D_H,D_S, D_{nt}, and D_{fm} are defined as the period of the lunar cycle, hatch date, spawning date, the date of the closest neap tide, and date of the closest full moon date, respectively.

Tidal phase is therefore defined as

$$\text{phase} = cos\left(\frac{2\pi}{lc/2}(D_{H/S} - D_{nt})\right), -1 \leqslant \text{phase} \leqslant 1. \tag{4.4}$$

Hence, a phase value of 1 corresponds to a neap tide. Hatch/spawning and neap tide dates are used to produce phase values for each year in the study period. We define the mean 10-year tidal phase as x_{obs}. Ten random phase values are generated from a uniform distribution with range $\frac{lc}{2}$, and the mean phase is calculated. Step 2 is repeated 10,000 times to derive a probability distribution of the mean of ten random tidal phases. The observed 10-year mean tidal phase x_{obs} is compared with the distribution to find the probability of observing a more extreme value, i.e. $p = Pr(X \geq x_{\text{obs}})$, where X is the mean of 10 phases. The corresponding p-value for spring tide cued hatching/spawning is simply $1 - p$. Tidal cued spawning is tested by changing the period in equation 4.4 to $\frac{lc}{4}$. Lunar cued hatching/spawning is tested in a similar way.

4.3 Results

4.3.1 Year-to-year changes in juvenile length

The decline in 0-group length was highly significant (p < 2.2e-16, $R^2 = 0.136$; Figure 4.5). Length decreased from 6.6 cm in 2000 to 4.9 cm by 2009, corresponding to a 66% reduction in calorific value (Figure 4.5). Length decreased by 25%, equal to a rate of 0.18 cm year^{-1}. The proportion of large fish decreased substantially towards the end of the decade. For example, 32% of 0-group exceeded 7 cm in 2000, compared to only 11% in 2009. This reduction in length corresponded to a 66% reduction in calorific value.

4.3.2 Environmental cues for hatching

Median hatch date varied over the 10-year period between day 67 in 2009 and day 85 in 2008. The 10-year mean of median hatch date was day 74 (s.d. = 5.3 days) (Figure 4.6). Hatch interval (10^{th} - 90^{th} percentiles) varied between 23 days in 2000 and 50 days in 2005

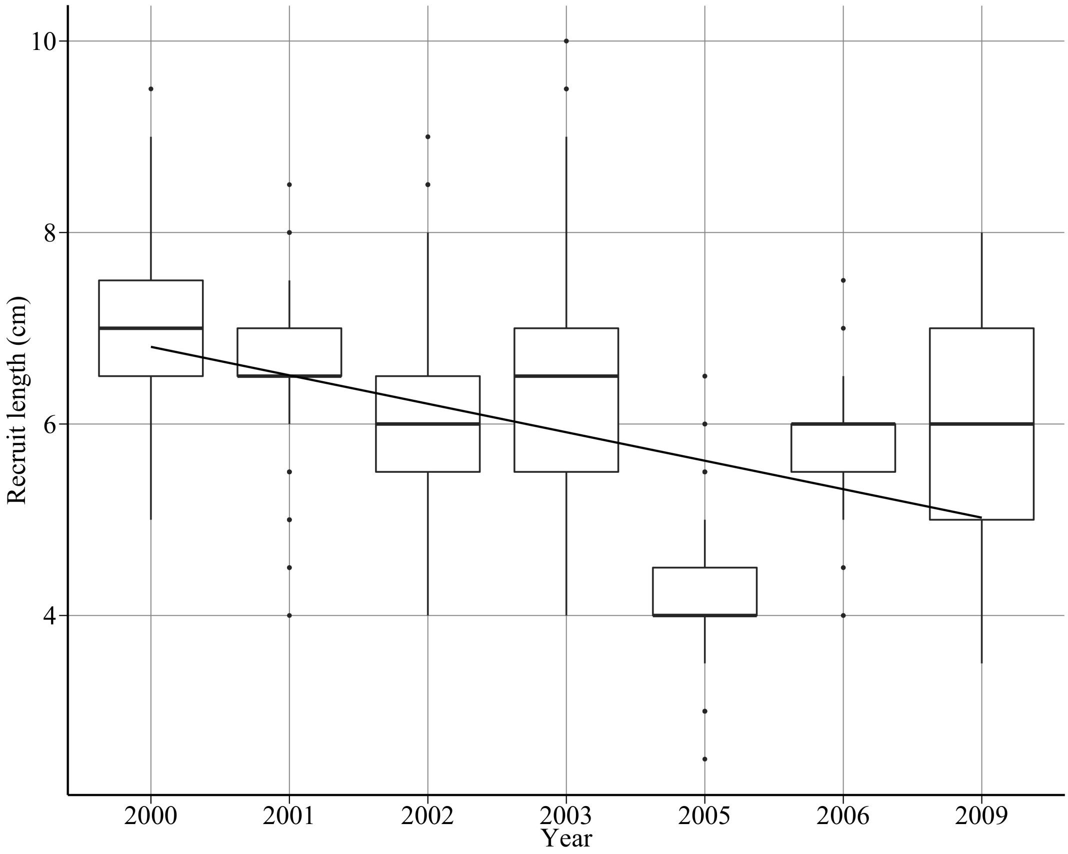


FIGURE 4.5: Decline in sandeel 0-group length between 2000 and 2009. The solid diagonal line represents the significant decline in length ($p < 2.2e\text{-}16$, $R^2 = 0.136$). Length = 378.51 - 0.186 Year.

(mean duration = 38 days, s.d. = 8 days). Annual minimum temperature (T_{min}) varied between 5.7°C in 2001 and 6.9°C in 2007 (Figure 4.7). $D_{T_{\mathrm{min}}}$ occurred an average 12 days after hatch onset, and 8 days before median hatch date. The relationship between the hatch end date and $D_{T_{\mathrm{min}}}$ was statistically significant (adjusted R^2: 0.44, $p = 0.022$) (Figure 4.8) ($D_{He} = 35.8097 + 0.8512\ D_{T_{\mathrm{min}}}$). No significant relationships were found between median hatch date and $D_{T_{\mathrm{min}}}$ ($p = 0.19$), or hatch start date and $D_{T_{\mathrm{min}}}$ ($p = 0.85$). Further, there was no relationship between hatch date and temperature (Table 4.3). In addition, no significant relationship was found between hatch date (D_{Hs}, D_{Hm} and D_{He}) and lunar or tidal events (Table 4.3).

4.3.3 Hindcasting spawning dates between 2000 and 2009

The estimated spawning interval was short compared to the hatching interval (Figure 4.6), suggesting spawning is more or less synchronous on a given date. Further, in 5

TABLE 4.3: P-values for relationships between environmental events and hatching and spawning using the statistical test outlined in section 4.2.6. Significant values are denoted by an asterisk.

	D_S	D_{H_s}	D_{H_m}	D_{H_e}
Neap tide	0.0226*	0.127	0.258	0.914
Spring tide	0.978	0.873	0.742	0.0859
Neap & spring tide	0.183	0.535	0.954	0.550
Full moon	0.37	0.356	0.283	0.612
New moon	0.63	0.644	0.717	0.389
Full & new moon	0.8	0.458	0.947	0.114
Temperature	0.478	0.681	0.986	0.347

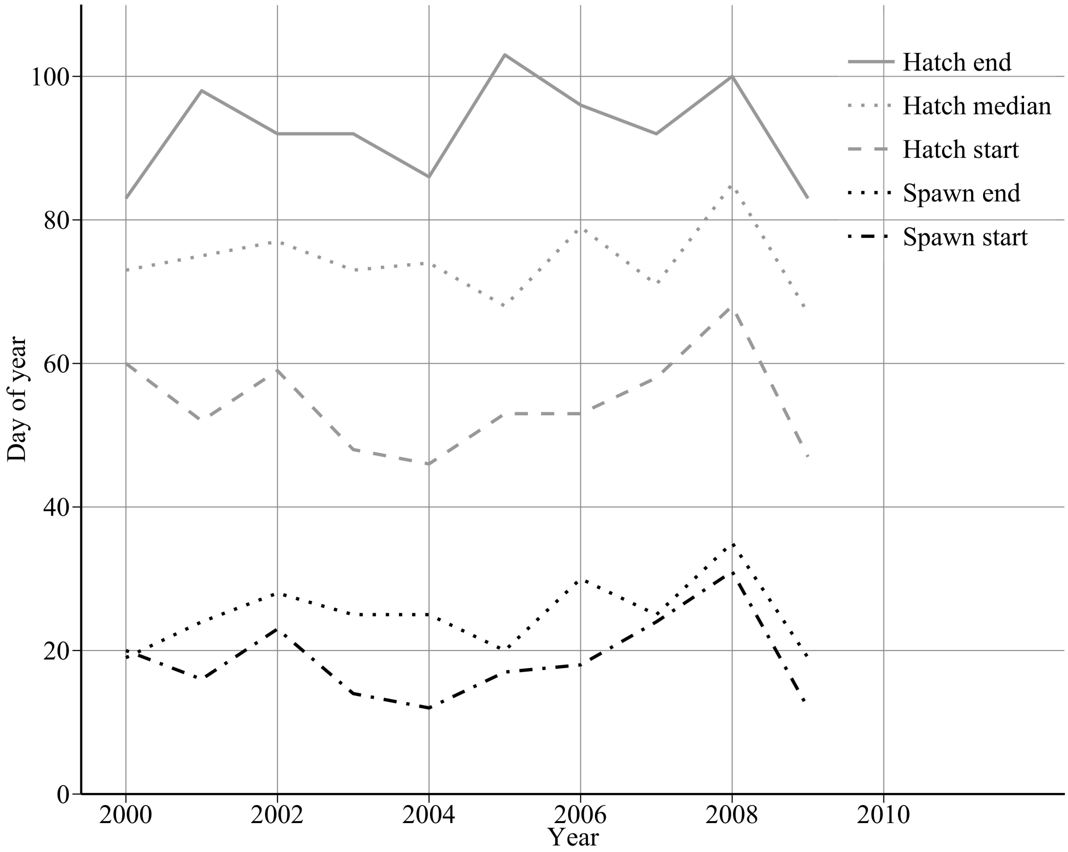


FIGURE 4.6: Year-to-year changes in spawning and hatch dates. The top three lines show median hatch date (dotted grey line) enclosed by hatch start and end dates (dashed and solid grey lines, respectively). The bottom two lines show the estimated spawning interval derived by backtracking from hatch dates.

out of 10 years, the two spawning day estimates diverged by 5 days or less (Table 4.4). Mean spawning date was day 21.5 (S.D.= 5.2 days), varying between day 15 in 2009, and day 33 in 2008. A high proportion of variability was due to 2008 and 2009. Excluding these years, the mean spawning date was day 20.9 (s.d. = 3 days). The sensitivity of

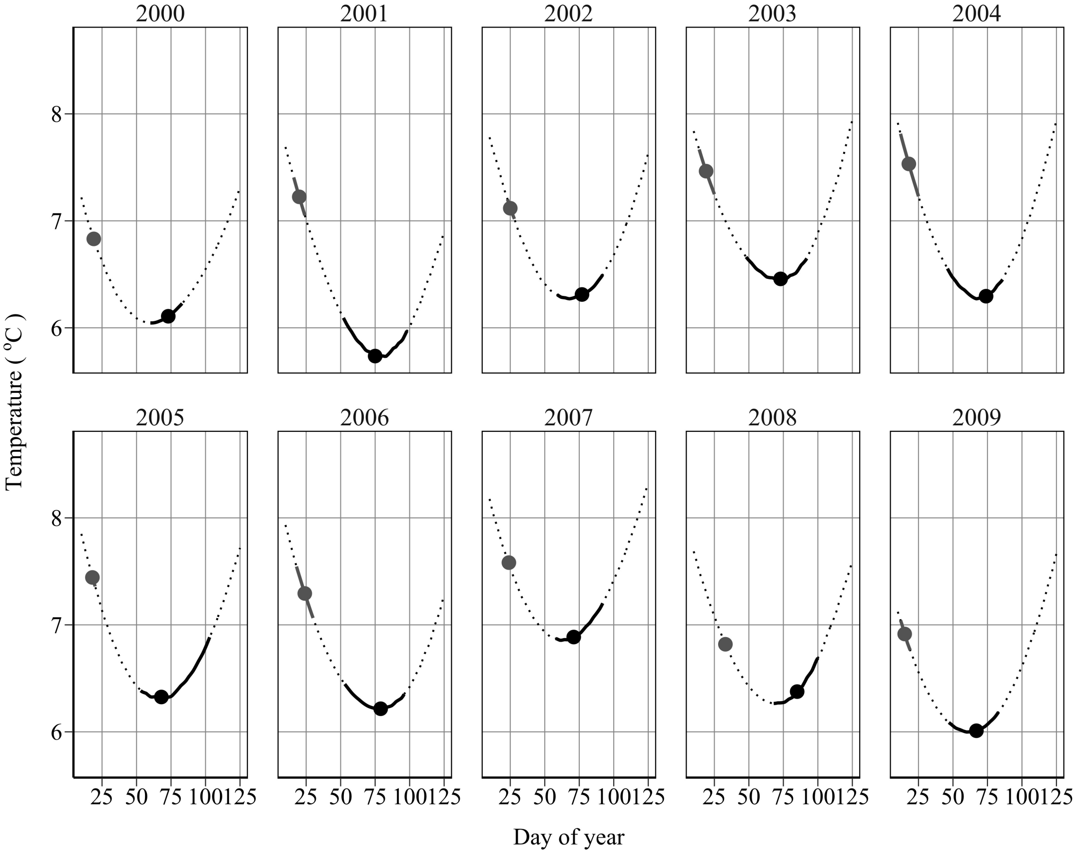


Figure 4.7: Spawning and hatch dates in relation to temperature. Shown is the temperature profile at 45m depth with overlaid spawning and hatch dates between 10th January and 1st May. Filled grey and black circles denote the synchronous spawning and median hatch dates, respectively. Solid grey and black lines denote the spawning and hatch intervals (10% percentile to the 90% percentile), respectively.

our 10-year mean spawning date to the choice of development rate equation (equation 4.2) was tested by calculating spawning date using *A. americanus* and *A. personatus* egg incubation data separately. Using data for *A. americanus* (Smigielski et al., 1984) and *A. personatus* (Yamashita and Aoyama, 1985) separately produced mean spawning dates of 21.5 (s.d. = 5.2 d) and 23 (s.d. = 4.9 d), respectively. The predicted hatch date distribution was estimated given a synchronous spawning day and temperature-dependent incubation period. To do this, the development time equations (equation 4.2) were used to track forward from the synchronous spawning date to calculate the expected hatch start, hatch median and hatch end dates. The error (days) between this generated hatch date distribution and the observed hatch date distribution was calculated. Mean errors of 3 days (s.d.=3.4 days) and -4 days (s.d. = 2.5 days) were associated with hatch onset and median dates respectively, however the corresponding error for hatch end date was 13.3 days (s.d. = 6.6 days). Forward-tracked hatch end

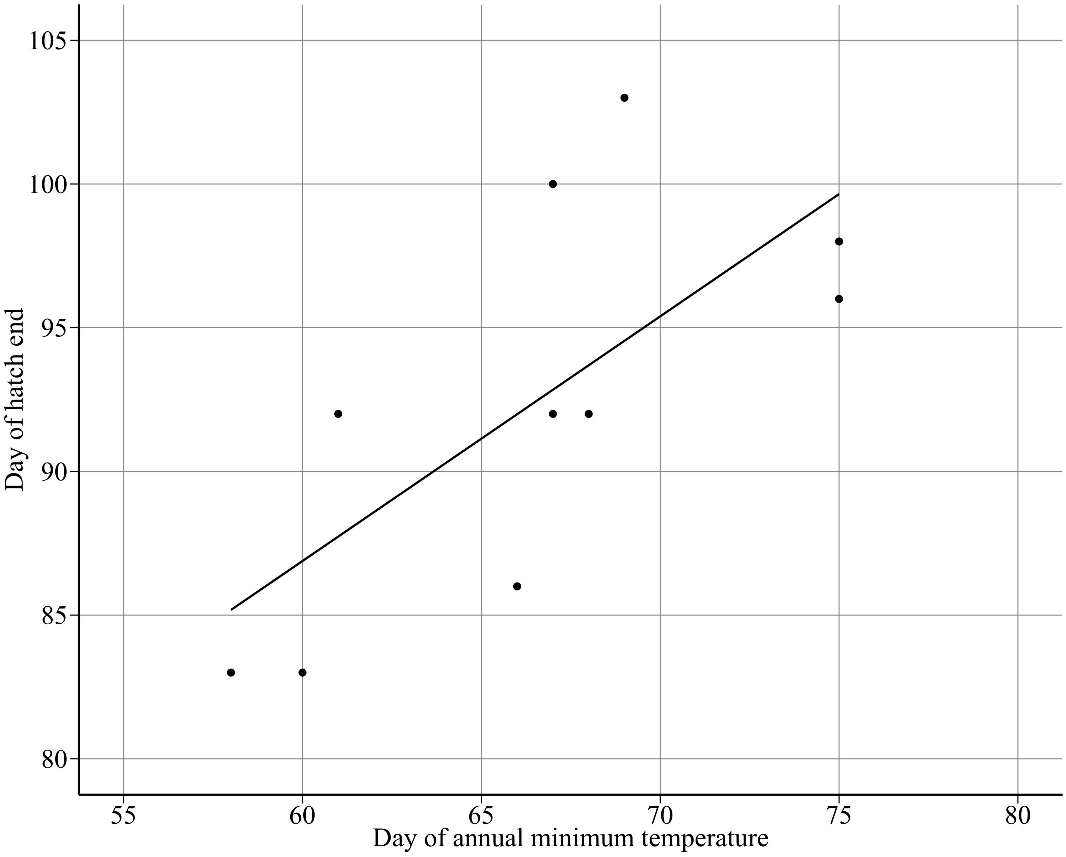


FIGURE 4.8: Relationship between day of hatch end D_{He} and the day of annual minimum temperature ($R^2 = 0.44$, $p = 0.022$, $D_{He} = 35.8097 + 0.8512\ D_{T_{\text{min}}}$).

dates occurred consistently later than observed hatch end dates, and were associated with the highest error. Results were consistent with early hatching.

TABLE 4.4: Estimates of synchronous spawning days between 2000 and 2009. Shown are the spawning start, spawning end days and synchronous spawning day. The synchronous spawning day is the average of the spawning start and spawning end days. Bold values indicate a spawning interval of 5 days or less.

Year	Spawning start	Spawning end	Synchronous spawning day
2000	19	19	20
2001	16	24	20
2002	23	28	25
2003	14	25	19
2004	12	25	18
2005	17	20	18
2006	18	30	24
2007	24	25	24
2008	31	35	33
2008	12	19	15

4.3.4 Environmental cues for spawning

A statistically significant relationship was found between spawning date and neap tide date (Table 4.3). Spawning dates and neap tides were within a day apart in 2001, 2002, 2004 and 2006. The mean number of days separating a spawning day and the closest occurring neap tide throughout the study period was <2.16 days. There was no evidence that a combination of neap and spring tides triggered spawning (p=0.183). Results do not support full moon or new moon cued spawning, however, the possibility that spawning is cued by a combination of lunar and tidal cues cannot be ruled out. In addition, there was no evidence that spawning was cued by temperature (Table 4.3).

4.3.5 Hindcasting historical hatch dates between 1973 and 1999

Historical hatch dates were estimated using d SST data under the assumption of a fixed spawning day. Median hatch date declined significantly between 1973 and 2009 (p-value < 0.001, $R^2 = 0.321$). Hatch day became earlier at a rate of 0.16 days year^{-1}, changing from day 71 in 1973 to day 65 in 2009 (mean = 68.14, s.d. = 2.87, range = 63—75).

4.4 Discussion

This study marks the first attempt at estimating spawning dates using sandeel field data and provides evidence of synchronous spawning. Synchronous spawning day varied between 15th January and February 2nd over the study period. These estimates are consistent with previous observations of spawning *A. marinus* (Winslade, 1971), which spawned between 15th and 29th January in the laboratory over a 3-year period (1969—1971). There are ecological reasons for synchronous spawning. Weaker currents during neap tides reduce gamete dispersal and potentially increase fertilisation rates (see for example Coral reefs, Babcock et al., 1986). Other sandeel species may spawn on a semi lunar cycle. For example, *Ammodytoides pylei* and *A. tobianus* spawn 3-5 days before a full moon (Thomopoulos, 1954; Randall et al., 1994). A similar forage fish, Atlantic herring *Clupea harengus*, is known to spawn at neap tides (Clarke and King, 1985; Hay, 1990).

Results show that given a synchronous spawning day, predicted hatch end dates occurred consistently later than observed dates. In addition, the hatch interval is smaller in the field than in laboratory experiments. *A. personatus* hatch within a period of 59 d at 6.5 ^{o}C (Yamashita and Aoyama, 1985), while the corresponding figure is 43 days at 7 ^{o}C for *A. americanus* (Smigielski et al., 1984). In comparison, the mean hatch duration of *A. marinus* between 2000 and 2009 was 38.1 days under a mean temperature of 6.33 ^{o}C. If there is little interspecific difference in egg development time, then the hatching period for *A. marinus* is smaller than expected. This could arise because tranquil conditions in laboratory studies may produce artificially long incubation times, which would be problematic for estimating spawning time (Smigielski et al., 1984). Alternatively, this inconsistency can be explained by some eggs hatching early in response to an environmental cue, which experimental studies do not allow for. This is likely represented by the significant relationship between hatch end day and day of annual minimum temperature.

The shift from decreasing to increasing temperature in spring appears to trigger hatching (Figure 4.7). This appears to be the first evidence of temperature-phase cued fish hatching, which is more common in reptiles and amphibians (Doody, 2011; Spencer and Janzen, 2011; Warkentin, 2011). There may be several reasons for this hatch cue. Newly hatched larvae require adequate food supply in the form of copepod nauplii (Ryland, 1964). Estimated median hatch dates occured in March, the time of peak egg production in the important calanoid copepod *C. finmarchicus* (Jønasdøttir et al., 2005). However, the timing of copepod egg production is likely to show more variation across the North Sea than the timing of the annual minimum temperature. Hence, in regions where the timing of copepod egg production is generally later than elsewhere, we may expect poor growth and survival of sandeel larvae, and therefore poor productivity of sandeels. However, using the temperature cycle to time important life cycle events may act as a buffer against climate change.

It is generally accepted that egg incubation periods are primarily temperature dependent (Pauly and Pullin, 1988) which, under changing temperature conditions, may cause vulnerability for species and food webs. A terrestrial illustration of such vulnerability is the relationship between great tits *Parus major* and winter moths *Operophtera brumata.* Increased temperature causes winter moths to hatch earlier leading to a mismatch between caterpillar availability and great tit peak food demand (Visser et al., 1998; Visser and Holleman, 2001). Since sandeels use rising spring temperatures as a hatch cue, it is possible that, similar to other birds (Schaper et al., 2012), sandeel-dependent seabirds use the same cue to time reproduction.

Between 2000 and 2009 sandeel length declined at a rate 5 times greater than between 1973 and 2000 (Wanless et al., 2004). No trend in hatch dates were evident during this period therefore changes in hatch date was likely not the cause. Decreasing 0-group length can be caused by a reduction in growth rate and survival with respect to hatch date (Wright and Bailey, 1996; Frederiksen et al., 2011). There has been no decline in the growth rate of 0-group (Wanless et al., 2004), or young larvae (Heath et al., 2012), so the only potential for a decline in growth rate is through the late-larval stage. 0-group length has also declined in the southern north sea, and has been linked to a reduction in copepod size (van Deurs et al., 2014). This could have affected the growth rate of late-stage larvae, especially as metamorphosis is a particularly vulnerable stage to reduction in food availability.

There is a discrepancy between hatch dates estimated in this study and those of Frederiksen et al. (2011). Mean hatch dates in the latter study occur on average 12 days earlier (2000-2006). Likely drivers of divergence in hatch dates are spatial variation in hatching time and the result of using CPR data to estimate hatch dates. A current drawback of using CPR data to measure sandeel abundance is that the CPR cannot distinguish sandeel species. There are multiple spring hatching sandeel species e.g. *H. lanceolatus*, *A. tobianus*, that may represent a significant proportion of sandeel larvae at various times of year (Heath et al., 2012; Lynam et al., 2013). For example, *H. lanceolatus* accounts for over 20% of the sandeel larval catch on the Scottish east coast by April and is the most abundant larvae from May until the end of the year (Figure 4.2). If the CPR catches sandeel species that hatch before *A. marinus*, this could explain why mean hatch dates calculated by Frederiksen et al. (2011) occured 12 days earlier than those estimated in the present study.

Sandeel hatch dates are likely to be influenced by a combination of prey phenology and temperature (Wright and Bailey, 1996; Wright et al., 2017). It is unclear as to what extent the former plays a role in sandeel hatch dates. However, it appears that temperature variations alone should not significantly alter hatch dates. For instance, changes in temperature between 2000 and 2009 contributed little to the variability in hatch dates. This was clear from the similar standard deviations of the synchronous spawning and hatch median dates. Moreover, the effect of temperature on incubation time is relatively weak (Smigielski et al., 1984; Yamashita and Aoyama, 1985). Temperature changes during the egg incubation period should not have significantly influenced hatch dates over the past few decades. Given a fixed synchronous spawning day of January 21st, increases in temperature on the Scottish east coast between 1973 and 2009 during egg incubation would have caused median hatch date to become 6 days earlier. Median hatch date would have varied between March 4th and March 16th. This is inconsistent with Frederiksen et al. (2011) who estimated a range of two months.

Chapter 5

Modelling changes in growth rates of sandeels

5.0.1 Sandeel growth

Marked differences in sandeel growth exist across the North Sea. The fastest growing populations are located in the southern and central north sea e.g. Dogger Bank, and off the Norwegian coast, while the slowest growing reside in northern UK waters and off the Scottish east coast (Wright and Bailey, 1993; Bergstad et al., 2002; Boulcott et al., 2007). There appears to be a correlation between growth rate and population productivity, which suggests that growth rate is a strong driver of population dynamics.

Seabird breeding success is highly sensitive to changes in quality and abundance of post-metamorphic sandeels. In particular, the timing of post-metamorphic 0-group sandeels (∼4—5 mm) is critical for seabird breeding success since chicks are fed a diet exclusively comprised of these fish (Lewis et al., 2001). Factors which determine this timing are sandeel hatch dates, larval growth rates and larval mortality (Frederiksen et al., 2011). However, a lack of long term data sets on these factors makes it difficult to attribute changes in post-metamorphic 0-group size-at-date to a single factor (Heath et al., 2012; Frederiksen et al., 2011). Wright and Bailey (1993) found significant differences in larval growth rates and hatch dates off Shetland between 1990 and 1992. While the timing of post-metamorphic 0-group sandeels was not significantly affected, it showed that hatch dates and growth rates have the potential to cause large inter-annual changes in post-metamorphic 0-group length. Sandeel growth is highly seasonal, with the largest increase in size observed between April and June (Bergstad et al., 2002; Winslade, 1974). Growth ceases altogether during winter (Macer, 1966; Cameron, 1958). The most important period of growth arguably takes place in the first year. There are several factors that support this reasoning. First, because of a high natural mortality, sandeel populations are dominated by younger age classes (age <2) (Pedersen et al., 1999), underlining the importance of early maturation. Most North Sea sandeels will reproduce for the first time in their second winter at age 1 (Boulcott et al., 2007). However, the sandeel stock off the Norway coast, one of the most productive populations in the North Sea, mature much earlier than their slow-growing Northern counterparts; the incidence of maturation at age 0 being significantly higher in this region than elsewhere (Boulcott et al., 2007). In addition to earlier maturation, rapid early growth may also have other benefits. For example, there is likely a decrease in starvation and predation mortality with increasing length (Sogard, 1997). Here, I estimate changes in sandeel growth rate between 1997 and 2006.

5.0.2 Sampling methods

Sampling of post-metamorphic sandeels by pelagic trawl has taken place annually off the Firth of Forth between 1997—2003 and 2005—2009 (56^o 00N and 56^o 30N and longitudes 003^o 00W and 001^o 00W, Figure 5.1). This covered the main sandbanks, the Wee Bankie, Marr Bank, and Berwick's Bank, which are prime habitat for sandeels in this area (Proctor et al., 1998; Pedersen et al., 1999). Sampling was undertaken by the FRV *Clupea* for the majority of the study period (1997-2007), before it was replaced by the FRV *Alba na Mara* (2008-2009). In each year, trawling was carried out between 0400h and 1800h GMT between late May and early July.

Sandeel larval sampling was undertaken in 2000 and 2001 at Stonehaven, and again in 2002 across a large expanse of the northwestern North Sea during a survey by FRV Scotia between 9-23 April 2002 (Figure 5.2). An ARIES high-speed sampler (Dunn et al., 1993; mouth area 0.1 m^2, mesh size 200m) and opening-closing Methot trawl (mouth area 2.25m^2, mesh size 2 mm) were used to sample small and large sandeel larvae, respectively. All sandeel larvae were extracted from the samples and preserved in 4%

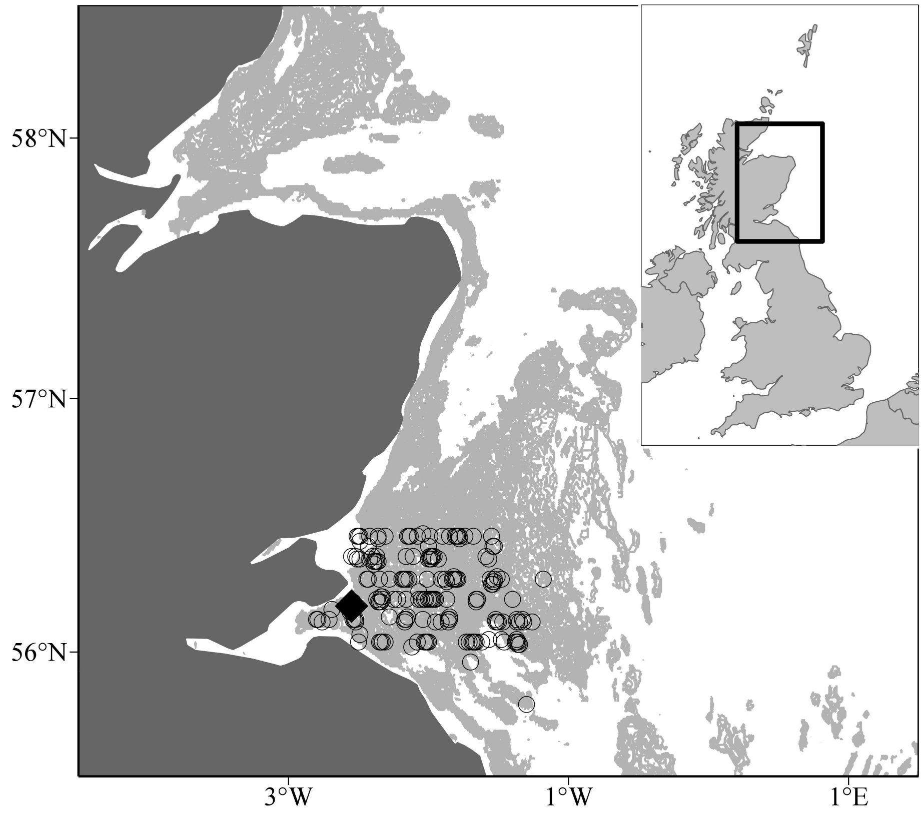


FIGURE 5.1: Pelagic trawl locations off the Scottish east coast. Open circles represent pelagic trawl locations. The black diamond and triangle denotes the Isle of May seabird colony and Stonehaven, respectively. The pale grey shaded area indicates water depths between 30 and 70m, the range of depth sandeels are most commonly found (Wright et al., 2000), and marks out the 3 main sandbanks, Wee Bankie, Marr Bank and Berwicks Bank.

formaldehyde. *A. marinus* larvae were measured to the nearest 0.1 mm in standard (notochord) length. A subset of fish was selected for otolith analysis. Daily increments on larval sagitta otoliths were used to calculate sandeel age (Wright, 1993). Larval hatch date was estimated by subtracting age from date at capture. For sampling methods at Stonehaven, see Chapter 4. In addition, weekly chlorophyll sampling was carried out between 1997 and 2008 at Stonehaven (Figure 5.3). Chlorophyll concentration mg m^{-3} was determined by collecting a 10 m integrated hose sample from the surface. To ensure natural 'clumping' of chlorophyll in the surface layer would not give a misleading estimation of concentration, the water was mixed before being transferred to bottles. Analysis was done using a spectrophotometer.

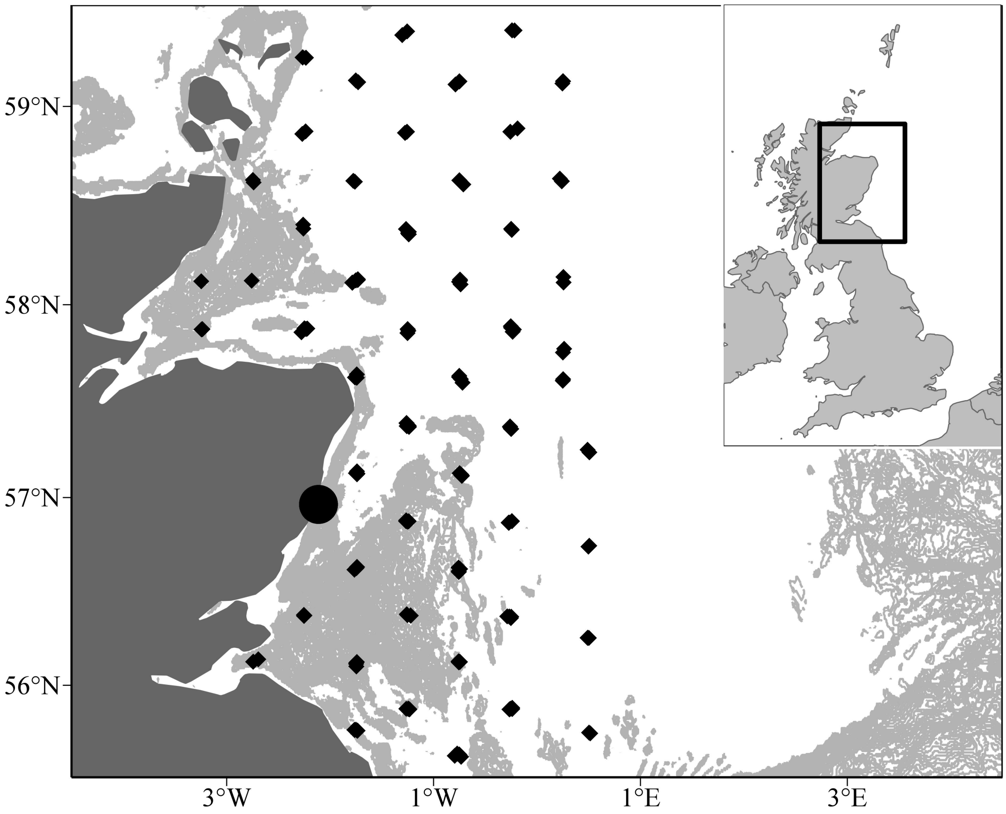


Figure 5.2: Locations of larval surveys between 2000 and 2002. Larval sampling was conducted at Stonehaven in 2000 and 2001 (circle) and across the northwestern North Sea in 2002 (diamonds).

5.0.3 Age-length analysis

Length-stratified subsamples were taken and otoliths were extracted to determine age length keys for each cruise. Total lengths (anterior tip of maxillae to tip of caudal fin) of a random sample of fish were accurately determined to 0.5 cm. A subsample was then removed for age determination. Annual rings form on sandeel otoliths (ICES 1995). Therefore age can be determined by counting the number of rings. Table 5.1 shows the number of otoliths collected by pelagic trawling between 1997 and 2009 (excluding 2004 and 2007), grouped by age class and year.

Sandeel abundance at age and length was determined using the following method. First, a biomass at length distribution was estimated by applying a year-specific weight at length relationship to the length frequency of sandeels caught in all trawls. Probability distributions of ages for each 5 mm length class were determined using the continuation-ratio logit method for each survey (Kvist et al., 2000; Rindorf and Lewy, 2001; Stari

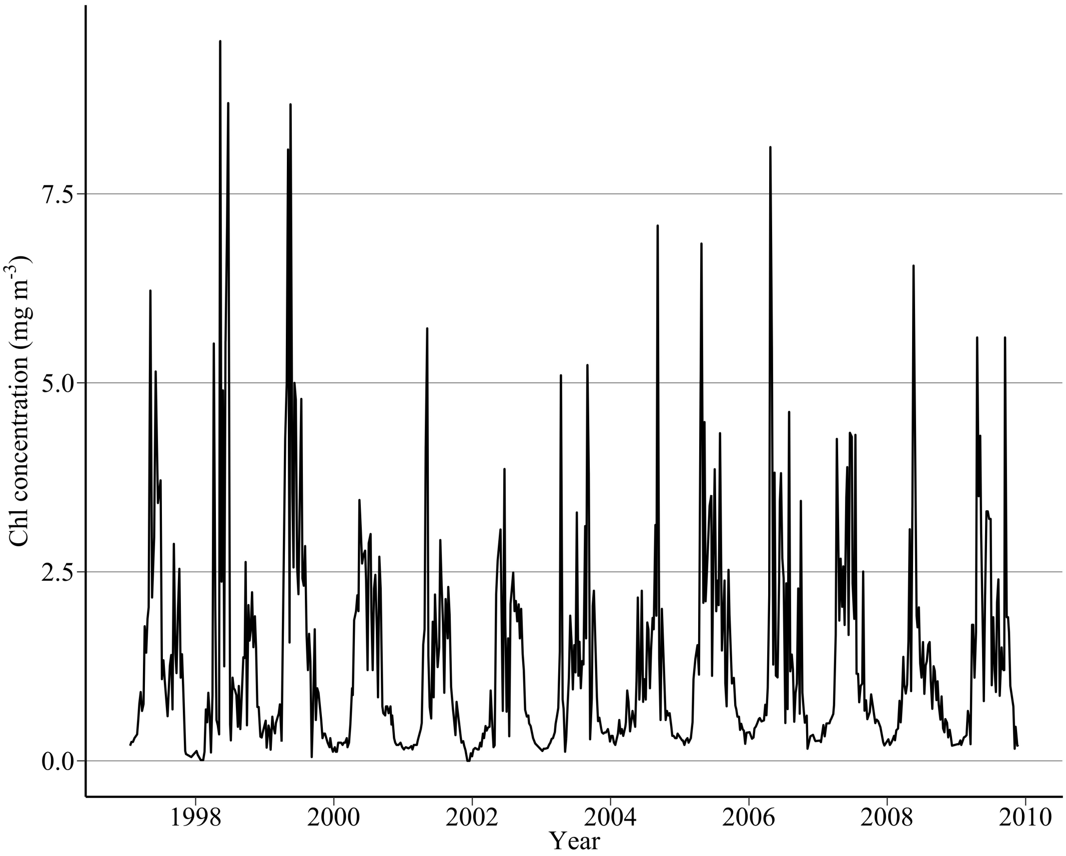


FIGURE 5.3: Chlorophyll concentration (mg m^{-3}) at Stonehaven (56^o 83N and 2^o 6.74W) between 1997 and 2008. The spring bloom was absent in 2004, which was marked by a low chlorophyll concentration.

TABLE 5.1: The number of sandeels sampled for otolith analysis between May and July. Otolith counts are seperated by age class.

Year	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	TotalOtolith
1997	2	46	9	26	3	2	0	1	0	0	89
1998	0	31	23	9	2	0	0	0	0	0	65
1999	133	154	208	114	13	6	1	0	0	0	629
2000	235	344	107	110	38	8	0	0	0	0	842
2001	95	395	559	87	89	34	6	0	0	0	1265
2002	238	9	0	72	38	41	16	0	1	1	416
2003	289	410	184	287	122	9	3	1	0	0	1305
2005	103	63	334	197	57	112	37	1	2	0	906
2006	22	140	8	28	3	0	2	0	0	0	203
2008	0	48	7	29	15	24	17	2	2	0	144
2009	90	89	40	17	36	8	10	2	2	1	295

et al., 2010). Then, changes in distribution of age at a given length, as a function of length, were estimated using Generalised Linear Modelling. Fitting was performed using Maximum Likelihood code (Stari et al., 2010). The resultant probability matrices of age-given-length were multiplied by biomass-at-length to give matrices of biomass-at-age-and-length. While these biomass-at-age-and-length matrices give accounts of biomass caught by trawling, they are not a measure of biomass at the scale of the Firth of Forth sandbanks (Figure 5.1). To obtain the true biomass of sandeels in the study area, correction factors must be applied to biomass-at-age-and-length matrices. Greenstreet et al. (2010) measured the biomass of Firth of Forth 0-group and 1+ group sandeels between 1997 and 2009. Correction factors are derived using these estimates and are estimated in the following way:

0-group biomass at year in the pelagic trawl y ($B_{0,\mathrm{PT},y}$) is related to 0-group biomass at year y in the study area ($B_{0,\mathrm{GREEN},y}$) using a correction factor ($CF_{0,y}$),

$$CF_{0,y} = \frac{B_{0,\mathrm{GREEN},y}}{B_{0,\mathrm{PT},y}} \tag{5.1}$$

The biomass of 1+ group sandeels in the study area is found in a similar way, using a correction factor for 1+ group sandeels ($CF_{1+,y}$).

Hence,

$$CF_{1+,y} = \frac{B_{1+,\mathrm{GREEN},y}}{B_{1+,\mathrm{PT},y}} \tag{5.2}$$

Next, abundance-at-age-and-length was estimated by multipling probability matrices of age-given-length by abundance-at-length. This produced abundance-at-age-and-length matrices of sandeels caught by trawling. These matrices were then multiplied by the appropriate correction factors defined above to give abundance-at-age-and-length of sandeels in the study area. From this, mean length-at-age for a cohort was calculated. Trends in length at age over time were estimated using linear and piecewise regression.

5.0.4 Estimating growth rates from length-at-age data

Fish usually grow according to the von Bertalanffy law (von Bertalanffy, 1938), That is, growth rate decreases with time, eventually becoming zero, Hence,

$$L(a) = L_{\infty}(1 - e^{-g(a-a_0)}) \tag{5.3}$$

where $L(a)$ is the length at age (years) , L_{∞} is the asymptotic length (cm), g is growth rate (year^{-1}) and a_0, is the age at which length is zero. a_0 is usually treated a fitting parameter and usually does not have any biological meaning. The von Bertalanffy law is limited because it assumes a constant environment over an animal's lifespan. However, due to its simplicity and usefulness in determining animal growth rates over a long time scale, it is widely used in ecology.

5.0.5 Relationship between larval growth and length of 0-group sandeels

I investigated whether larval growth rate and 0-group sandeel length was correlated during the stock decline. A significant relationship would provide further evidence that a long term decline in 0-group length at date is being driven by a reduction in growth rate, and not changes in hatch dates (see Chapter 4).

5.0.6 Length distributions

33,412 sandeels were measured for length from pelagic trawls between 1997 and 2009. Only 6 sandeels were retained in 2007, therefore this year was excluded from analysis. Annual length distributions of sandeels measured for length is shown in Figure 5.4. Length distributions show a consistent bimodal pattern through the study period (Figure 5.4). All distributions had 2 distinct peaks, representing 0-group fish and older fish, with the exception of 2008 when no 0-group sandeels were caught (In 2008 no 0-group otoliths were measured and sampled sandeels were $>$ 12cm).

5.0.7 Probability of age given length

6,159 otoliths in total were available over the study period. Most importantly, a sufficient amount was available in any year to gain a precise estimation of the probability of age given length. Age ranged from 0 to 9 years old, however, there were few otoliths for ages greater than 6 (Figure 5.5). This is likely because the lifespan of these animals is around 6-7 years (Macer, 1966). An example of a probability distribution of age given length is shown in Figure 5.6.

Catches were dominated by 0-group and 1-group fish in all years except in 2008 when older fish dominated (Figure 5.7). 0-group and 1-group fish constituted an average of

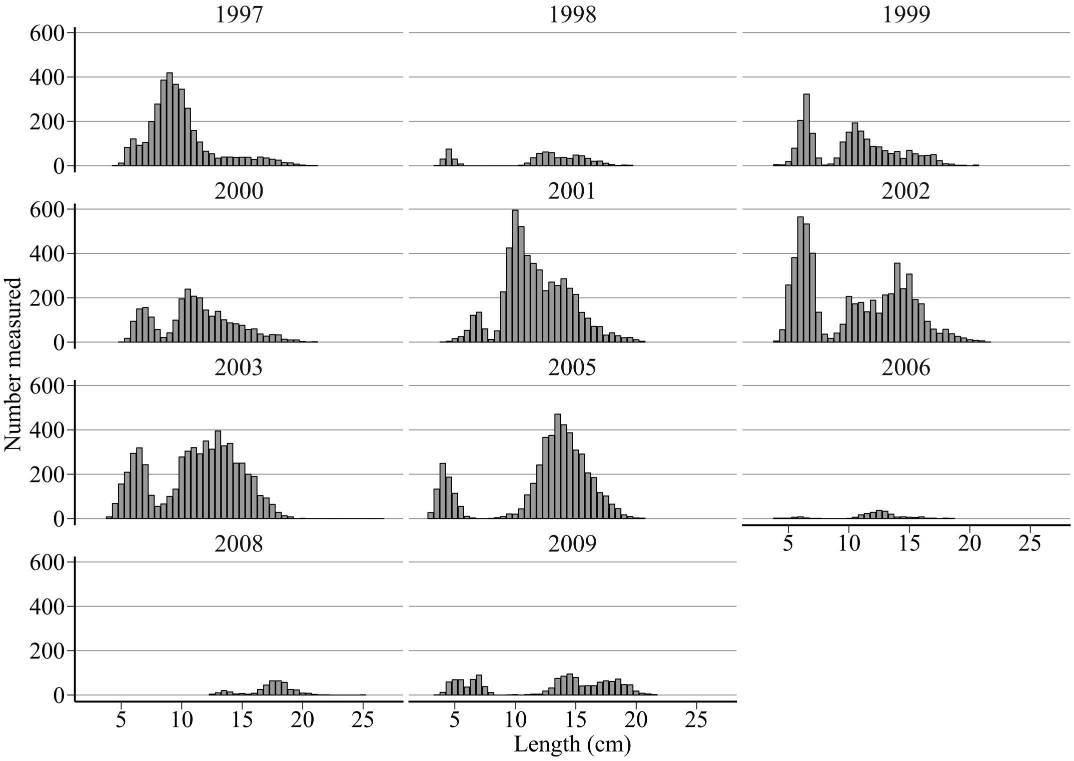


FIGURE 5.4: Length frequency distributions (number measured at length) of sandeels in pelagic trawl samples.

83% of the population (range =(12%,100%), S.D. = 30%). The proportion of 1-group individuals showed a significant decrease during the study period ($p < 0.04$, $R^2 = 0.48$).

5.0.8 Changes in growth rate between 1997 and 2006

Figure 5.8 shows changes in mean length at age during the study period. There was a pattern of decreasing length between 1997 and 2005 and increasing length between 2005 and 2009 for most age classes. Piecewise linear regression identified break points for several age classes. Significant break points were found for lengths of age 1, age 2, age 5 and age 6 sandeels in 2002, 2005, 2007 and 2005, respectively.

Figure 5.9 shows von Bertalanffy fits to mean length of sandeels off the Scottish east coast between 1997 and 2009. There was marked variation in growth trajectories of different cohorts over the study period. This is illustrated by year-to-year changes in the shape of the fitted curve in Figure 5.9.

Figure 5.10 shows changes in von Bertalanffy growth parameters L_∞ and g. There was marked variation in cohort growth rate and asymptotic length over the study period.

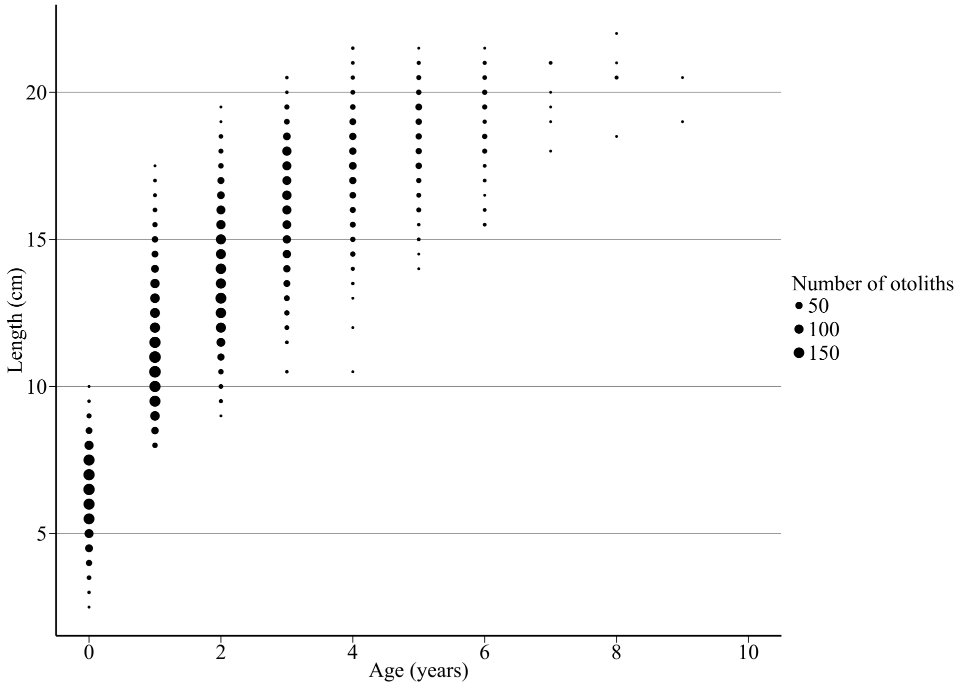


FIGURE 5.5: Individual length and age estimates for all years. The size of the point represents the amount of individuals in a given age-length class.

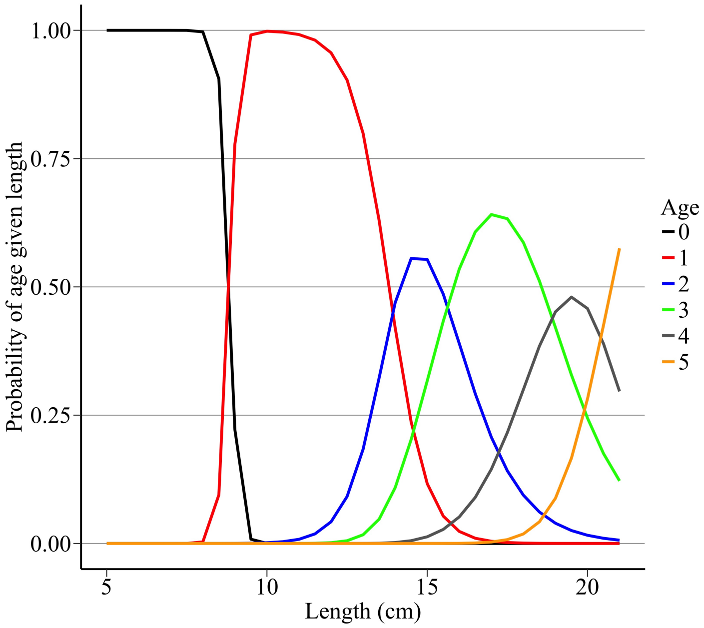


FIGURE 5.6: Fitted probability distributions of age given length from pelagic trawling in 2000. The probability that a large sandeel is old increases with length. The clustering of lines after 12 cm indicates a slow down in growth rate once sandeels are 2 or older.

Cohort growth rate varied from 0.126 year^{-1} in 2004 to 1.308 year^{-1} in 2006. In biological terms, this meant that sandeels born in 2006 approached their maximum asymptotic length at a rate 10 times faster than individuals born in 2004. An outlier test showed

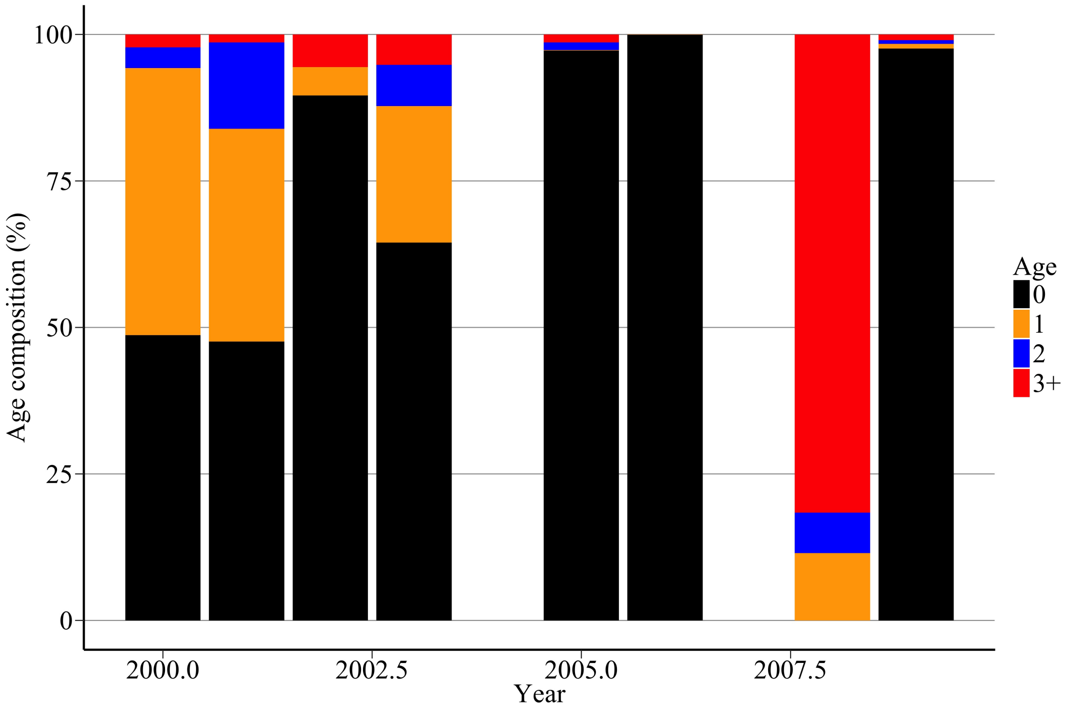


Figure 5.7: Age composition of sandeels catches by pelagic trawl (numbers). 3+ indicates all fish age 3 and older. The population largely consists of fish younger than age 2.

that growth rates for individuals born in 2005 and 2006 were statistically different ($p < 0.05$).

The asymptotic length of cohorts (L_∞) varied from 17.95 cm in 1999 to 34.25 cm in 2004. Outlier tests revealed that the asymptotic lengths L_∞ for sandeels born in 2003 and 2004 were statistically different ($p < 0.0001$).

There was a significant inverse relationship between growth rate and asymptotic length. This took the form $L_\infty = 5.6789/g$ (s.e. =0.7593, P< 1e-04). Hence, fast growing sandeels reached lower maximum lengths than slower growing individuals (Gislason et al., 2008).

There was a significant negative relationship between asymptotic length off the Firth of Forth L_∞ and mean chlorophyll concentration at Stonehaven (mg m^{-3}) during the primary sandeel foraging period (March-June) ($R^2 = 0.4355$, $p < 0.03$, $n = 10$, intercept $= 29.77$, slope $= -4.21$). The relationship between growth rate g and mean chlorophyll concentration (mg m^{-3}) during the primary sandeel foraging period was also significant ($R^2 = 0.3276$, $p < 0.05$, $n = 10$, intercept $= -0.047$, slope $= 0.27$).

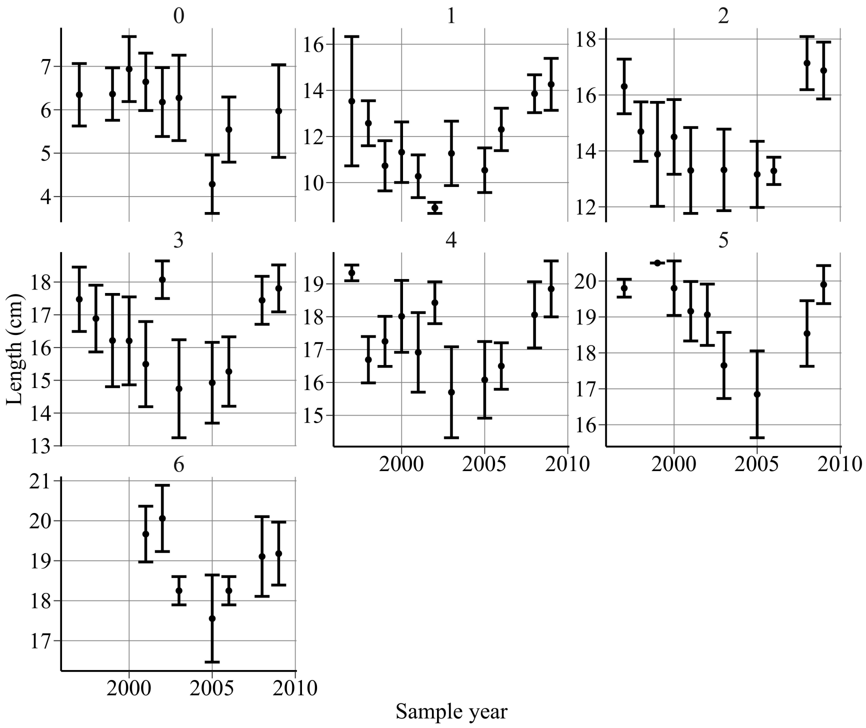


Figure 5.8: Changes in sandeel mean length at age between 1997 and 2009 off the Firth of Forth (black points), estimated from pelagic trawl data. Error bars indicate ±1 standard deviations. Length at age decreased between 1997 and 2005, and increased between 2005 and 2009.

5.0.9 Relationship between larval growth and length of 0-group sandeels

Larval length-at-age data revealed marked year-to-year changes in growth rate (Table 5.2). Between 2000 and 2002, larval growth rate ranged from 0.468 mm day^{-1} in 2000 to 0.338 mm day^{-1} in 2002. Metamorphosis dates are estimated by assuming a fixed hatch date (see Chapter 4) and metamorphosis length of 40 mm (Wright and Bailey, 1996; Cameron, 1958; Macer, 1965). Tracking forward from median hatch dates between 2000 and 2001 (14^{th}, 17^{th} and 19^{th} March, respectively), larval growth rates in these two years correspond to metamorphosis days of 28^{th} May, 13^{th} June and 28^{th} June, respectively. Hence, larval phase durations between 2000 and 2002 were 76, 89 and 102 days, respectively. There was a statistically significant relationship between 0-group length in June ($L_0$and larval growth rate g_l between 2000 and 2002 ($L_0 = 4.1891 + 5.9152 * g_l$,n=3, $R^2 = 0.995$, $p < 0.04$, Figure 5.11). A 28% reduction in larval growth rate between 2000 and 2002 corresponed to an 11% decrease in mean length in June.

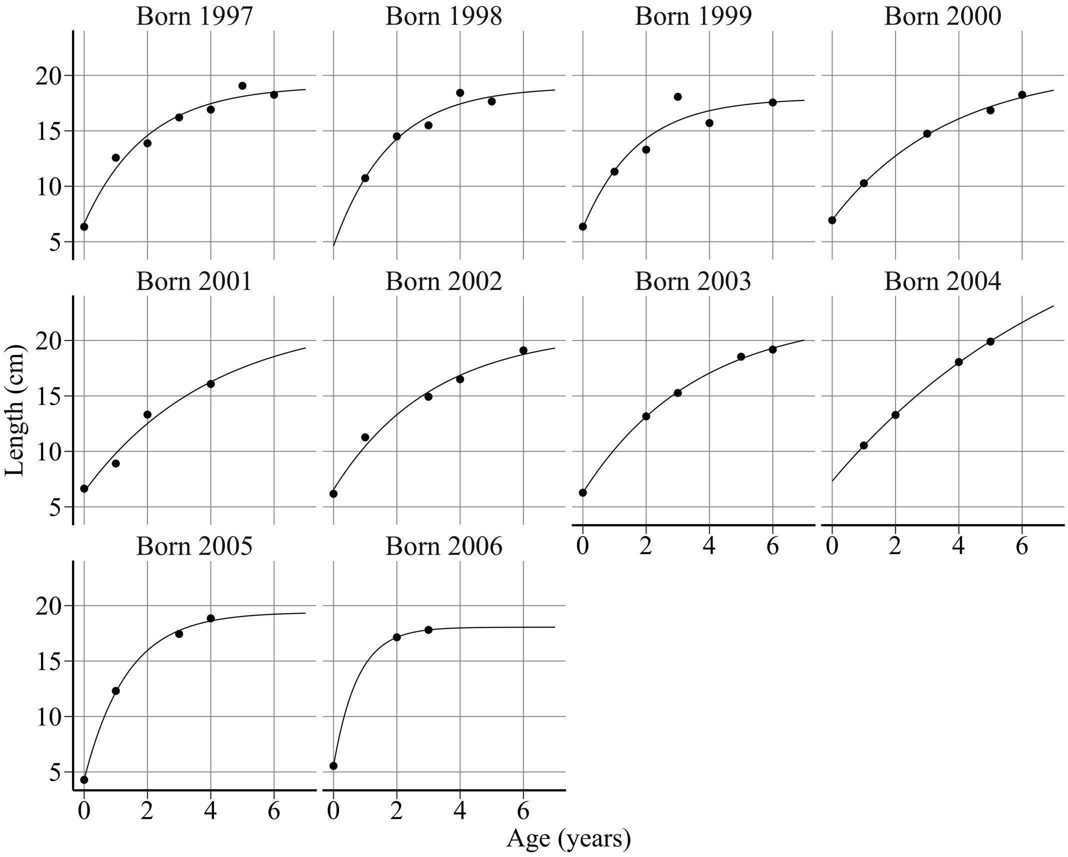


FIGURE 5.9: Fitted von Bertalanffy curves for sandeels between 1997 and 2009 off the Firth of Forth. The solid line denotes the von Bertalanffy fit through observed length at age (black points). Marked variation in von Bertalanffy curves indicates corresponding variation in cohort growth rate throughout the study period.

TABLE 5.2: Results from linear regressions between age (years) and length (mm) for larval *A. marinus* (Length (age) = Hatch length + Growth rate*age). Individuals were caught off the Scottish east coast in 2000, 2001 and 2002.

Year	Hatch length (mm)	Growth rate (mm day^{-1})	R^2
2000	4.62	0.47	0.97
2001	4.71	0.4	0.9
2002	5.65	0.34	0.55

5.1 Discussion

The length of post-metamorphic 0-group sandeels in June was significantly related to larval growth rates off the Scottish east coast (Figure 5.11). During this time hatch dates were relatively fixed in time, ranging from day 73 in 2000 to day 77 in 2002 (see Chapter 4). The implication is that changes in growth rate were responsible for variability in 0-group length at date. While changes in mortality with respect to hatch date could explain changes in 0-group length at date, this appears unlikely. Therefore,

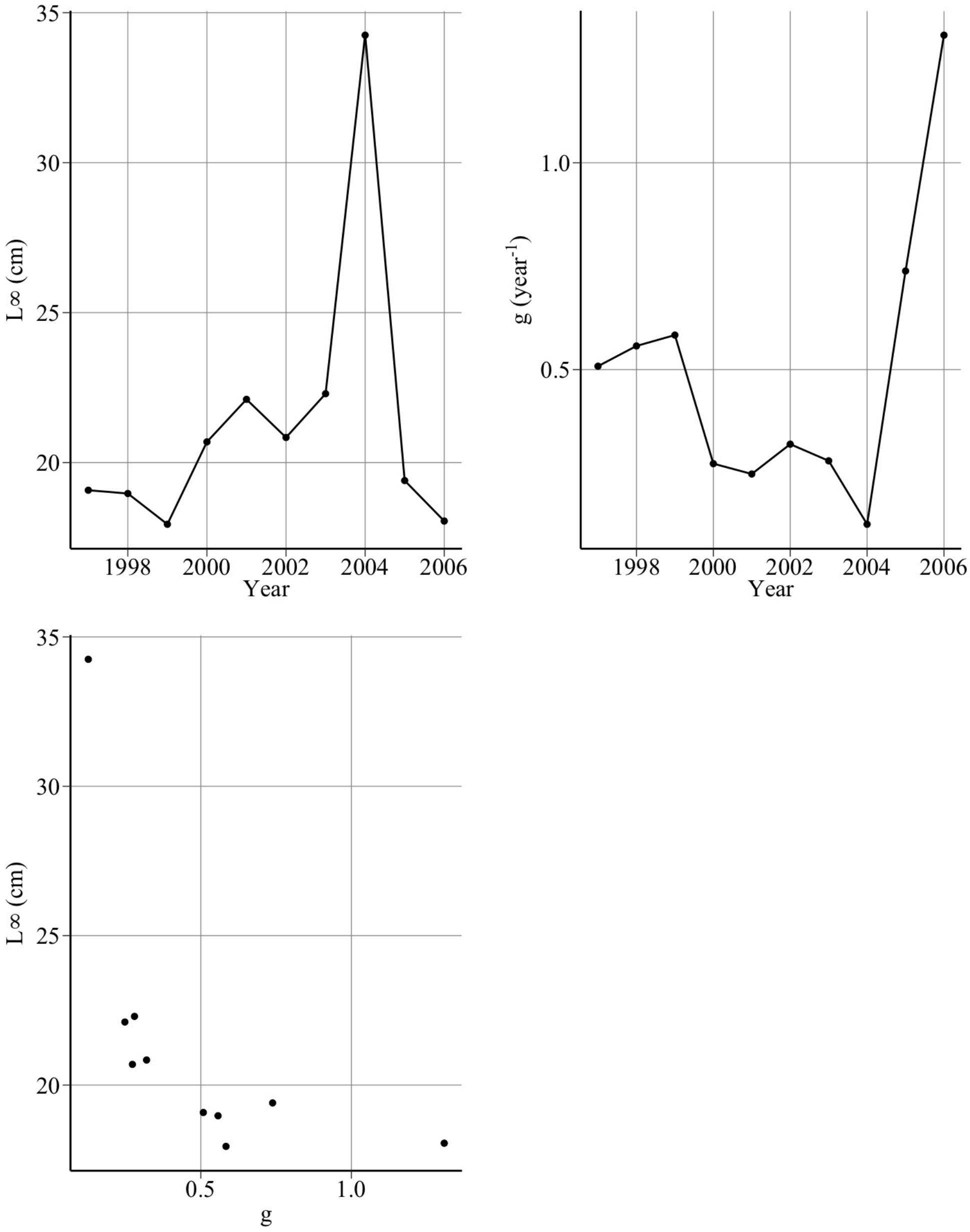


FIGURE 5.10: Changes in growth rate g and asymptotic length L_∞ between 1997 and 2009 off the Firth of Forth. g was relatively low between 2000 and 2004 but increased rapidly towards the end of the study period. Mean growth rate was 0.49 year^{-1} and ranged between 0.13 and 1.31 year^{-1} over the study period. Mean L_∞ was 21.4 cm and ranged between 18 and 34 cm over the study period. This large variation was due to the year 2004. Excluding this year, L_∞ ranged between 18 and 22 cm. There was a significant inverse relationship between growth rate and asymptotic length. This took the form $L_\infty = 5.6789/g$ (s.e. =0.7593, P< 1e-04). Hence, fast growing sandeels reached lower maximum lengths than slower growing individuals.

the significant correlation observed between larval growth rate and post-metamorphic 0-group length supports the hypothesis that changes in food and/or temperature are leading to decreased larval growth rates, and hence lower prey quality for breeding seabirds (Frederiksen et al., 2011).

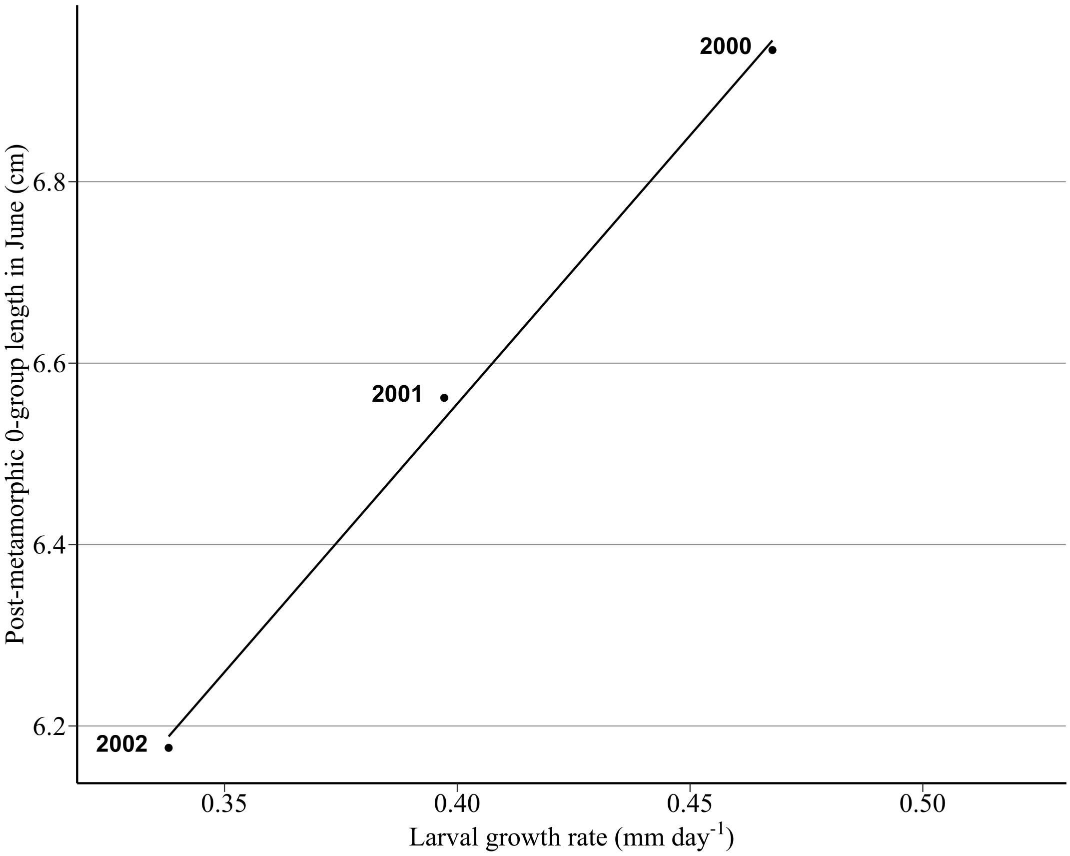


FIGURE 5.11: Regression between 0-group length (cm) in June and larval growth rate. The solid line denotes a statistically significant linear relationship through data (black points) (mm d^{-1}) (R^2= 0.995, $p < 0.04$).

Years of low food abundance may exert a negative effect on larval (> 7 days old) mortality, specifically older larvae around metamorphosis, which is likely an extremely energy demanding process (Brewster, 1987; Gwak et al., 2003). Achieving settlement size in years of low copepod abundance requires larvae to feed longer in the water column, where predation risk is much higher than in the sediment. This may be why years of high 0-group abundance tend to correlate with a larger size-at-date (Eliasen et al., 2011).

The hypothesis of negative food-driven changes in sandeel growth rate is also supported by the coincidence of historic low spring chlorophyll concentration and low sandeel energy values in 2004. The spring bloom is defined as the first time in the year in which chlorophyll concentration in the surface layer exceeds 2 mg m^{-3} for five consecutive days (Scott et al., 2006). But this did not occur in the spring of 2004. Incidentally, this was the year that unexpectedly low energy values were found for sandeels, and this was linked to catastrophic seabird breeding failures on the Scottish east coast (Wanless et al., 2005). In addition, although no measurements of abundance were taken in 2004, changes in seabird breeding output indicated low sandeel availability (Wanless et al., 2005). Larval starvation mortality could have increased if prey abundance was insufficient, especially since first feeding larvae prey exclusively on phytoplankton (diatoms and dinoflagellates) (McGurk, 1992; Monteleone and Peterson, 1986; Covill, 1959; Ryland, 1964). Sandeels born in 2004 had the lowest growth rate and highest asymptotic length of any cohort between 1997 and 2006 (Figure 5.10), which provides evidence that copepod abundance or energy value between 2004 and 2005 may have been poor.

Our results demonstrate an inverse relationship between growth rate and asymptotic length. There are two reasons why this may be the case. First, rapid early growth may increase age-specific metabolism to such an extent that sandeels use all energy for metabolism, and none for somatic growth, while slow growing sandeels, which have lower age-specific metabolism, have energy for somatic growth. This is the biological theory on which the von Bertalanffy growth curve is based upon. An alternative hypothesis is that the inverse relationship between growth rate and asymptotic length arises from variation in maturation at age. For instance, resource allocation models result in growth curves resembling bertalanffys if the difference between anabolism and catabolism increase monotonically with size, but after maturation an increasing fraction goes into reproduction (Czarnoleski and Kozlowski, 1998). Hence, rapid early growth leads to earlier maturation at age and increased energy allocation to reproduction, which is associated with decreased somatic growth.

However, copepod abundance was not significantly different from previous years therefore the proximate cause for a substantial decline in energy content would be a decline in copepod energy content. Hence, the discovery of an absent spring bloom provides evidence of a bottom-up trophic cascade on seabirds. However, zooplankton abundance data does not show any significant changes in this period. The remaining possibility would be that due to a lack of chlorophyll, zooplankton energy content was low, and this cascaded through to the seabirds.

It is possible that starvation mortality contributed to the decline in stock abundance. It may not be coincidental that year-to-year changes in 0-group length reflect trends in stock abundance, especially since starvation mortality generally declines with increasing length (Sogard, 1997). Length increased between 1997 and 2000 and decreased until its lowest value in 2005. Field data shows that stock abundance increased between 1999 and 2001 and decreased thereafter. The steepest decline in 1+ group biomass recorded took place between 2005 and 2006, the period after the lowest recorded 0-group length on record, when the abundance of this group fell by 2 orders of magnitude (Greenstreet et al., 2010).

Fish experiencing poor growth conditions tend to have delayed maturation (Berrigan et al., 1994). Indeed, variation in sandeel growth rate may account for differences in age-at-maturity across the North Sea (Boulcott et al., 2007). Stock abundance is likely sensitive to age-at-maturation, especially since the stock is dominated by fish younger than age 2 (Chapter 2, page 18,19). Therefore, successive years of poor growth, as observed between 2000 and 2004, could decrease stock abundance.

Although sandeel growth has been studied before in the field (Rindorf et al., 2016), this study is the first to analyse year-to-year changes in growth rate. Length-at-age decreased until 2005, and increased thereafter. The 2004-year class had the lowest growth rate, and highest asymptotic length.

Part III

A dynamic energy budget model for sandeels

Chapter 6

Model description

6.1 Introduction

Previous sandeel modelling studies have been hampered due to the lack of empirically derived physiological data. (Table 6.1). However, there has been an expansion in knowledge of how sandeel physiological rates relate to food and temperature (Van Deurs et al., 2010; van Deurs et al., 2013, 2014, 2015). These data can provide a more realistic model of sandeel growth, since the number of biological assumptions can be reduced. Previous modelling studies have modelled length using the von Bertalanffy equation and assumed a fixed relationship between weight and length (Baistrocchi, 2003; Christensen et al., 2009, 2013). Here I use a different approach to modelling growth.

I build and test a new dynamical energy budget (DEB) model for sandeels. There are two central aims of the model. First, the hypothesis that starvation mortality contributed towards the sandeel stock decline off the Scottish east coast between 2000 and 2008 is tested. Second, the relative influence of temperature and food on sandeel physiology is assessed. However, there is another useful model application: the estimation of inter-annual changes in energy available to seabirds.

A DEB model has several advantages over traditional models using length and weight. Starvation mortality cannot be easily modelled using length and weight as state variables. Modelling energy dynamics allows a more direct measure of sandeels ability to withstand starvation (Broekhuizen et al., 1994). DEB models provide an accessible way of modelling energy reserves dynamics and have been applied to a diverse range of species

(Pecquerie et al., 2009; Muller et al., 2010; Pouvreau et al., 2006; van der Veer et al., 2003).

The model hindcasts changes in energy content, weight and length of sandeels off the Firth of Forth off the Scottish east coast. The geographic domain is shown in Figure 6.1.

Table 6.1: Sandeel growth modelling studies.

Paper	Model	Location
Kishi et al. (1991)	Population model	Seto Inland Sea, Japan
Gilman (1994)	Zooplankton consumption	Georges Bank, Western Atlantic
Baistrocchi (2003)	Spatial Population model	western North Sea
Christensen et al. (2009)	Spatial Population Model	North Sea
Van Deurs et al. (2010)	Growth	NA
Christensen et al. (2013)	Spatial Population model	North Sea
van Deurs et al. (2013)	Growth	Dogger bank, North Sea
van Deurs et al. (2014)	Growth	Dogger bank, North Sea
van Deurs et al. (2015)	Growth	Dogger bank, North Sea

6.2 Model framework

Only postmetamorphic sandeels are modelled; egg and larval stages are omitted. The model is split into two post larval components, immature and mature sandeels. Individuals are modelled in terms of structural mass, reserve mass and gonad mass.

In the absence of fishing, sandeels incur several types of mortality. These are natural mortality, predation mortality and starvation mortality. Natural mortality covers all causes of mortality except predation and starvation. That is, factors such as disease, spawning stress, starvation, and old age. Starvation mortality occurs when sandeels exhaust energy reserves. While natural and predation mortality are not modelled, starvation mortality is.

Sandeel energy is largely comprised of reserve energy, structural energy and gonad energy. First, sandeels mobilize energy reserves to survive a long overwintering period, suggesting reserves are a key component (Winslade, 1974; van Deurs et al., 2011). Second, sandeel gonads constitute approximately a third of total body mass, suggesting considerable energy in gonad formation (Gauld and Hutcheon, 1990). Last, structure represents the skeleton among other vital parts, which form a large part of the body.

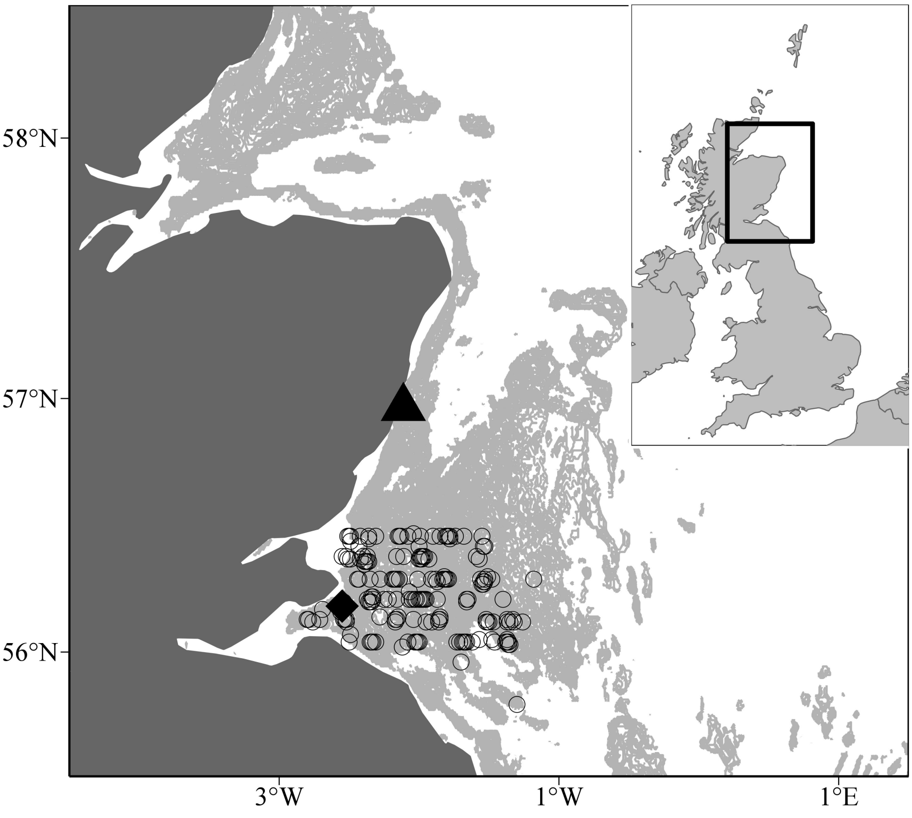


FIGURE 6.1: Location of the model study region site off the Scottish east coast (between latitudes 56^o 00 N and 56^o 30 N and longitudes 003^o 00 W and 001^o 00 W). Open circles represent pelagic trawl locations. The black diamond denotes the Isle of May seabird colony. The pale grey shaded area indicates water depths between 30 and 70m, the range of depth sandeels are most commonly found (Wright et al., 2000), and marks out the 3 main sandbanks, Wee Bankie, Marr Bank and Berwicks Bank.

An important concept in the model is energy allocation. Allocation to structure is length-dependent (Robards et al., 1999). Small sandeels preferentially allocate energy towards growth (Robards et al., 1999). However, large sandeels allocate little energy towards growth. Further, they reach a maximum length suggesting allocation to structure eventually becomes zero. Energy allocation to structure must therefore be a decreasing function of structure.

The aim of the model is to model the changes in energy of sandeel cohorts. The abundance of different size classes of age 0 and age 1 group individuals can be estimated (see methods, chapter 4). Therefore, the decision was made to begin model simulations using these field estimates of energy content and abundance. Tracking changes in individual energy content and the distribution across cohorts will therefore be informative of the influence of environmental drivers. This model was then parameterised and tested using field data as discussed in section 7.4.

Sandeel condition is an important component of the model. Condition influences models of energy allocation, starvation mortality and ingestion. Previous DEB models have used the reserve ratio, defined as the ratio of reserve energy to structural energy, as a proxy for condition (Broekhuizen et al., 1994; Jones et al., 2002). I use the ratio of reserve energy to structural and gonad energy ($\rho = \frac{\text{reserve energy}}{\text{structural energy+gonad energy}}$) as a proxy for condition, and refer to this as the 'reserve ratio', or simply condition.

6.3 Model ordinary differential equations

Individual sandeels are modelled in terms of energy content of structure (S), reserves (R) and gonads (G), with kilojoules as a unit of energy. The rate of change of R, S and G is modelled separately using 3 ordinary differential equations.

The metabolic cost of sustaining the life of an individual is prioritised over growth and reproduction. Therefore, energy allocation to gonad and structure should only occur after metabolic costs are covered. This is modelled using the following assumptions: 1. All assimilated energy enters reserves. 2. Metabolic costs are subtracted from reserves. 3. Once metabolic costs have been paid a fraction of remaining assimilated energy is allocated to structure and gonads.

The rate of change of reserve energy is given by:

$$\boxed{\frac{dR}{dt} = A - M - \frac{dS}{dt} - \frac{dG}{dt}} \tag{6.1}$$

where A is the rate at which an animal assimilates energy (kJ d^{-1}) and M is the rate at which animals lose energy to metabolism (kJ d^{-1}).

The rate of change of structural energy is given by:

$$\boxed{\frac{dS}{dt} = C(\rho, S) \max(0, A - M)} \tag{6.2}$$

where ρ is the sandeel reserve ratio and $C(\rho, S)$ is the fraction of assimilated energy remaining after metabolism that is used to form structure.

$C(\rho, S)$ takes the form

$$C(\rho, S) = \begin{cases} f\left(S_1 - S_2 \log(S)\right), & \text{if } \rho > \rho_0 + \rho_w \\ f\left(\frac{S_1 - S_2 \log(S)[\rho - \rho_0]^+}{\rho_w}\right), & \text{otherwise} \end{cases} \tag{6.3}$$

where S_1 and S_2 are constants for the maximum proportion of energy allocated to structure, ρ_0 is the defended reserve ratio and ρ_w is the allocation switch width. The function $f(\cdot)$ constrains energy allocation $C(\rho, S)$ between 0 and 1, thus $f(X) = \max(0, \min(1, X))$ There are two reasons for the rather complicated form of $C(\rho, S)$. First, small sandeels appear to use much more energy to build structure than larger sandeels (Robards et al., 1999). Hence, $C(\rho, S)$ must be a decreasing function of length. Second, individuals with a high reserve ratio allocate more energy to structure than those with poor reserve ratios. Therefore, $C(\rho, S)$ must be an increasing function of the reserve ratio. It is easier to understand the processes involved in equation 6.3 if we visualize changes in energy allocation of individuals of different length and condition (left panel in Figure 6.2).

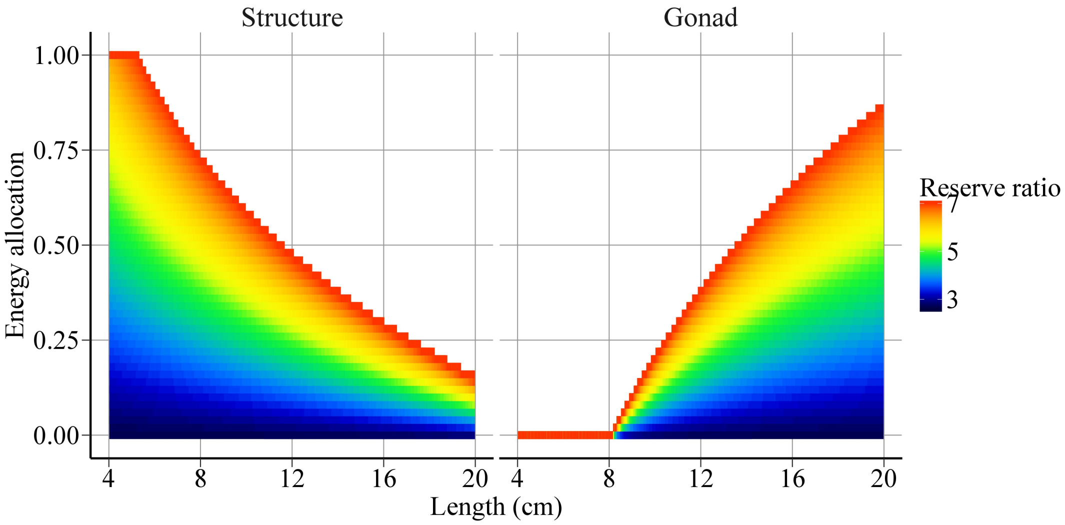


FIGURE 6.2: Energy allocation to structure and gonads. The left and right panels show energy allocation to structure ($C(\rho, S)$) and gonads ($G(\rho, S)$), respectively. No allocation to structure or gonads occurs below a reserve ratio of ρ_0.

The rate of change of gonad energy is given by:

$$\boxed{\frac{dG}{dt} = G(\rho, S)\, R} \tag{6.4}$$

where $G(\rho, S)$ is the fraction of reserve energy directed to gonads. *A.marinus* are capital breeders, meaning energy stores gained during the summer feeding period are used to form gonads (Boulcott and Wright, 2008; Macer, 1966). I assume that gonad energy allocation occurs between 1st October and 21st January. This is because field data shows that gonad size increases substantially after September (Bergstad et al., 2001) and the mean spawning day off the Scottish east coast is 21st January (see Chapter 4). The efficiency of gonad formation is assumed to be 100%. Age-at-maturity is set at age 1 (Boulcott et al., 2007). Male and female sandeels appear to incur similar energy losses during spawning (Table 6.2).

$G(\rho, S)$ takes the form

$$G(\rho, S) = \begin{cases} f\left(G_1 + G_2 \log(S)\right), & \text{if } \rho > \rho_0 + \rho_w \text{ \& } 1^{\text{st}} \text{ October} < \text{date} < 21^{\text{st}} \text{ January} \\ f\left(\frac{G_1 + G_2 \log(S)[\rho - \rho_0]^+}{\rho_w}\right), & \text{if } \rho \leq \rho_0 + \rho_w \text{ \& } 1^{\text{st}} \text{ October} < \text{date} < 21^{\text{st}} \text{ January} \\ 0, & \text{otherwise,} \end{cases} \tag{6.5}$$

where G_1 and G_2 are constants for the maximum proportion of energy allocated to gonads. It is easier to understand the processes involved in equation 6.5 if we visualize changes in energy allocation of individuals of different length and condition (right panel in Figure 6.2).

Table 6.2: Maximum gonad weight as a percentage of wet body weight (GSI) from sandeel maturation studies. Sandeels gonads comprises around a third of total body weight, reflecting a large energetic investment in reproduction. Note that all calcualations for *A. dubius* are in terms of dry weight.

Species	Sex	Number measured	GSI	Wet weight (g)	Gonad weight (g)	Length (cm)	Source
A. Americanus	F	27	29	10.99	3.15	14.88	Smigielski et al. (1984)
	M	44	26	10.63	2.72	14.47	
A. Hexapterus	F	32	31	10.94	3.38	13.80	Robards et al. (1999)
	M	27	26	11.71	3.09	14.40	
A. Dubius	F	7	26	1.22	0.322	12.7	Gilman (1994)
	M	1	14	1.23	0.176	13.2	
A. marinus	F	70	28	NA	NA	NA	Gauld and Hutcheon (1990)
A. personatus	F	32	32	NA	NA	NA	Okamoto et al. (1989)
	M	38	25	NA	NA	NA	

6.3.1 Metabolism

Metabolism is determined by temperature and body mass. Metabolic rates of an organism usually follow a Q_{10} relationship; that is, for every 10 ^{o}C increase in temperature metabolism increases by a factor of Q_{10}. Moreover, metabolism scales with body weight to a power less than 1 i.e. metabolism body weight$^p, p < 1$ (Clarke and Johnston, 1999). Hence, larger fish usually have lower weight-specific metabolism than smaller fish. Sandeel metabolism is higher during feeding season than overwintering due to activity associated with foraging. *A. marinus* only forage during daylight (Ryland, 1964) and spend 2 times standard metabolic rate (SMR) when doing so (van Deurs et al., 2015). The energy lost to metabolism can therefore be written in terms of temperature T and body weight w.

Hence, the metabolism of feeding animals is the sum of standard metabolic rate and activity costs:

$$\begin{aligned} M_{\text{feed}} &= \text{Standard metabolic rate} + \text{Activity} \\ &= M_f\, Q_{10,M_f}^{T/10}\, w^r + P_d M_f\, Q_{10,M_f}^{T/10}\, w^r \\ &= M_f\, Q_{10,M_f}^{T/10}\, w^r + P_d M_f\, Q_{10,M_f}^{T/10}\, (\frac{R_{\text{dry}}}{E_R} R + \frac{S_{\text{dry}}}{E_S} S + \frac{G_{\text{dry}}}{E_G} G)^r \end{aligned} \tag{6.6}$$

M_f is the metabolic cost rate scale during the feeding season (kJ g^r d^{-1}), $Q_{10,M_f}^{T/10}$ is the Q_{10} for feeding metabolism, w is wet weight (g) and r is the metabolic rate exponent. The term P_d in equation 6.13 represents the proportion of the day with daylight. R_{dry} ,S_{dry} and G_{dry} are dry-wet weight conversion factors for reserve, structural and gonad tissue. E_R, E_S and E_G are energy densities of reserve, structural and gonad dry tissue.

The metabolism of overwintering animals requires a different formulation:

$$\begin{aligned} M_{\text{OV}} &= M_o\, Q_{10,M_o}^{T/10}\, w^r \\ &= M_o\, Q_{10,M_o}^{T/10}\, (\frac{R_{\text{dry}}}{E_R} R + \frac{S_{\text{dry}}}{E_S} S + \frac{G_{\text{dry}}}{E_G} G)^r \end{aligned} \tag{6.7}$$

where M_o is the metabolic cost rate scale in winter (kJ g^r d^{-1}) and Q_{10,M_o} is the Q_{10} for winter metabolism.

The effect of body mass on *A. marinus* overwintering metabolism has not been quantified in the literature. However, this can be estimated using published respiration data from the closely related species, *A. hexapterus* (Quinn and Schneider, 1991). Quinn and Schneider (1991) measured *A. hexapterus* respiration rates of animals of different weights at 12 ^{0} C (Figure 6.3). The range of body weights is sufficient to estimate a scaling exponent for metabolism.

A respiration rate model of the form: respiration rate = $a{*}w^r$ was fitted to *A. hexapterus* oxygen consumption data using non-linear least squares (R^2 = 0.84, p<0.001, Figure 6.3).

$$\text{Respiration rate}(\mu\text{l}\, O_2\, \text{h}^{-1}) = 110.05\, w^{0.645} \tag{6.8}$$

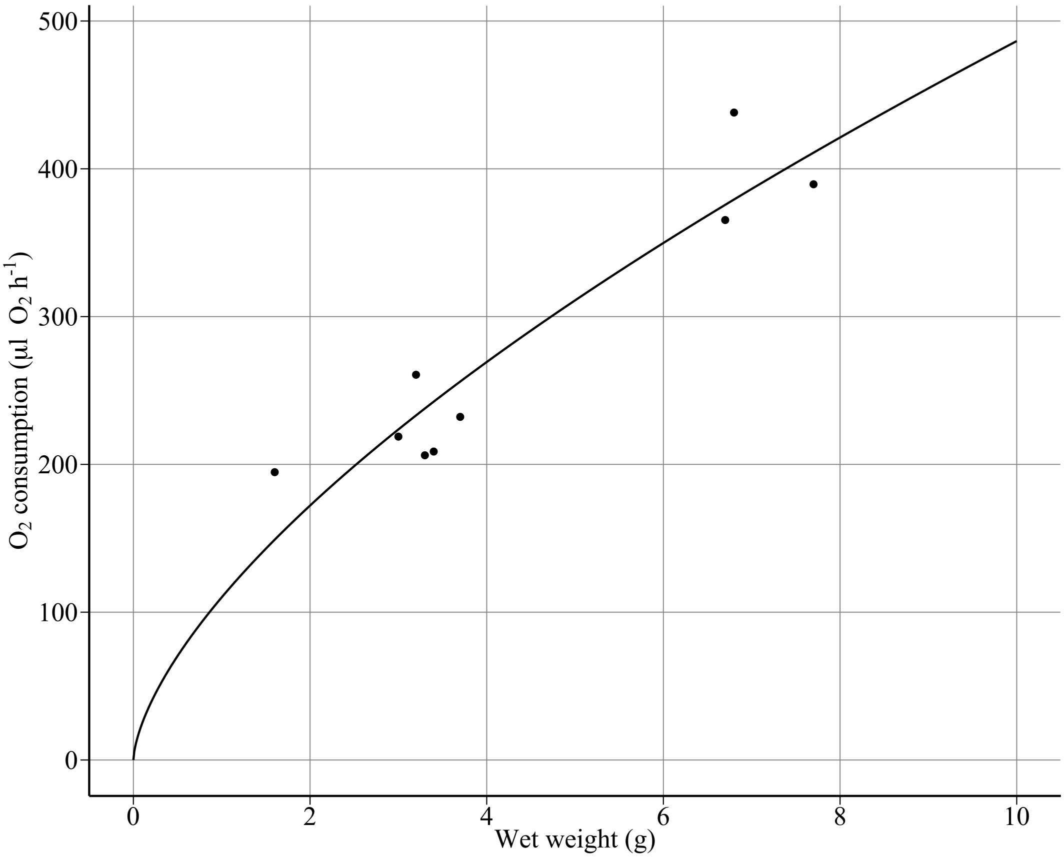


FIGURE 6.3: *A. hexapterus* resting oxygen consumption. Oxygen consumption scales with body weight to the power 0.65. Therefore, the relative metabolic rate of a sandeel decreases substantially with weight. Data digitized from figure 1 in Quinn and Schneider (1991).

The effect of temperature on *A. marinus* metabolism has not been quantified. However, the influence of temperature on overwintering metabolism has been estimated for two similar species, *A. tobianus* (van Deurs et al., 2011) and *A. hexapterus* (Quinn and Schneider, 1991). These species display remarkably different metabolic responses to temperature. Overwintering *A. tobianus* have a Q_{10} of 4.06 (van Deurs et al., 2011), while the corresponding value for *A. hexapterus* is 1.46 (Quinn and Schneider, 1991). I therefore reviewed Q_{10}s for metabolism in other fish (Clarke and Johnston, 1999). This showed fish species typically have a Q_{10} close to 2 (Clarke and Johnston, 1999). Therefore, the Q_{10} for *A. tobianus* is uncommonly high. The Q_{10} for overwintering metabolism was thus set to 1.46.

There are even fewer studies to guide the choice of the feeding Q_{10}. Only one study has measured the effect of temperature on feeding sandeels (Quinn and Schneider, 1991). Quinn and Schneider (1991) found a value of 1.8 for the Q_{10} for *A. hexapterus* metabolism The Q_{10} for feeding metabolism was thus set to 1.8.

THe response of metabolism to temperature and body size has been estimated. The final step in deriving equations for metabolism is to estimate the metabolic cost rate scales M_f and M_o (equations 6.13 and 6.15). Oxygen consumption data for summer and winter acclimatised *A. hexapterus* is used (Table 6.3). First, oxygen consumption rates O_2 (μl 0_2 g^{-1} h^{-1}) are converted into energy depletion rates E (kJ d^{-1}) Thus,

$$\begin{aligned} E &= 24 \times 10^{-6} \times A \times B \times w \times O_2 \\ &= 24 \times 10^{-6} \times 1.43 \times 14 \times 3 \times 0_2 \\ &= 0.00144\, 0_2 \end{aligned} \tag{6.9}$$

where A is the number of grams of oxygen gas required to make 1 litre of oxygen gas, B is a general oxycaloric coefficient (J mg^{-1}) (van Deurs et al., 2011), w is the wet weight of animals in respiration experiments (g) and O is oxygen consumption rate (μl 0_2 g^{-1} h^{-1}). Derived energy depletion rates are shown in (Table 6.3).

TABLE 6.3: *A. hexapterus* oxygen consumption rate (μl O_2 h^{-1}) according to season and temperature. Rates are adjusted to a standard body weight of 3 g.

Season	Temperature	Oxygen consumption (μl O_2 g^{-1} h^{-1})	Energy depletion rate (kJ d^{-1})
Summer	5	38.4	0.0553
	12	57.9	0.0834
Winter	5	29.3	0.0422
	12	38.3	0.0552

Thus, to calculate the summer metabolic cost rate M_f, nonlinear regression is used to solve

$$M_{\text{feed}} = M_f\, 1.8^{T/10}\, 3^{0.645} \tag{6.10}$$

with summer energy depletion rates given in Table 6.3. Equation 6.10 represents the standard metabolic rate of feeding sandeels, since the animals in the respiration experiments were completely inactive (Quinn and Schneider, 1991). Therefore, equation 6.10 is exactly the same as equation 6.13, except the activity parameter P_d to zero.

The winter metabolic cost rate M_o is calculated in a similar way

$$M_{\mathrm{OV}} = M_o\, 1.46^{T/10}\, 3^{0.645} \tag{6.11}$$

with winter energy depletion rates given in Table 6.3. Modelled metabolic costs of summer and winter acclimatised animals at 12 ^{o}C are illustrated in Figure 6.4.

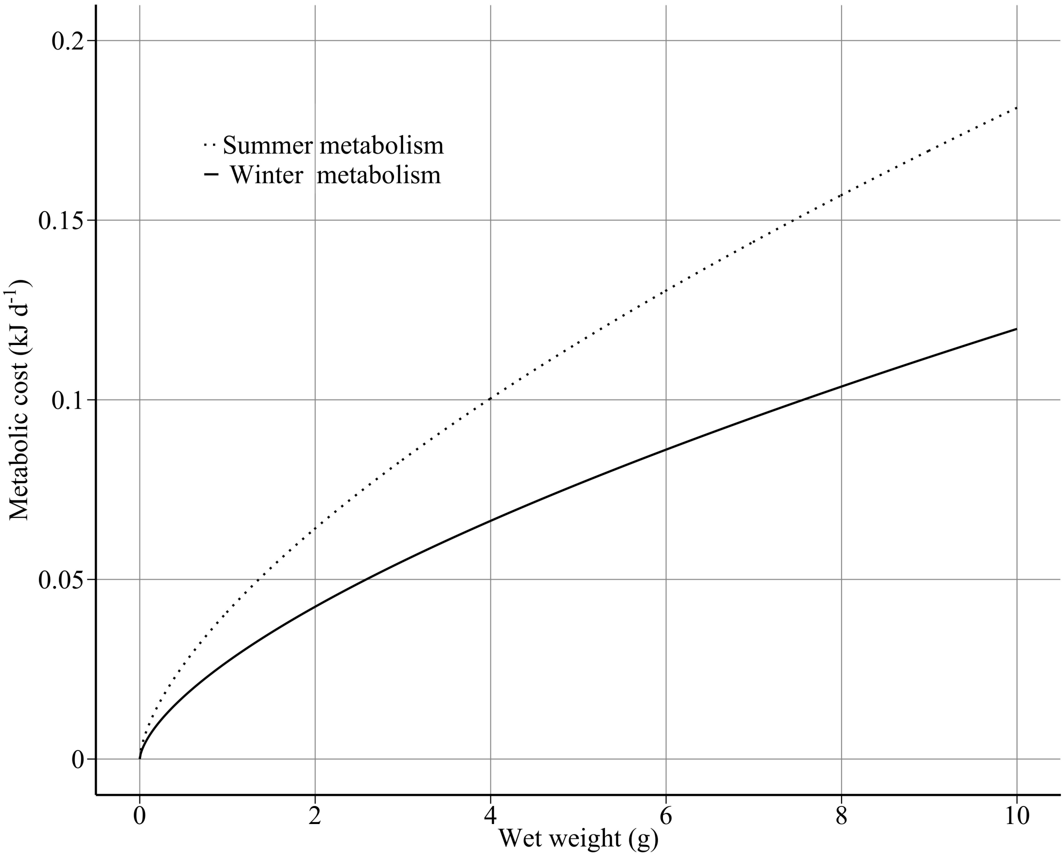


FIGURE 6.4: Modelled seasonal variation in sandeel standard metabolic rate at 12 ^{o}C. Metabolism of feeding sandeels is twice as high as overwintering individuals. Metabolic rates derived from Table 1 in Quinn and Schneider (1991).

The energy lost to metabolism can therefore be written in terms of temperature T and body weight w.

Hence, the metabolism of feeding animals is

$$\begin{aligned} M_{\mathrm{feed}} &= \text{Standard metabolic rate} + \text{Activity} \\ &= M_f\, Q_{10,M_f}^{T/10}\, w^r + P_d M_f\, Q_{10,M_f}^{T/10}\, w^r \\ &= M_f\ (1+P_d)\ Q_{10,M_f}^{T/10}\, \left(\frac{R_{\mathrm{dry}}}{E_R} R + \frac{S_{\mathrm{dry}}}{E_S} S + \frac{G_{\mathrm{dry}}}{E_G} G\right)^r \end{aligned} \tag{6.12}$$

Hence,

$$\boxed{M_{\text{feed}} = 0.02026\ (1 + P_d)\ 1.8^{T/10}\,(\frac{R_{\text{dry}}}{E_R} R + \frac{S_{\text{dry}}}{E_S} S + \frac{G_{\text{dry}}}{E_G} G)^{0.645}} \tag{6.13}$$

$M_f = 0.02026$ is the metabolic cost rate scale during the feeding season (kJ g^r d^{-1}), $Q_{10,M_f} = 1.8$ is the Q_{10} for feeding metabolism and $r = 0.645$ is the metabolic rate exponent.

The metabolism of overwintering animals requires a different formulation:

$$\begin{aligned} M_{\text{OV}} &= M_o\, Q_{10,M_o}^{T/10}\, w^r \\ &= M_o\, Q_{10,M_o}^{T/10}\,(\frac{R_{\text{dry}}}{E_R} R + \frac{S_{\text{dry}}}{E_S} S + \frac{G_{\text{dry}}}{E_G} G)^r \end{aligned} \tag{6.14}$$

Hence,

$$\boxed{M_{\text{OV}} = 0.01722\, 1.46^{T/10}\,(\frac{R_{\text{dry}}}{E_R} R + \frac{S_{\text{dry}}}{E_S} S + \frac{G_{\text{dry}}}{E_G} G)^{0.645}} \tag{6.15}$$

where $M_o = 0.01722$ is the metabolic cost rate scale in winter (kJ g^r d^{-1}) and $Q_{10,M_o} = 1.46$ is the Q_{10} for winter metabolism.

6.3.2 Ingestion

Modelled ingestion rate is related to temperature, body size, condition, photoperiod and zooplankton community abundance and composition. Before outlining the details of the ingestion model, a brief summary of the existing knowledge of the biology and ecology of sandeel feeding is provided. The model is a mathematical synthesis of this understanding.

Sandeels live in the sediment during darkness and feed on calanoid copepods during daylight hours (Macer, 1966; Ryland, 1964; van Deurs et al., 2013). When feeding, individuals are either engaged in searching for food or handling food. A sandeel continually searches for food until a prey item is encountered and consumed. Animals take time to digest prey and so must temporarily stop searching.

Sandeels appear to actively search for larger prey items, ignoring smaller ones (van Deurs et al., 2014). This is supported by field observations which show sandeels do not filter feed; they consume large copepods and only feed on small copepods when the former are absent (van Deurs et al., 2014).

Body size has a critical influence on ingestion rate. Larger sandeels swim faster than smaller individuals so they encounter more prey items. Further, the guts of larger individuals can hold more prey items than smaller sandeels.

There is evidence that sandeels increase their ingestion rates when in poor condition. This is supported by the fact that animals grow extremely rapidly after going more than two-thirds of the year without feeding. Indeed, it may only take 2 months for these animals to double their energy content (Hislop et al., 1991).

Ingestion rates for sandeels feeding on a prey field of two copepod groups are influenced by a variety of factors. This will depend on large and small copepod abundance (n_L, n_S), energy content (E_L, E_S, kJ) and the search time (t_s, fraction of day). However, there are several other important factors that determine ingestion rate. Two factors, swimming speed and gut size, relate to sandeel size. As the size of the gut increases, it will be able to hold more prey items. An increase in swimming speed will allow sandeels to catch more prey items. These two factors are represented by S^q in equation 6.16. Finally, ingestion rate is dependent on attack rates on large and small copepods (a_L, a_S, $\frac{1}{\mathrm{kJ}^q \mathrm{days}}$).

Combining this information, ingestion rate (kJ day^{-1}) during a search time t_s (fraction of day) is

$$I = a_L t_s n_L E_L S^q + a_S t_s n_S E_S S^q \tag{6.16}$$

No quantitative information exists on the effect of sandeel body size on search rate, so the choice of scaling exponent is tricky. A common theoretical assumption is that search rate should scale with the surface area of the individual. A scaling of $q = 2/3$ is adopted, a value assumed in an experimental study on *A.marinus* consumption of herring larvae (Christensen, 2010).

Search time t_s is found by subtracting the total time handling prey (fraction of day) from the total time foraging (fraction of day)

$$t_s = P_d - a_L t_s n_L h_L S^q + a_S t_s n_S h_S S^q. \tag{6.17}$$

Rearranging for t_s,

$$t_s = \frac{P_d}{1 + a_L n_L h_L S^q + a_S n_S h_S S^q}, \tag{6.18}$$

The Ingestion rate (kJ day^{-1}) is therefore

$$I = P_d \, \frac{a_L n_L E_L S^q + a_S n_S E_S S^q}{1 + a_L n_L h_L S^q + a_S n_S h_S S^q}. \tag{6.19}$$

One might expect the two handling times to be different since adult calanus are an order of magnitude larger than adult calanoid copepods of other species. Modelled handling time is proportional to copepod weight. Note that this is copepod energy (E_i) divided by their energy density (Ed_i, kJ g^{-1}). Hence handling time is $h_i = \phi w_i = \phi \frac{E_i}{Ed_i}$, where ϕ is a variable. Later in the derivation, we shall see handling time is an increasing function of copepod energy, and a decreasing function of structure S and temperature T.

$$I = P_d \, \frac{a_L n_L E_L S^q + a_S n_S E_S S^q}{1 + a_L n_L \phi \frac{E_L}{Ed_L} S^q + a_S n_S \phi \frac{E_S}{Ed_S} S^q}. \tag{6.20}$$

Large and small copepod energy concentration is written as $F_i = n_i E_i$ (kJ).

Thus,

$$I = P_d \, \frac{\frac{1}{\phi}(a_L F_L + a_S F_S) S^q}{\frac{1}{\phi} + (\frac{a_L F_L}{Ed_L} + \frac{a_S F_S}{Ed_S}) S^q}. \tag{6.21}$$

Assuming that maximum ingestion rate ($I_{\max}$) is reached for extremely large prey concentrations,

$$\frac{E_d \, P_d}{\phi} = I_{max}, \tag{6.22}$$

where prey energy density E_d is

$$E_d = \frac{Ed_L a_L n_L + Ed_S a_S n_S}{a_L n_L + a_S n_S} \tag{6.23}$$

Equation 6.21 is restated as

$$I = \frac{\frac{I\text{max}}{E_d}(a_L F_L + a_S F_S) S^q}{\frac{I\text{max}}{E_d P_d} + (\frac{a_L F_L}{Ed_L} + \frac{a_S F_S}{Ed_S}) S^q}. \tag{6.24}$$

Three biological factors determine sandeel maximum ingestion rate. These are the rate at which food leaves the stomach (referred to as the digestion rate), the maximum stomach capacity, and the reserve ratio. The latter influences maximum ingestion rate because sandeels appear to increase their consumption rates if condition falls below a threshold value. Referred to as compensatory growth, this phenomena is an adaptation to highly variable food availability, and has been demonstrated in a number of species (Christensen and McLean, 1998; Jobling and Johansen, 1999; Xie, 2001). The fact that sandeels grow very rapidly over a extremely short time after emerging from the overwintering period suggests a compensatory growth response.

Hence, maximum ingestion rate can be expressed in terms of a digestion rate Q (day^{-1}), maximum stomach weight $SW\text{max}$ (g), and function of reserve ratio($\Lambda(\rho)$:

$$I\text{max} = P_d \, \Lambda(\rho) \, Q \, SW\text{max}. \tag{6.25}$$

where

$$\Lambda = \begin{cases} \lambda, & \text{if } \rho < \tau \\ 1, & \text{otherwise.} \end{cases} \tag{6.26}$$

Hence, sandeels increase their maximum ingestion rate if the reserve ratio falls below a critical threshold τ. When this happens, maximum ingestion rate is multiplied by a term λ. The maximum ingestion rate of a sandeel with reserve ratio less than τ is therefore greater than that of a sandeel with identical structural weight and reserve ratio greater than τ.

Next, I derive the form of equation 6.25 for sandeels with high condition (for the case $\Lambda = 1$, $\rho < \tau$). No experimental data on *A. marinus* digestion rate and maximum stomach weight is available. Fortunately, this data is available for a closely related species, *A. tobianus*. Therefore, the maximum ingestion rate of a sandeel can be estimated.

Digestion rate is a function of temperature T (°C) and prey energy density E_d (kJ (g WW)$^{-1}$).

From van Deurs et al. (2015), sandeel digestion rate Q (day^{-1}) is

$$Q = \frac{3.696}{E_d}\, e^{0.054\,T} \tag{6.27}$$

It should be noted this is the gastric evacuation rate and not the true digestion rate. However, both rates should be similar due to sandeel's ability to rapidly digest prey (Christensen, 2010).

Using data on the relationship between length and maximum stomach weight (Figure 6.5), estimated from supplementary material in Van Deurs et al. (2010)),

$$SW_{\text{max}}(g) = 0.000436\, L^3 \tag{6.28}$$

The maximum energy ingested is found my mulpliying maximum stomach weight (g) by prey energy density E_d

$$SW_{\text{max}}(\text{kJ}) = 0.000436\, E_d\, L^3 \tag{6.29}$$

Next, length is expressed in terms of structural energy (equation 7.18 from section 7.6),

$$\begin{aligned} SW_{\text{max}}(\text{kJ}) &= 0.000436\, E_d\, \frac{S}{0.00465} \\ SW_{\text{max}}(\text{kJ}) &= 0.0937\, E_d\, S \end{aligned} \tag{6.30}$$

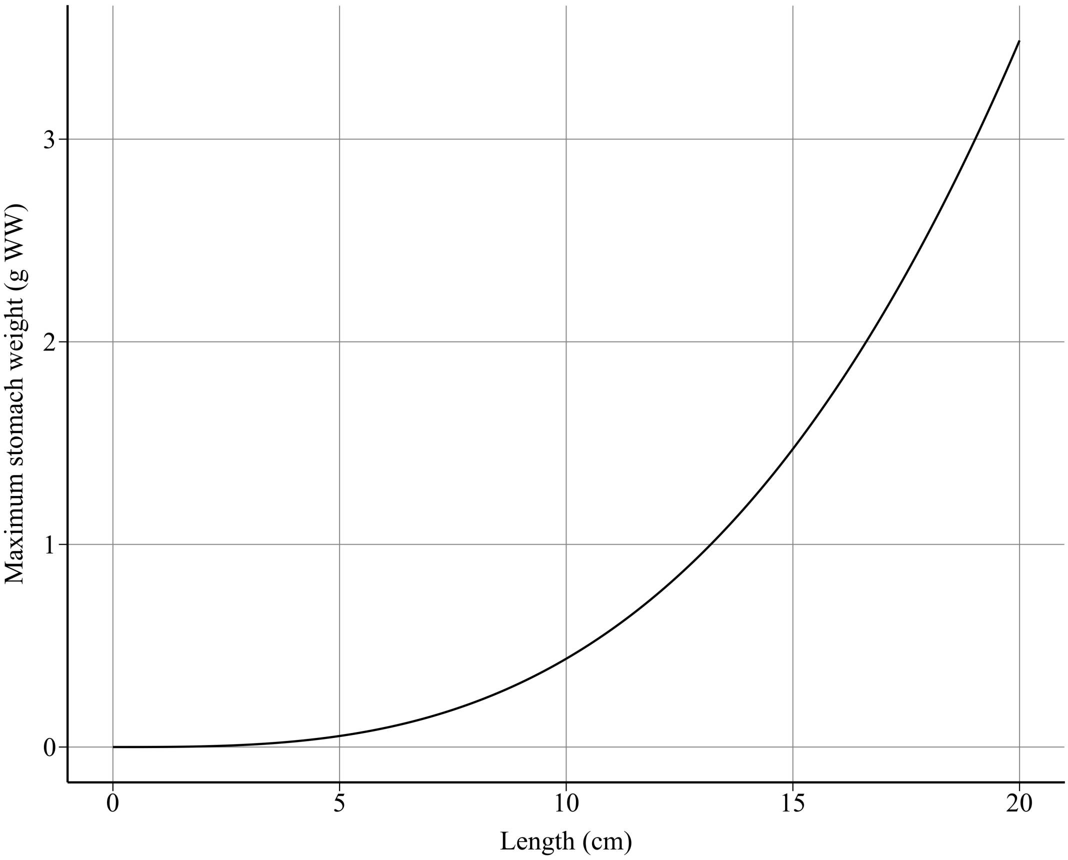


FIGURE 6.5: Maximum stomach weight in relation to length. A sandeel stomach shows isomorphic growth. Relationship was derived from supplementary material in Van Deurs et al. (2010).

$$\begin{aligned} I_{\max} &= P_d\,\Lambda(\rho)\,Q\,SW_{\max} \\ &= P_d\,\Lambda(\rho)\,\frac{3.696}{E_d}\,e^{0.054\,T}\,0.0937\,E_d\,S \\ &= P_d\,\Lambda(\rho)\,0.346\,e^{0.054\,T}\,S \end{aligned} \tag{6.31}$$

The temperature effect term $e^{0.054\,T}$ is rewritten as $Q_{10,U}^{T/10}$. Hence, maximum ingestion rate (kJ d^{-1}) is expressed as

$$I_{\max} = P_d\,\Lambda(\rho)\,0.346\,Q_{10,U}^{T/10}\,S \tag{6.32}$$

Ingestion rate (I , kJ d^{-1}) is written as

$$I = P_d \frac{\frac{I_0 \, \Lambda \, Q_{10,U}^{T/10} \, S^p (a_L F_L + a_S F_S)}{E_d}}{\frac{I_0 \, \Lambda \, Q_{10,U}^{T/10} \, S^{p-q}}{E_d} + (a_L w_L + a_S w_S)} \tag{6.33}$$

Hence,

$$\boxed{I = P_d \frac{\frac{0.346 \, \Lambda \, 1.72^{T/10} \, S (a_L F_L + a_S F_S)}{E_d}}{\frac{0.346 \, \Lambda \, 1.72^{T/10} \, S^{0.33}}{E_d} + (a_L w_L + a_S w_S)}} \tag{6.34}$$

where

$$\Lambda = \begin{cases} \lambda, & \text{if } \rho < \tau \\ 1, & \text{otherwise.} \end{cases} \tag{6.35}$$

where $I_0 = 0.346$ is the maximum ingestion scale (kJ g^{-p} d^{-1}), $Q_{10,U} = 1.72$ is the effect of temperature on uptake rate, $p = 1$ is the maximum ingestion rate exponent and $q = 2/3$ is the effect of search rate exponent.

6.3.3 Overwintering timing

In the model sandeels must cease feeding and overwinter for a prolonged period. Further, this overwintering period must end as animals return to the water column to feed (Reeves, 1994). Field evidence shows that sandeels emerge within a short window between the beginning of March and the end of April (Reeves, 1994). However, the causes of timing are not understood. I therefore make the simplifying assumption that all animals exit on April 1$^{\text{st}}$.

It remains unclear what causes an animal to start overwintering. Photoperiod, fat content, food abundance and temperature have been proposed as possible triggers (Winslade, 1974), However, the only hypothesis that is consistent with the evidence is that overwintering commencement is related to fat content.

Declining food abundance has been proposed to be a trigger (Winslade, 1974). However, this does not appear to be credible. Closely related species have been observed to stop feeding during the time of year when plankton production reaches a maximum

(Tomiyama and Yanagibashi, 2004). Furthermore *A. marinus* overwinters at a time when there is a large bloom in the prey species *C. helgolandicus* (Edwards et al., 2010).

Variation in overwintering start dates is too great for photoperiod to be a critical influence. Overwintering onset is protracted and appears to range between May and October (Reeves, 1994).

Modelled sandeels are assumed to overwinter when a reserve ratio threshold is reached. Animals must survive for up to 8 months without feeding which requires a minimum amount of energy reserves per weight (van Deurs et al., 2011). The timing of this overwintering threshold is size-specific; smaller sandeels require higher reserve ratios to overwinter than larger sandeels at length. This is because smaller animals have higher weight specific respiration rates and therefore deplete energy reserves at a relatively faster rate. This assumption is justified by the fact that smaller animals spend 1—2 months longer feeding (Macer, 1966; Reeves, 1994; Kvist et al., 2001). Therefore, the overwintering threshold OV_{thresh} is a decreasing function of length. Modelled individuals begin overwintering once the reserve ratio $\frac{R}{S+G}$ exceeds a critical value OV_{thresh}.

Hence,

$$OV_{\text{thresh}} = \frac{OV_1 - OV_2\, d}{S^{OV_3}} \tag{6.36}$$

where d stands for julian day, OV_1 is the overwinter threshold intercept (kJ^c), OV_2 is the overwinter threshold slope (kJ^c) and OV_3 is the overwinter threshold length-dependent exponent. Figure 6.6 shows OV_{thresh} for different sizes of sandeels.

Hence, the term S^c in equation 6.36 reflects the need of smaller fish to attain a higher reserve ratio than larger fish before overwintering. OV_{thresh} is a decreasing function of time because the reserves necessary to begin overwintering in July exceed those required to begin overwintering in December.

6.3.4 Modelling starvation mortality

Modelled sandeels incur condition-dependent starvation mortality. While a sandeel with no energy reserves is likely to suffer mortality, starvation may start to occur once the

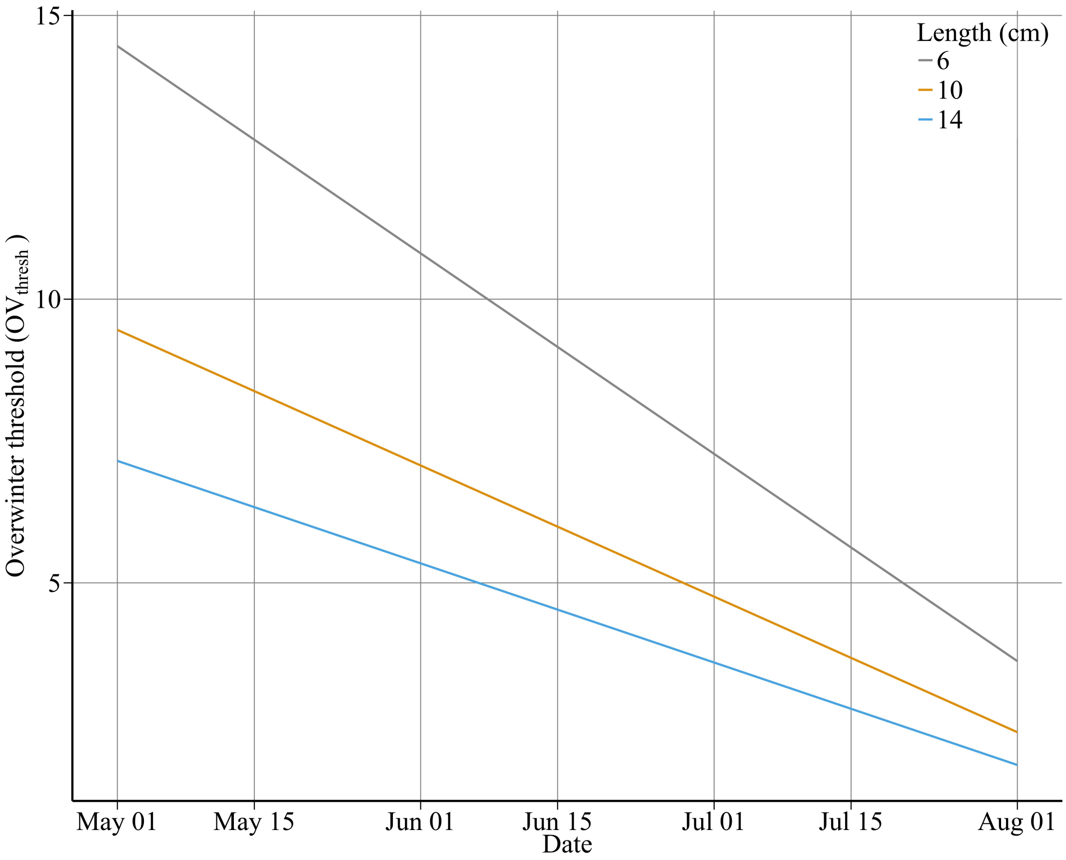


FIGURE 6.6: Overwintering onset threshold OV_{thresh} between 1st May and 1st August for 6, 10 and 14 cm sandeels. Smaller sandeels must be in better condition than larger sandeels to overwinter.

reserve ratio falls below a critical value. Starvation is regarded as a probabilistic process, so a given fraction of the population is removed. Hence,

$$\boxed{P(\text{Survival}) = \frac{1}{1 + e^{-\sigma_1\left(\frac{R}{S+G} - \sigma_2\right)}}} \tag{6.37}$$

where σ_1 is the starvation response shape parameter and σ_2 represents the reserve ratio at 50% survival.

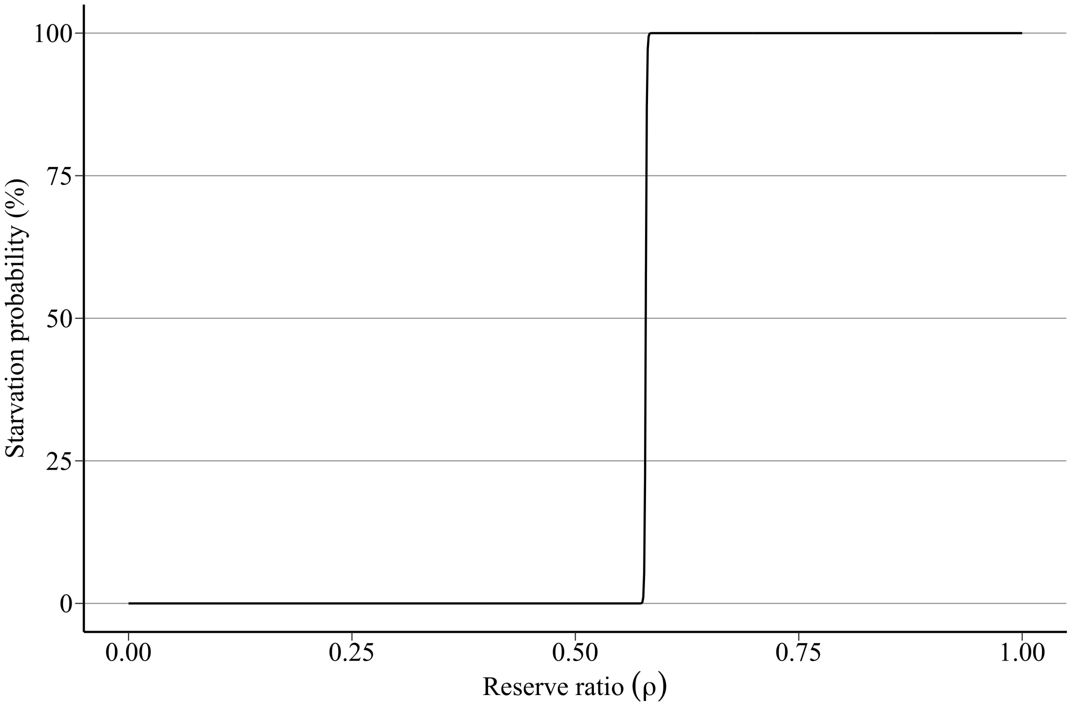


FIGURE 6.7: Starvation probability in relation to the reserve ratio $\rho = \frac{R}{S+G}$.

Chapter 7

Application of dynamic energy budget to sandeels off the east Scottish coast

7.1 Introduction

Sandeel abundance off the Scottish east coast increased markedly 2000 and 2001 due to high levels of recruitment (Greenstreet et al., 2010; Heath et al., 2012) However, the stock underwent a sustained decline thereafter. The stock decline was so severe that average abundance after the decline (2002—2007) was 35% of the average abundance before the decline (1990—2001). Although larval abundance declined, recruitment has been maintained due to an increasing larval survival rate (Heath et al., 2012). This means that the number of sandeels less than 1 year old in summer has not changed dramatically over time, while the number of older sandeels has continued to decline.

Two main factors have been proposed as responsible for the decline in sandeel abundance, increases in overwinter and predation mortality. Sandeels show significant weight loss during the overwintering period (Boulcott et al., 2007; Boulcott and Wright, 2008), and it is speculated that increased temperature will increase this rate of loss due to elevated metabolism. The energy required by overwintering animals must be accumulated the previous summer, so unless warming is accompanied by increased scope for summer feeding, which does not appear to be the case (Wanless et al., 2004; Boulcott et al., 2007), then the net effect is likely to be reduced overwinter survival (van Deurs et al., 2011).

Considerable size dependent overwinter mortality is not uncommon in fish (Schultz et al., 1998; Oliver et al., 1979; Kirjasniemi and Valtonen, 1997; Biro et al., 2004). This mortality risk decreases with increasing size. Hence, sandeels entering their first winter are most vulnerable to overwintering mortality. While partly the effect of predation, lipid depletion appears to be the dominant driver (Huss et al., 2008). 0-group individuals require more time to accumulate the necessary energy reserves to overwinter than older individuals. This is supported by the fact that 0-group sandeels require at least 1 month extra feeding time than older sandeels (Macer, 1966; Reeves, 1994; Kvist et al., 2001). Due to differences in metabolism, starvation risk declines with increasing size (Shuter and Post, 1990; Schultz and Conover, 1999; Post and Parkinson, 2001). Hence, a trend towards smaller overwintering size can increase mortality (van Deurs et al., 2011). Indeed, there has been a long-term decline in 0-group length. Data from chick-feeding Atlantic puffins *Fratercula arctica* and Continuous Plankton Recorder samples indicate that the size-at-date of 0-group sandeels has declined substantially since 1973 (Wanless et al., 2004).

The importance of lipid reserves for the survival of young-of-the-year fish is highlighted in a paired experimental and field study on rainbow trout *Onchorhynchus mykiss* (Biro et al., 2004). The overwhelming majority of 0-group trout that begin overwintering eventually succumb to starvation, and excluding other forms of mortality, as little as 10% may survive winter (Biro et al., 2004). Hindcasted starvation mortality was greater than 95% for sandeels born in 2002 and 2005.

Despite having a much longer overwintering phase than young-of-the-year sandeels, older individuals do not appear vulnerable to winter starvation. The ability of mature sandeels to withstand long periods without feeding is highlighted in an experimental study (van Deurs et al., 2011). Animals larger than 11 cm can survive for at least 10 months without feeding period (van Deurs et al., 2011). However, sandeels in the wild will likely overwinter for a much shorter time, so should be unlikely to starve.

7.2 Model environmental drivers

The model is driven by temperature T (^{o}C), and copepod biomass concentration (kJ m^{-3}). High resolution food and temperature data were not available for the Firth of Forth. Therefore, food and temperature from a location approximately 60 km north of the centre of our study region was used. Weekly zooplankton sampling and temperature readings at surface and seabed depth (45 m) were carried out in Stonehaven (56° $57.83'$N, 002° $06.74'$W), between January 1997 and December 2008. For full details on plankton sampling methods, see Bresnan et al., 2015. Surface and seabed temperature is used in the model to account for temperature variation experienced by sandeels when they are feeding and overwintering, respectively. This is a slight approximation, since sandeels feed at the surface only before the thermocline forms, and feed at the thermocline thereafter. Weekly measurements of copepod abundance were available between 2000 and 2008. Copepod abundance was grouped by species and stage. Field data indicates sandeels feed primarily on the dominant calanoid copepods ; *Calanus*, *Pseudocalanus*, *Temora*, *Centropages*, *Acartia*, *Paracalanus*, *Oithona* and *Microcalanus* (Macer, 1966; van Deurs et al., 2013, 2014, 2015). Sandeels were assumed to prey exclusively on these copepods, expect nauplii stages (van Deurs et al., 2013, 2014, 2015).

Total food abundance F was split into two prey groups, large copepod biomass concentration FL, and small copepod biomass concentration FS. To this end, large copepods were defined as any of the advanced calanus stages (Table 7.1). Small copepods were defined as being any of the major calanoid copepod species (Table 7.2). Converting copepod prosome length to energy content involved the following steps: First, a weight-length relationship was used to estimate copepod wet weight (van Deurs et al., 2015),

$$W_c = 5\left(\frac{10^{3.13\,log_{10}(1000PL)-8.18}}{10^{6}}\right) \tag{7.1}$$

Next, wet weight was converted into energy content. This was done by multiplying wet weight by an energy density for small and large copepods. van Deurs et al. (2013) derived energy densities for small ($<$ 1.3 mm) and large copepods ($>$ 1.3 mm) from data on the monthly energy content of four North Sea copepod species in spring (Corner and OHara, 1986). Energy densities of 5.6 kJ g^{-1} and 3.2 kJ g^{-1} were assumed for large and small copepods, respectively.

Table 7.1: Energy content of large copepods. Prosome lengths (PL) of adult *C. finmarchicus* and *C. helgolandicus* were available from field data in Jønasdøttir et al. (2005). C6 male *C. helgolandicus* PL was assumed to be equal to C6 female *C. helgolandicus* PL. Other prosome lengths were derived from using the relationship between temperature and PL for *C. finmarchicus* in Campbell et al. (2001), assuming a temperature of 10 °C, which is the 10-year average surface temperature from Stonehaven.

Genus	Species	Stage	Length (mm)	Energy (J)
Calanus	*C. finmarchicus*	C6 Female	2.66	9.706
		C6 Male	2.61	9.146
		C5	2.33	6.412
	C. helgolandicus	C6 Female	2.53	8.297
		C6 Male	2.53	8.297
		C5	2.33	6.412
	Unidentified	C6 Female	2.6	9.037
		C6 Male	2.57	8.715
		C5	2.33	6.412
		C4	1.81	2.909
		C3	1.35	1.162

Table 7.2: Energy content of small copepods. Calanus prosome lengths were derived from using the relationship between temperature and PL for *C. finmarchicus* in Campbell et al. (2001), assuming a temperature of 10 °C, which is the 10-year average surface temperature from Stonehaven. Pseudocalanus PL was taken from Lynch et al. (2001). Temora and Centropages PL was taken from Hirst et al. (1999). Acartia PL was taken from Leandro et al. (2006). Paracalanus PL was taken from Davis (1984).

Genus	Species	Stage	Length (mm)	Energy (J)
Calanus	Unidentified	C2	1.04	0.293
		C1	0.74	0.101
Pseudocalanus	*Pseudocalanus minutus elongatus*	C6 Female	1	0.26
		C6 Male	1	0.26
		C5 Female	0.88	0.174
		C5 Male	0.88	0.174
		C4	0.73	0.097

		C3	0.62	0.05812
		C2	0.52	0.03351
		C1	0.42	0.01717
Temora	*Temora longicornis*	C6 Female	0.76	0.1099
		C6 Male	0.68	0.0776
		C5 Female	0.64	0.06419
		C5 Male	0.58	0.04717
		C5	0.61	0.05523
		C4	0.51	0.03154
		C3	0.44	0.01987
		C2	0.4	0.01474
		C1	0.34	0.008864
Centropages	*Centropages hamatus*	C5 Female	0.64	0.06419
		C6 Female	0.85	0.156
		C5 Male	0.68	0.0776
		C6 Male	0.8	0.1291
		C5	0.66	0.07068
		C4	0.55	0.03994
		C3	0.45	0.02131
		C2	0.37	0.01155
		C1	0.31	0.006639
	Centropages typicus	C6 Female	0.85	0.156
		C6 Male	0.8	0.1291
		C5	0.66	0.07068
		C4	0.55	0.03994
		C3	0.45	0.02131
		C2	0.37	0.01155
		C1	0.31	0.006639
Acartia	*Acartia clausi*	C6 Female	0.92	0.1999
		C6 Male	0.85	0.156

		C5 Female	0.79	0.1241
		C5 Male	0.77	0.1145
		C5	0.78	0.1192
		C4	0.66	0.07068
		C3	0.56	0.04226
		C2	0.46	0.02283
		C1	0.37	0.01155]
	Acartia longiremis	C6 Female	0.92	0.1999
		C6 Male	0.85	0.156
	Acartia discaudata	C6 Female	0.92	0.1999
		C6 Male	0.85	0.156
	Acartia bifilosa	C6 Female	0.92	0.1999
		C6 Male	0.85	0.156
Paracalanus	*Paracalanus parvus*	C6 Female	0.74	0.1011
		C6 Male	0.74	0.1011
		C5 Female	0.62	0.05812
		C5 Male	0.62	0.05812
		C5	0.62	0.05812
		C4	0.52	0.03351
		C3	0.41	0.01593
		C2	0.36	0.0106
		C1	0.28	0.004828
Oithona		C6 Female		0.156
		C6 Male		0.1291
		C4,C5		0.05531
		C3		0.02131
		C2		0.01155
		C1		0.006639
Microcalanus	*Microcalanus pusillus*	C6 Female		0.156

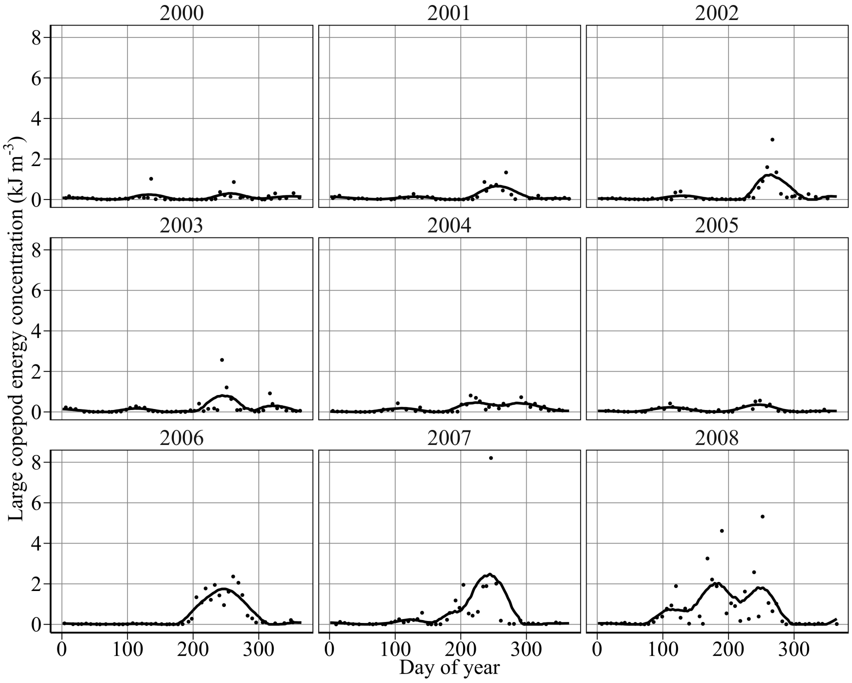
C6 Male	0.1291
C5	0.07068
C4	0.03994
C3	0.02131
C2	0.01155
C1	0.006639

To calculate copepod biomass concentration on a given day, a smooth (LOESS, span = 0.04) was fitted to the time series of copepod measurements and the food on each day was extracted (Figure 7.1). Figure 7.2 shows the mean daily energy concentration of small and large copepods during the main sandeel foraging period (1st April and 1st August). Abundance of the two copepod size classes was low between 2000 and 2006, but comparatively high between 2007 and 2008. This was especially true for large copepods. Curiously, the local trend in large copepods at Stonehaven was highly unusual given the expected climate warming effect on the dominant *Calanus* species. In fact, this trend contrasted with what was happening to the zooplankton community elsewhere in the Northern North Sea (Edwards et al., 2010).

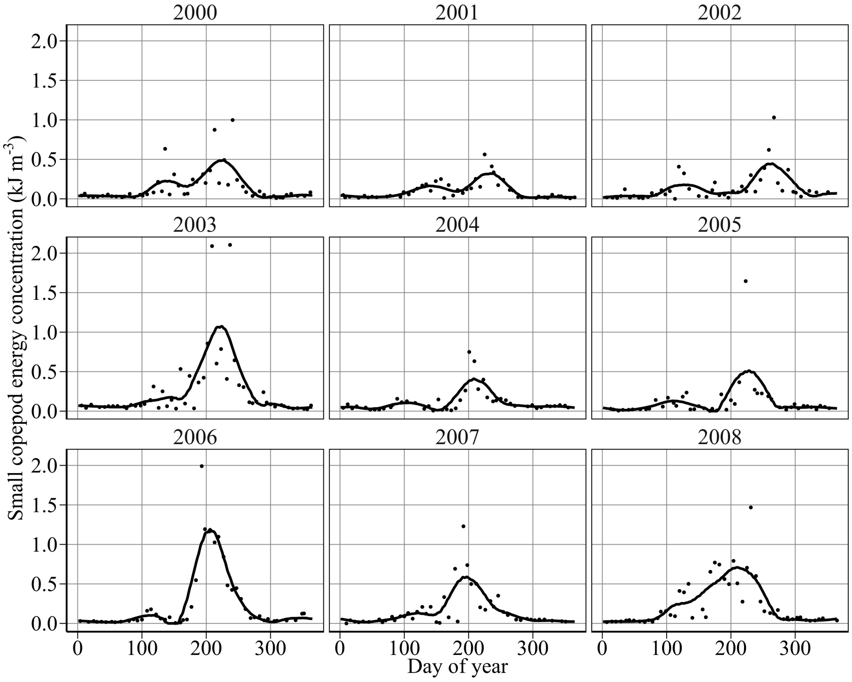
7.3 Initial conditions of the model

The model is run using reserve and structural energy of 0-group and age 1 fish in summer as initial conditions. Each cohort consists of a group of individuals, each characterised by a unique structural energy, reserve energy, and abundance. Unfortunately, no observations of sandeel energy between 2000 and 2008 were available; only length and weight estimates are readily available from survey data. However, structural and reserve energy can be estimated by relating length and weight to energy content.

For each survey, probability distributions of ages for each 5 mm length class were estimated using the continuation-ratio logit method (Kvist et al., 2000; Rindorf and Lewy, 2001; Stari et al., 2010). Changes in distribution of age at a given length, as a function of length, were estimated using Generalized Linear Modelling. Fitting was performed using Maximum Likelihood code (Stari et al., 2010) developed for the R statistical environment (R development Core Team, 2014). The resultant probability matrices of



(A)



(B)

FIGURE 7.1: Large (A) and small (B) calanoid copepod energy concentration. A loess smooth (span = 0.04) is fitted to weekly observations (points).

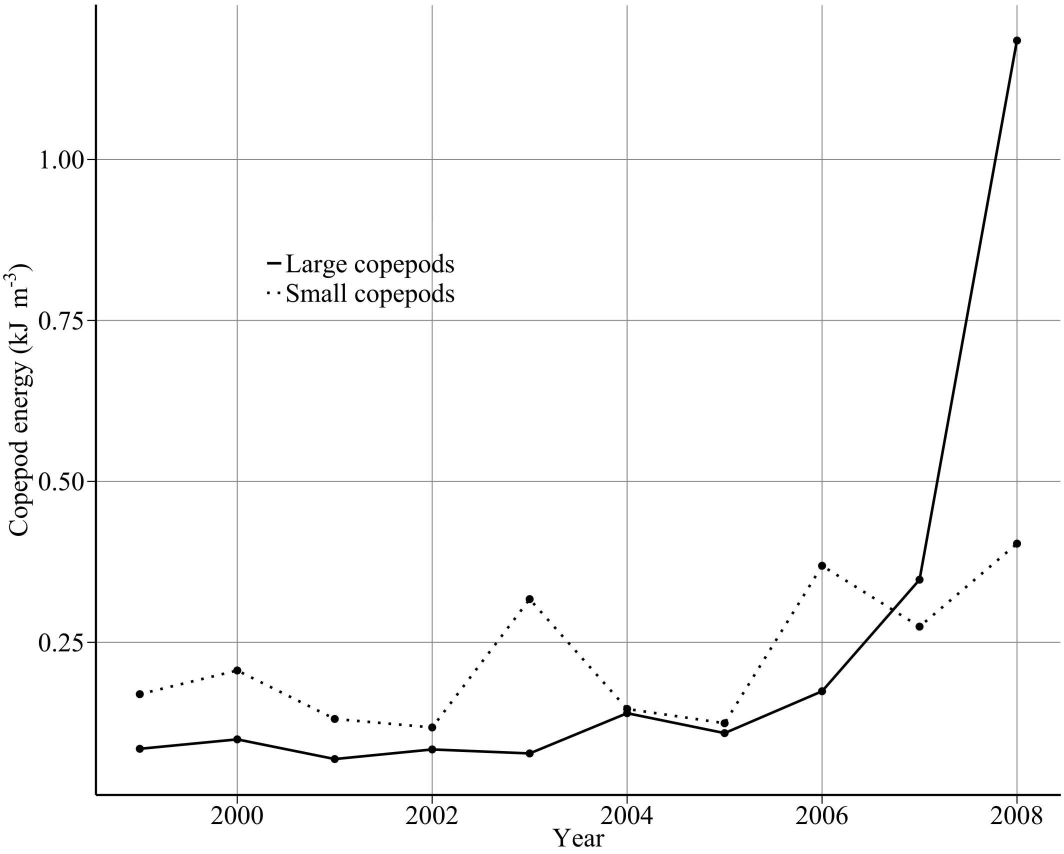


Figure 7.2: Mean daily energy concentration of small and large copepods between 1st April and 1st August, sandeels main foraging period.

age-given-length were multiplied by abundance-at-length to give matrices of abundance-at-age-and-length. That is, for a given age and cohort, each length carried an associated abundance. For example, 207 individuals of length 11 cm and age 1 were caught in 2000. The next step was to associate a weight with each individual. Otolith data was used to estimate the probability of weight given age and length. For example, given a sandeel of length 11 cm and age 1 in 2000, the probability of being 4 grams in weight is 5%. Therefore, $207 * 5/100 \approx 10$ individuals weigh 4 grams. Figures 7.3 and 7.4 show length and weight estimates of 1-group and 0-group sandeels, respectively.

Justifying the use of different initial conditions for each cohort requires that significant differences exist in length and weight between years. To do this, a t-test (equal variance) was used to determine if differences in cohort mean weight were statistically significant between years. This was done separately for 0-group and 1-group individuals. Mean weight varied significantly between cohorts, with the exception of the 0-group born in 2002 and 2003, and the 1-group born in 2000 and 2001.

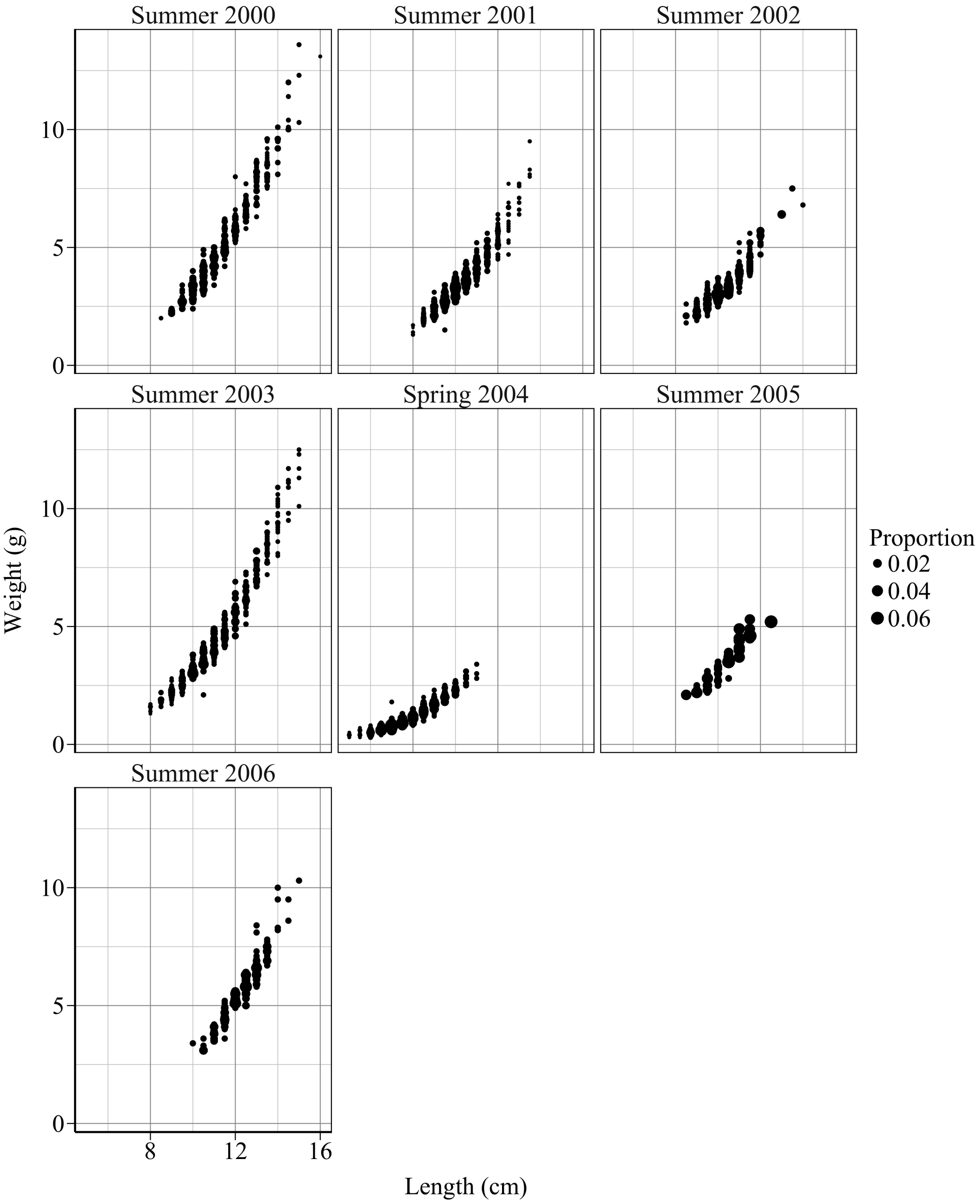


FIGURE 7.3: Year-to-year changes in length and weight at age 1. Each point represents a group of individuals with equal length and weight. The number of each individuals in a length-weight group is indicated by the size of the point. All fish were caught in summer trawl surveys with the exception of 2002 and 2004 where dredge data was used. This is because few age 1 fish were caught by pelagic trawl in 2002, and no trawling is conducted outside the summer months. No summer surveys were undertaken in 2004, therefore the model is run with age 1 fish caught in the spring dredge survey.

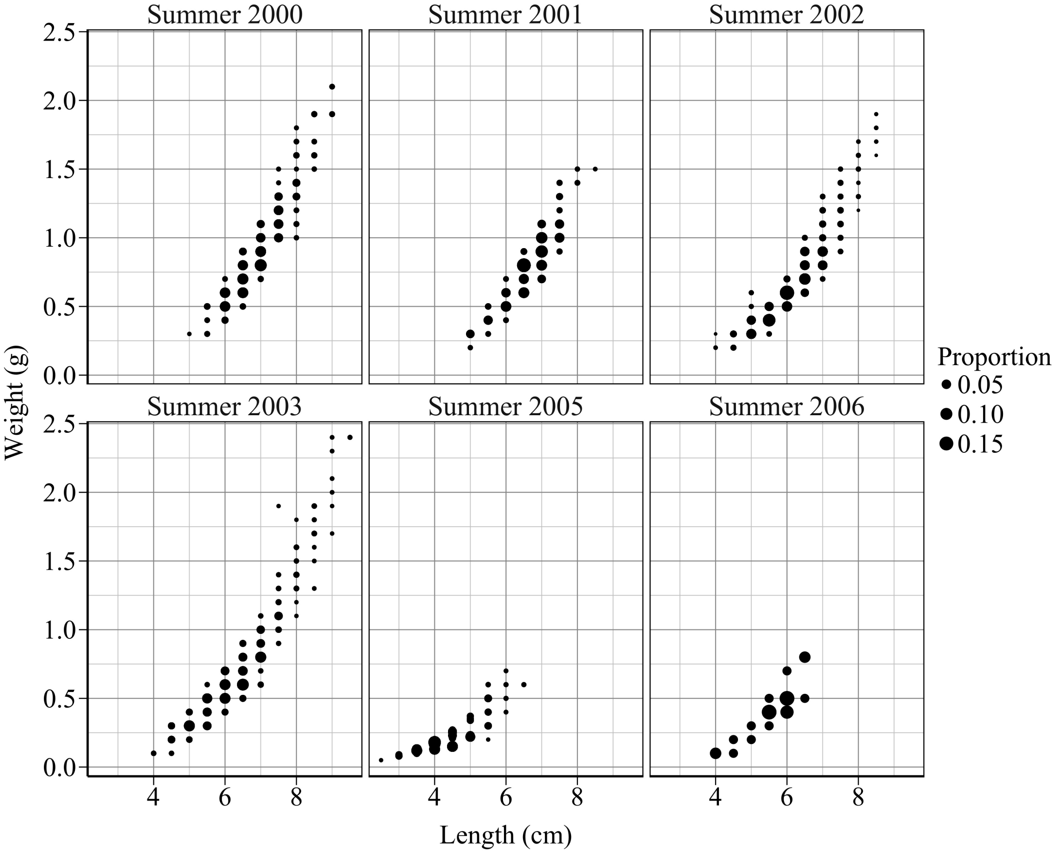


FIGURE 7.4: Year-to-year changes in length and weight at age 0. Each point represents a group of individuals with equal length and weight. The number of each individuals in a length-weight group is indicated by the size of the point. There is considerable year-to-year variation in sandeel 0-group size. For example, almost 60% of individuals caught in 2000 had lengths ≥ 7, while all sandeels caught in 2005 and 2006 were smaller than 7 cm. All fish were caught in summer trawl surveys.

7.4 Parameter estimation and model implementation

There are 34 parameters to estimate in the model. We find values for parameters using the following method. First, empirical data from the literature is used if available. If parameters are not available, they are derived using empirical data if possible. If a parameter is not available from the literature and cannot be derived, it is treated as a fitting parameter. Fitting parameters were found by fitting the model to length and weight data.

The model is implemented in C and parameterised in R. Ordinary differential equations (equations 6.2, 6.4, 6.1) were solved numerically using the Euler method with discrete daily time steps. To ensure the discrete differential equations converged to the continuous differential equations, model results using the Euler method and the ode45 method in the deSolve package (Team, 2015) were compared. The Euler method converged to the solution of the differential equations.

The model was fitted by selecting the set of 14 unknown model parameters (Ω) that minimized the following error

$$\begin{aligned}\text{Error} = \min_{\Omega} \Bigg(& \Big(\frac{\text{Modelled length} - \text{Observed length}}{\text{Observed length}}\Big)^2 + \\ & \Big(\frac{\text{Modelled weight} - \text{Observed weight}}{\text{Observed weight}}\Big)^2 + \\ & \Big(\frac{\text{Modelled reserve ratio} - \text{Observed reserve ratio}}{\text{Observed reserve ratio}}\Big)^2 \Bigg)\end{aligned} \tag{7.2}$$

This error was minimised by performing a random walk through parameter space. This was done because there are many local minima due to the complexity of the model.

7.5 Using sandeel abundance data to validate a model of starvation mortality

Total mortality is not a general predictable function in our model. Instead, it is observed from abundance-at-age data (Figure 7.5). However, the model does predict one component of mortality - starvation mortality. A signature of major starvation events may be that a normally constant cohort mortality is interrupted by a sudden decrease in abundance at one particular time. Hence, we determine if modelled starvation events explain trends in observed total cohort mortality.

We validate the model of starvation mortality using the following procedure: Two different mortality models were compared to validate the starvation mortality model. Models assumed a constant mortality, with starvation turned off in one model and on in the other. A model of constant mortality is represented by a linear fit through cohort abundance data (Figure 7.5). The two models of constant mortality with and without starvation mortality were compared using the Akaike Information Criterion (AIC), done seperately for each cohort (Akaike, 1974). The best mortality model was selected for each cohort on the basis of the AIC value, where lower values indicate better model fits.

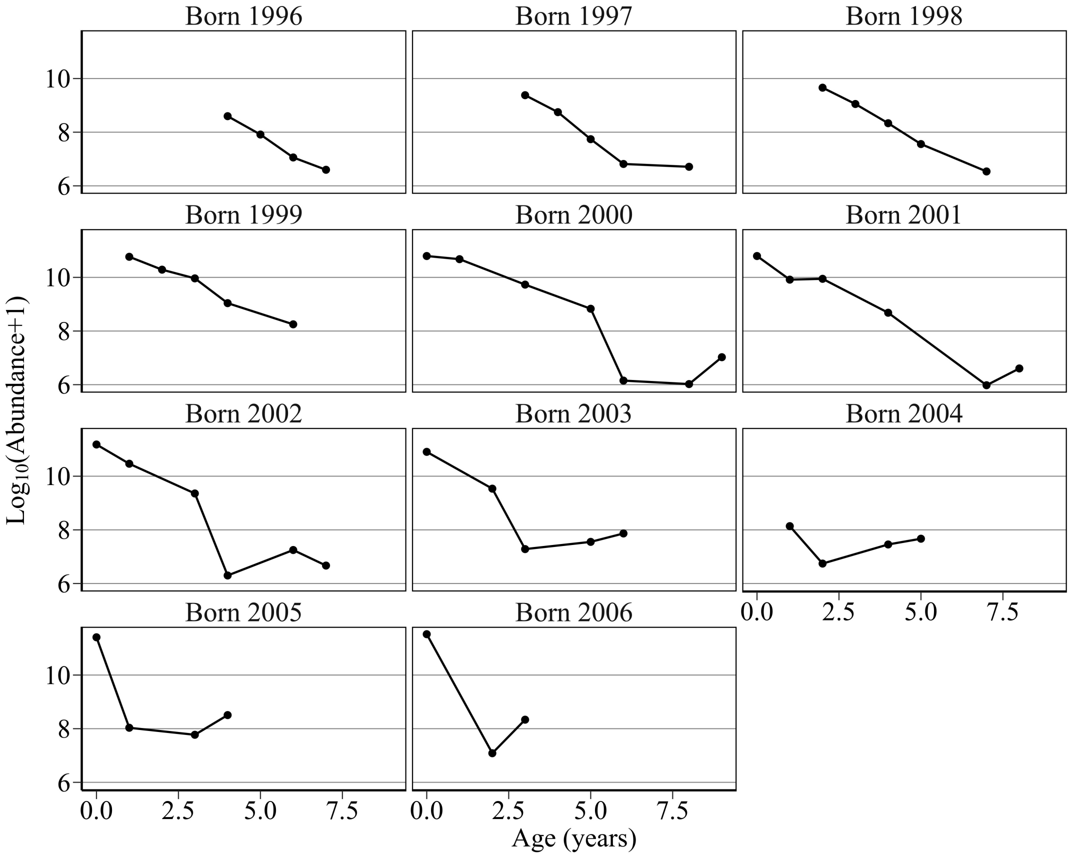


FIGURE 7.5: Estimated changes in total cohort abundance of sandeels in Wee Bankie. Total cohort abundance was estimated by applying correction factors to pelagic trawl abundance data (see text).

7.6 The relation of structure and reserve energy to length and weight

Sandeel energy data is required to fit our model and estimate unknown parameters. Ideally, this test data would be field measurements of sandeel energy content between 2000 and 2008 off the Firth of Forth. Unfortunately these data are not available, so a different approach is needed. First, sandeel energy content is related to length and weight. Then assuming this relationship holds, the model is validated against sandeel length and weight.

Estimates of sandeel length and weight were derived from Firth of Forth field data. See chapter 4 for full details on sampling methods.

Reserve, structural and gonad energy is converted into wet weight using two steps. First, R, S and G are converted to dry weight using dry weight energy densities. Then, reserve, structural and gonad dry weight is converted into wet weight using conversion factors.

$$W = \frac{R_{\text{dry}}}{E_r} R + \frac{S_{\text{dry}}}{E_s} S + \frac{G_{\text{dry}}}{E_g} G \tag{7.3}$$

R_{dry}, S_{dry} and G_{dry} is the ratio of wet weight to dry weight for reserve, structural and gonad tissue. E_r, E_s, E_g are energy densities for reserve, structural and gonad dry weight.

By definition, structure cannot decrease. Consequently, structure is a proxy for length. Several DEB models (Broekhuizen et al., 1994; Jones et al., 2002) assume this relationship takes the form:

$$L = (\frac{S}{\alpha})^{1/\beta} \tag{7.4}$$

where α and β are the length-structure scale and the length-structure exponent, respectively. Modelled sandeels are assumed to be isomorphic so they retain the same shape as they grow. Thus, $\beta = 3$ in equation 7.4. Isomorphism is common assumption in DEB models, having been assumed for countless species (Kooijman, 2010).

Wet weight can be separated into 2 components: water (w) and dry weight DW. Dry weight can be broken down further into reserve dry weight (R_{dry}), structural dry weight (S_{dry}) and gonad dry weight (G_{dry}).

$$\begin{aligned} W &= w + DW \\ &= w + R_{\text{dry}} + S_{\text{dry}} + G_{\text{dry}} \\ &= w + \frac{R}{E_r} + \frac{S}{E_s} + \frac{G}{E_g} \end{aligned} \tag{7.5}$$

The ultimate aim is to rewrite equation 7.5 purely in terms of reserve, structural and gonad energy. Thus, water weight must be expressed in terms of energy, and the energy densities of reserve, structural and gonad dry weight have to be determined.

To estimate the ratio of gonad wet weight to dry weight (G_{dw}) and gonad energy density (E_g), a study is used on the energetics of a similar species, Atlantic herring (Green, 1978).

To aid the estimation of parameters, let us imagine an immature sandeel, i.e. G_{dry}.

Hence,

$$W = w + R_{\text{dry}} + S_{\text{dry}} \tag{7.6}$$

Sandeel dry weight is composed almost entirely of fat, protein and ash. However, the contribution of these three elements to reserve, structure and gonad tissue is likely to vary. Reserves, the parts that a sandeel will use to burn energy will likely contain a higher fat content than structural tissue, which is primarily comprised of skeletal tissue and organs.

The first step in doing this is to express water weight (w) in terms of reserve dry weight (R_{dry}). This is done by assuming that (R_{dry}) is proportional to sandeel fat weight (F). Then fat is expressed as a function of wet weight.

Sandeels accumulate a considerable amount of fat prior to the overwintering period, suggesting fat is a critical part of reserve energy (Winslade, 1974).

Reserve energy is assumed to be proportional to fat content. Hence,

$$aR_{\text{dry}} = F \tag{7.7}$$

Fat replaces water between April and August; fat content declines once sandeels begin overwintering in August (Figure 7.6). Fat and water content are inextricably linked in pelagic fish (Wallace and Hulme, 1977; Iles and Wood, 1965; Dubreuil and Petitgas, 2009). There is a significant relationship between sandeel fat and water content (Fat content (% wet weight) = - 0.777 x Water content (% wet weight) + 64.094, R^2 = 0.9, N = 143, $P < 0.001$, Hislop et al., 1991). Combining this relationship with the assumption that reserve weight is proportional to fat content, water content is expressed as

$$\begin{aligned} w &= 0.825\,W - 1.287F \\ &= 0.825\,W - 1.287aR_{\text{dry}} \end{aligned} \tag{7.8}$$

where $\gamma = 0.825$ is the maximum proportion of water in a sandeel and $b = 1.287$ is the water weight lost (g) when a sandeel gains a gram of fat.

Substituting this into equation 7.5 yields

$$W = 0.825\,W - 1.287aR_{\text{dry}} + R_{\text{dry}} + S_{\text{dry}} \tag{7.9}$$

The minimum possible weight of an immature individual is structural dry weight (S_{dry}) and water. Setting R_{dry} and G_{dry} to be zero in equation 7.6 yields a minimum wet weight in terms of structural dry weight S_{dry}

$$W_{\text{min}} = 5.711\,S_{\text{dry}} \tag{7.10}$$

The corollary is that the proportion of water in a sandeel cannot exceed 83 percent.

Equation 7.9 can be rewritten as

$$W = 0.825\,W - 1.287aR_{\text{dry}} + R_{\text{dry}} + \alpha L^3 \tag{7.11}$$

Now, the wet weight of a sandeel can be written as

$$\begin{aligned} W &= 0.825\,W - 1.287aR_{\text{dry}} + R_{\text{dry}} + \alpha L^3 \\ &= 5.711\left(R_{\text{dry}}\,(1 - 1.287a) + S_{\text{dry}}\right) \\ &= 5.711\Big(\left(DW - \alpha L^3\right)(1 - 1.287a) + \alpha L^3\Big) \end{aligned} \tag{7.12}$$

Sandeel energy content is determined by fat and protein. Fat and protein have energy densities of 39.6 and 23.7 kJ g^{-1}, respectively (Crisp, 1971). Using these values for energy density of fat (g) and protein (g) the energy content (kJ) of a sandeel can be written as

$$\begin{aligned} E &= 39.6\,\text{Fat} + 23.7\,\text{Protein} \\ &= 39.6\,\text{Fat} + 23.7\,\left(DW - \text{Fat} - \text{Ash}\right) \\ &= 39.6\,aR_{\text{dry}} + 23.7\left(R_{\text{dry}} + S_{\text{dry}} - aR_{\text{dry}} - \text{Ash}\right) \end{aligned} \tag{7.13}$$

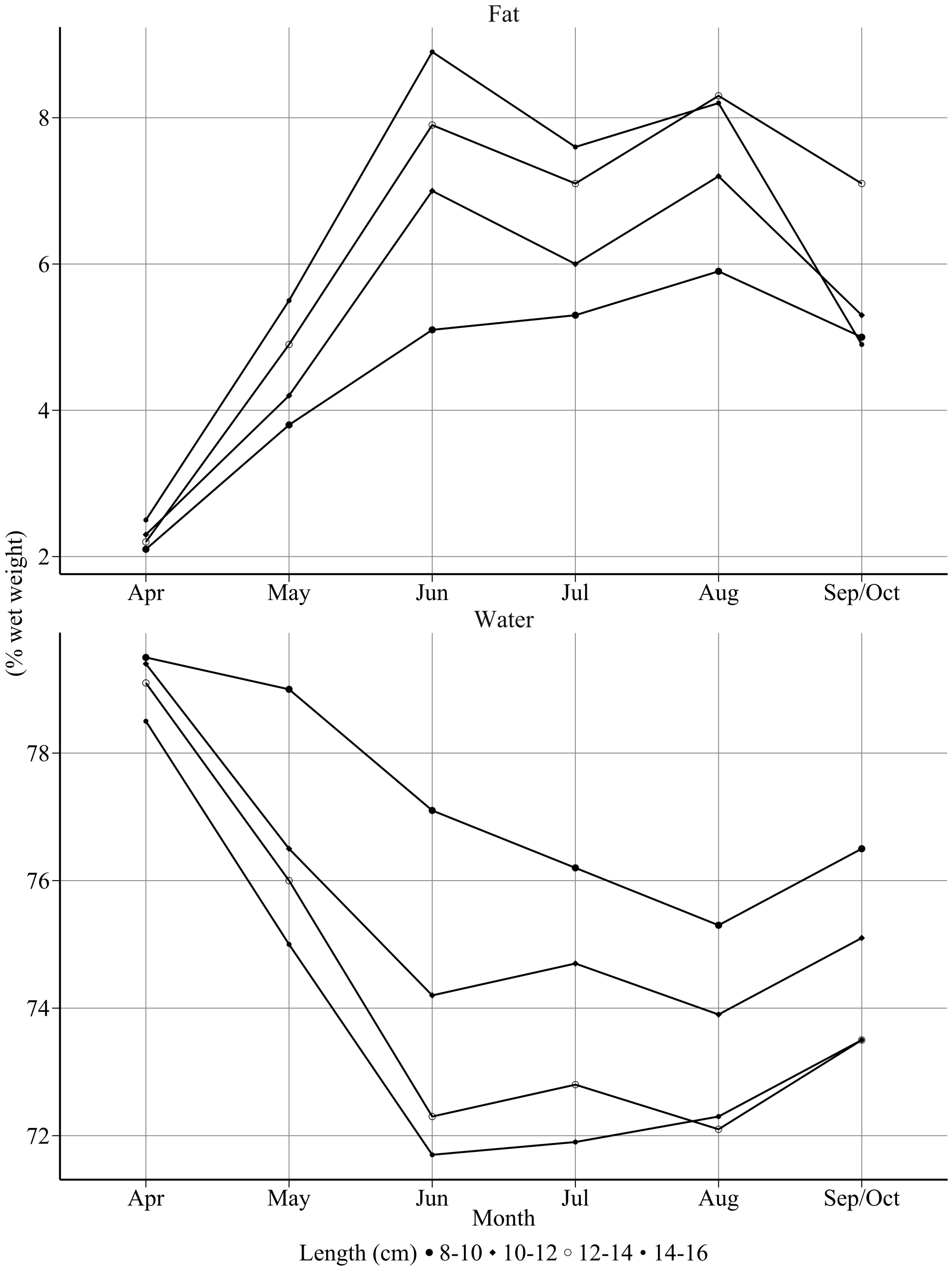


FIGURE 7.6: Seasonal changes in *A.marinus* body composition from field data. The proportion of wet weight comprised of fat and water is shown for several length groups. There is a sharp increase in fat content, corresponding to a decrease in water content between April and June. The opposite trend occurs in August—September as animals begin overwintering. Body composition data taken from appendix V in Hislop et al. (1991).

Now, ash content is related to reserve energy, structural energy and wet weight. *A.hexapterus* data is used to relate dry weight to water content (Figure 7.7).

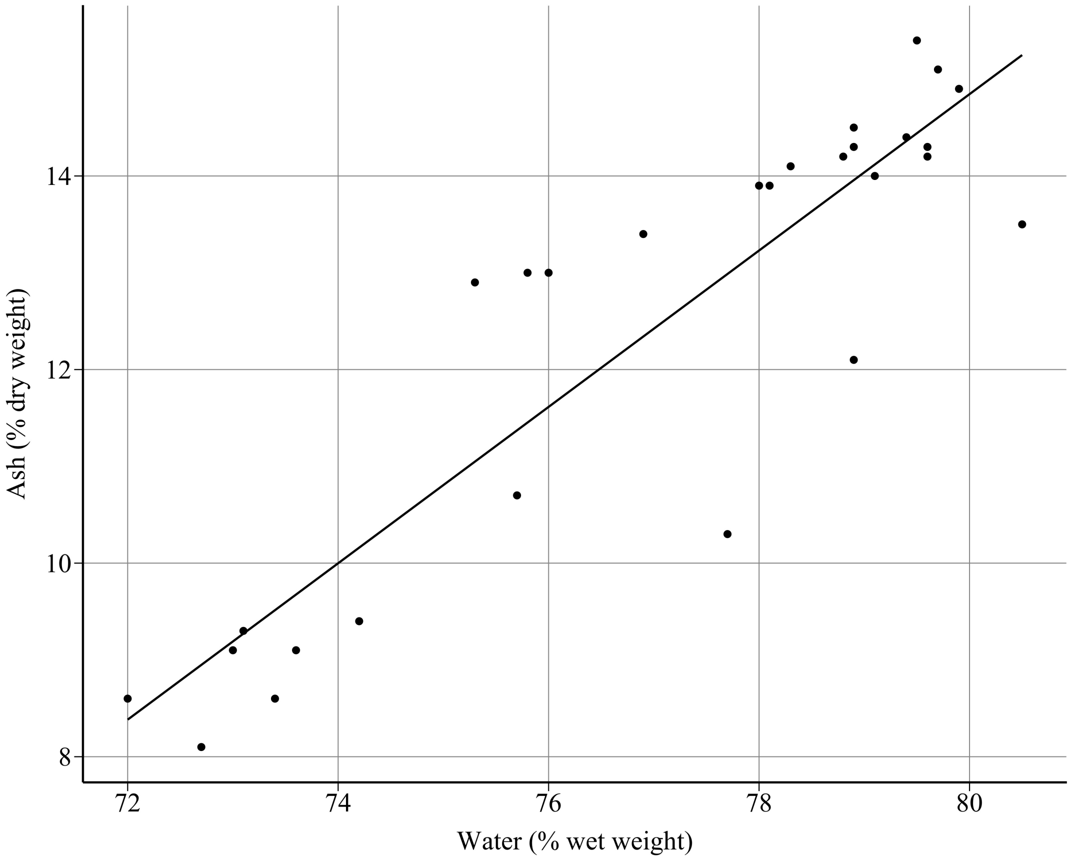


FIGURE 7.7: Relationship between water content (% wet weight) and ash content (% dry weight) in *A. hexapterus* (Robards et al., 1999) (intercept = -49.77837, slope = 0.80780 , $r^2 = 0.81$, n = 20 , $p < 1e-10$).

There is a strong linear relationship between the percentage of ash in dry weight and percentage of water in wet weight (Equation 7.14).

$$\text{Ash}\,(\%\,\text{dry weight}) = -49.778 + 0.808\,\text{water}\,(\%\,\text{wet weight}) \tag{7.14}$$

Hence, ash (g) is written as

$$\text{Ash} = -0.498DW + 0.808\frac{w}{W}DW \tag{7.15}$$

where $\text{ash}_x = 0.498$ and $\text{ash}_y = 0.808$.

Using this information in equation 7.13, the energy content of a sandeel is written as

$$\begin{aligned} E &= 39.6\, aR_{\text{dry}} + 23.7\, \Big(R_{\text{dry}} + S_{\text{dry}} - aR_{\text{dry}} - \text{Ash}\Big) \\ &= 39.6\, aR_{\text{dry}} + 23.7\, \Big(DW - aR_{\text{dry}} - \big(-0.498DW + 0.808\frac{w}{W}DW\big)\Big) \\ &= 39.6\, aR_{\text{dry}} + 23.7\, \Bigg(R_{\text{dry}} + S_{\text{dry}} - aR_{\text{dry}} - \Big(-0.498(R_{\text{dry}} + S_{\text{dry}}) + \\ &\quad 0.808(\frac{0.825W - 1.287aR_{\text{dry}}}{W})(R_{\text{dry}} + S_{\text{dry}})\Big)\Bigg) \end{aligned} \tag{7.16}$$

Empirical data is used to estimate unknown parameters a and α in equations 7.12 and 7.16. Doing this requires information on sandeel dry weight, wet weight, length and energy content. This collection of data is available for *A. marinus* (Appendix I, Hislop et al., 1991), however, it is not suitable for our purpose. There are two reasons for this. First, length was grouped into .5 cm classes, which is too imprecise. Second, estimates are mean values of a group of individuals, not a single individual. Fortunately, higher precision data is available from experiments on *A. tobianus* energy content (Figure 7.8).

Values for a and α are found by minimising the overall square relative error between predicted and observed energy content (kJ) and wet weight (g). Figure 7.9 illustrates the quality of fits to energy and weight data.

Finally, wet weight (g) is obtained in terms of R_{dry} and S_{dry},

$$W = 3R_{\text{dry}} + 5.7S_{\text{dry}} \tag{7.17}$$

Hence, every gram of reserve dry weight represents 3 grams of wet weight. Similarly, every gram of structural dry weight represents 5.7 grams of wet weight.

Length is written as a function of structural weight,

$$L = 5.989\, S^{1/3} \tag{7.18}$$

Total energy content (kJ) of a sandeel is obtained in terms of R_{dry} and S_{dry},

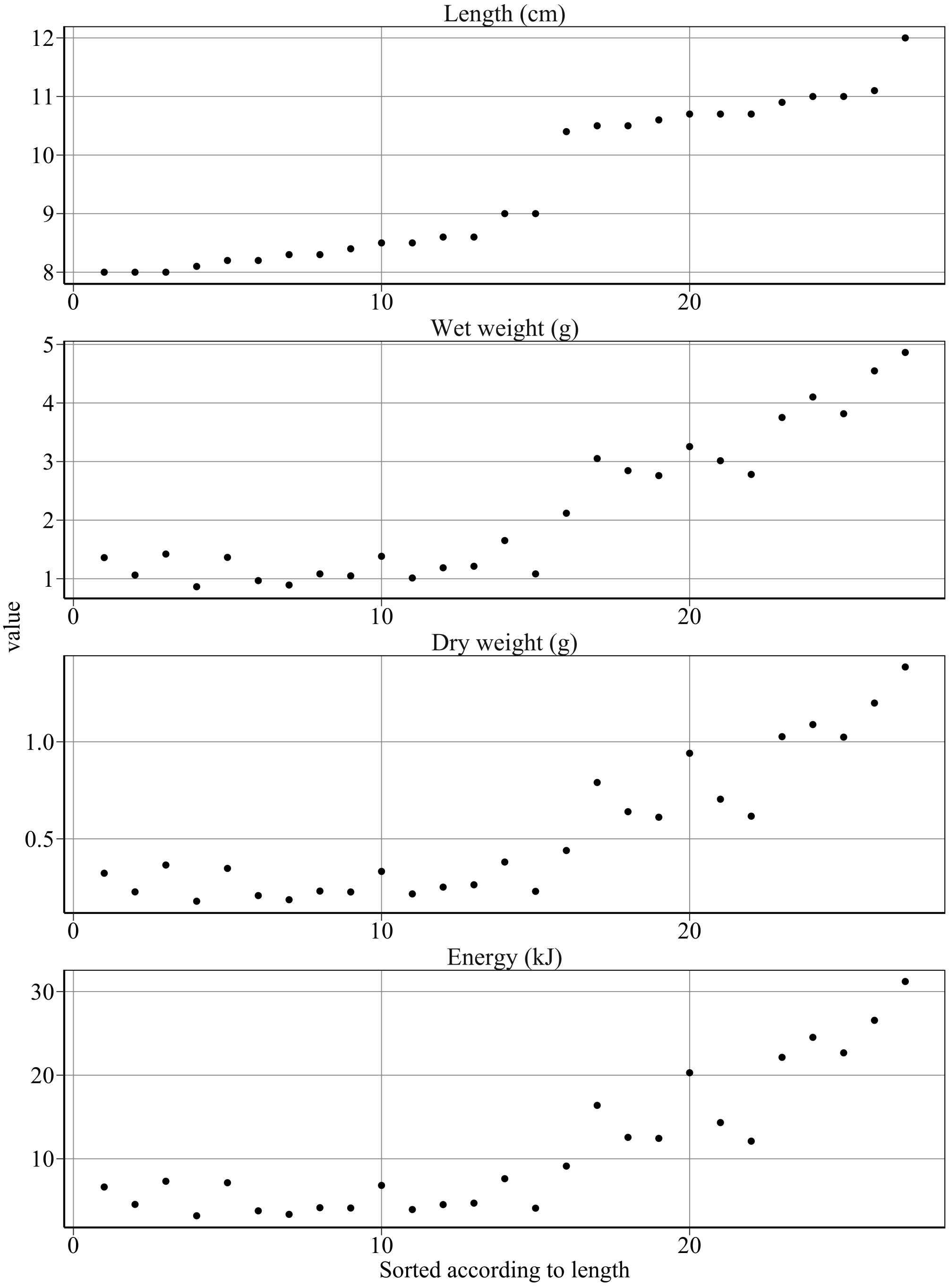


FIGURE 7.8: Length, wet weight, dry weight and energy content of 27 *A.tobianus* individuals derived from laboratory experiments.

$$E = \left(25.6 + 9.14\left(\frac{R_{\text{dry}} + S_{\text{dry}}}{W}\right)\right) R_{\text{dry}} + 19.7 S_{\text{dry}} \tag{7.19}$$

Note the $R_{\text{dry}} S_{\text{dry}}$ term is grouped into reserve energy, since the energy density of structure is assumed to be fixed. Thus, the estimated structural energy density is 19.7

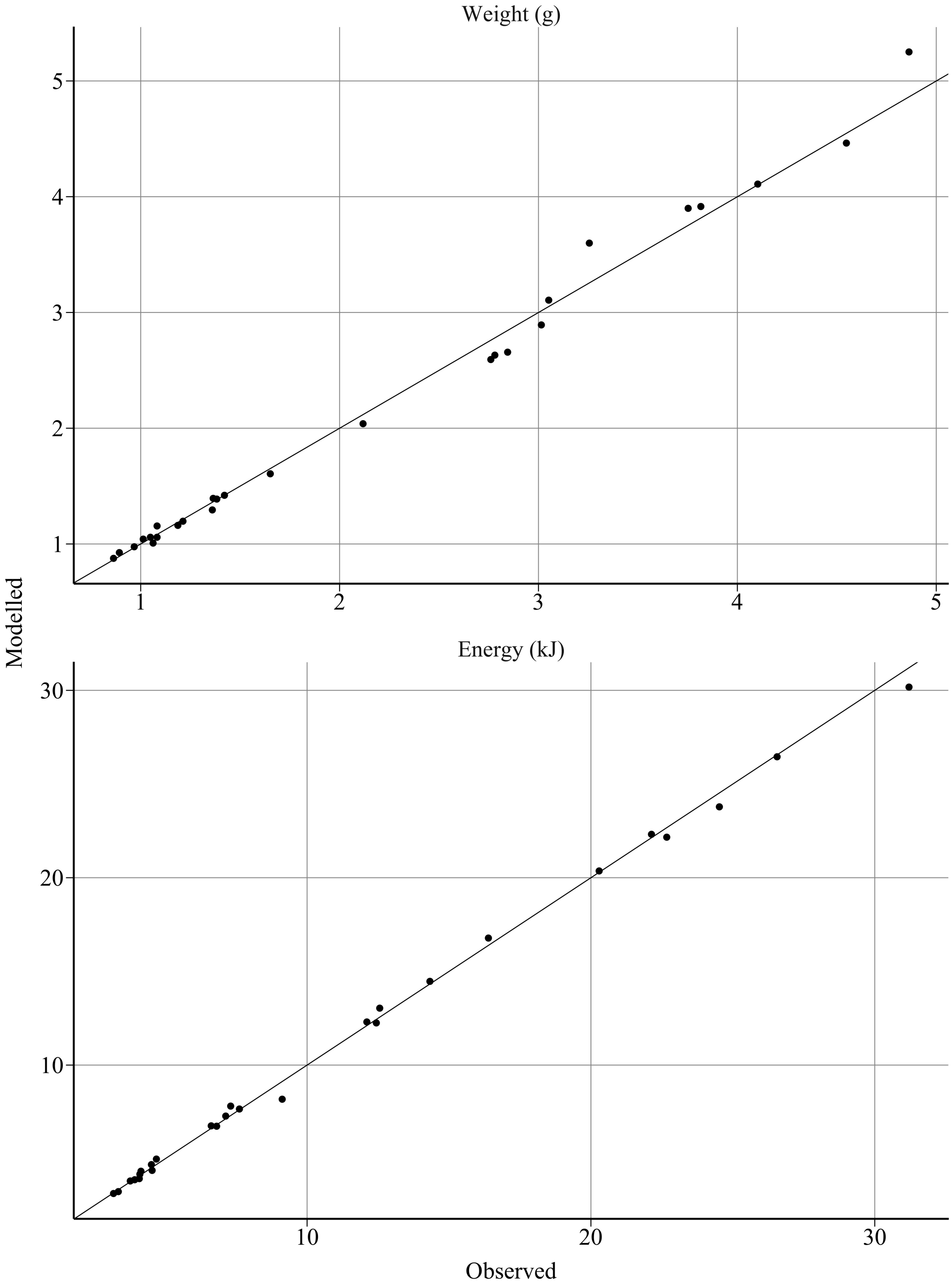


FIGURE 7.9: Modelled vs observed energy content and wet weight using equations 7.4, 7.16 and 7.12. The model provides excellent fits to weight and energy data ($R^2 = 0.998$ and $R^2 = 0.991$, respectively.).

kJ g^{-1}, which assuming little fat content, and negligible mineral mass, is 17% ash and 83% protein. Note that reserve energy density E_r is dependent on the ratio of dry weight to wet weight, i.e. sandeels with a high water content will have less energy per unit gram in the reserve mass.

7.7 Results

7.7.1 Model fitting

Model parameters are given in Table 7.3. Figure 7.10 shows model fits to length, weight and reserve ratio data. The model performs extremely well in reproducing changes in length, weight and reserve ratio of small sandeels (less than 10 grams). However, the model noticeably performs better at predicting the weight and reserve ratios of smaller individuals than larger individuals. This is to be expected since the model was fitted by minimising the relative square error of length, weight and reserve ratios.

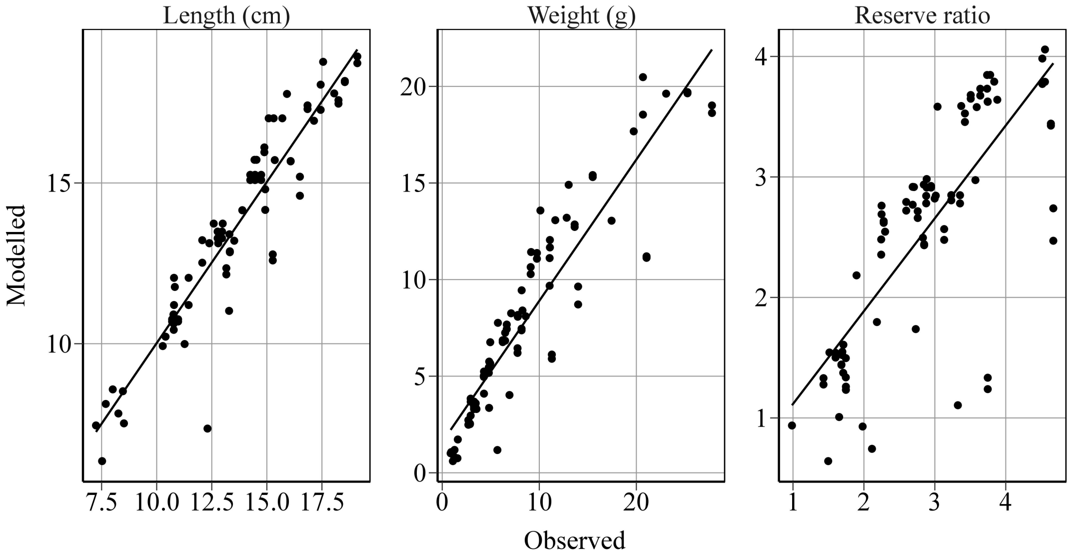


FIGURE 7.10: Comparison of modelled and observed weight, length and reserve ratio. Points represent cohort mean values at survey dates. Black lines represents linear fits through the data. The model provides excellent fits to weight (R^2 = 0.85, n= 83, intercept = 1.59, slope = 0.73) and length data (R^2 = 0.89, n= 83, intercept = -0.01, slope = 1), and a satisfactory fit to reserve ratio (R^2 = 0.59, n= 83, intercept = 0.35, slope = 0.77).

7.7.2 Estimates of overwinter starvation mortality

Figure 7.11 shows first year overwinter survival of sandeels born in 2000—2003 and 2005—2006. Overwinter survivorship ranged from approximately 0% in 2005/06 to 89% in 2000/01 (Figure 7.11). Sandeels born in 2002 and 2005 had lowest overwinter

Table 7.3: Model parameters. Parameters are either taken or derived from the literature, or chosen as a fitting parameter.

Parameter	Description	Value	Units	Source	Species
Conversion factors					
R_{dry}	Reserve dry to wet weight conversion factor	2.99	g WW g DW^{-1}		*A.marinus*, *A.hexapterus*, *A.tobianus*
S_{dry}	Structure dry to wet weight conversion factor	5.71	g WW g DW^{-1}		*A.marinus*, *A.hexapterus*, *A.tobianus*
G_{dry}	Gonad dry to wet weight conversion factor	4.167	g WW g DW^{-1}	Green (1978)	
β	Length-structure exponent	3	—	Kooijman (2010)	
α	Length-structure scale	0.000236	g cm $^{-\beta}$	Chosen	*A.marinus*, *A.hexapterus*, *A.tobianus*
Energy densities					
E_f	Energy density of fat	39.6	kJ g^{-1}	Crisp (1971)	
E_p	Energy density of protein	23.7	kJ g^{-1}	Crisp (1971)	
E_r	Reserve energy density	28	kJ g^{-1}	Derived in section 7.6	*A.marinus*, *A.hexapterus*, *A.tobianus*
E_S	Structure energy density	19.7	kJ g^{-1}	Derived in section 7.6	*A.marinus*, *A.hexapterus*, *A.tobianus*
E_G	Gonad energy density	23.7	kJ g^{-1}	Robards et al. (1999)	*A.hexapterus*
Ed_L	Large copepod energy density	5.6	kJ g^{-1}	van Deurs et al. (2015)	—
Ed_s	Small copepod energy density	3.2	kJ g^{-1}	van Deurs et al. (2015)	—
Feeding					
ϵ	Assimilation efficiency	$0.82 + 0.0076\ T$	—	Gilman (1994)	*A.dubius*
p	Maximum ingestion rate exponent	1	—	Derived in section 6.6	*A. tobianus*
q	Search rate exponent	0.67	—	—	—
$Q_{10,U}$	Ingestion rate Q10	1.72	—	Derived in section 6.6	*A. tobianus*
I_0	Ingestion scale	0.346	kJ^{1-p} d^{-1}	Derived in section 6.6	*A. tobianus*
λ	Hungry ingestion scaling factor	2	—	Miglavs and Jobling (1989)	Arctic charr *Salvelinus alpinus*
a_L	Large copepod encounter rate	2.03	—	Fitted	—
a_S	Small copepod encounter rate	1.62	—	Fitted	—
τ	Healthy threshold/ hungry threshold	3.22	—	Fitted	—
Metabolism					
$Q_{10,Mo}$	Q10 for winter metabolism	1.46	—	Quinn and Schneider (1991)	*A.hexapterus*
$Q_{10,Mf}$	Q10 for summer metabolism	1.8	—	Quinn and Schneider (1991)	*A.hexapterus*
r	Metabolic rate exponent	0.645	—	Derived from Quinn and Schneider (1991)	*A.hexapterus*
M_0	Overwinter metabolic cost rate scale	0.01722	kJ g^r d^{-1}	Derived from Quinn and Schneider (1991)	
M_f	Summer metabolic cost rate scale	0.02025882	kJ g^r d^{-1}	Derived from Quinn and Schneider (1991)	*A.hexapterus*
Overwintering					
OV_1	Overwinter threshold parameter	28.76	—	Fitted	—
OV_2	Overwinter threshold parameter	0.118	—	Fitted	—
OV_3	Overwinter threshold parameter	0.277	—	Fitted	—
OV_{end}	Julian day of overwintering exit	92	—	Chosen	
Survival					
σ_1	Survival parameter 1	1612.94	—	Fitted	—
σ_2	Survival parameter 2	0.58	—	Fitted	—
Allocation					
S_1	Structural allocation constant	2.51	—	Fitted	—
S_2	Structural allocation exponent	0.58	—	Fitted	—
G_1	Gonadal allocation constant	-0.78	—	Fitted	—
G_2	Gonadal allocation exponent	0.88	—	Fitted	—
ρ_w	Allocation switch width	11.91	—	Fitted	—
ρ_0	Defended reserve ratio	2.67	—	Fitted	—
Fat					
γ	Maximum proportion of water (wet weight)	0.825	—	Derived in section 7.6	*A.marinus*
b	Water lost (g) for every gram of fat	1.287	—	Derived in section 7.6	*A.marinus*
a	Proportion of reserves that are fat	0.371	—	Derived in section 7.6	*A.marinus*, *A.hexapterus*, *A.tobianus*
Ash					
ash_x	Ash parameter 1	0.498	—	Derived in section 7.6	*A. hexapterus*
ash_y	Ash parameter 2	0.808	—	Derived in section 7.6	*A. hexapterus*

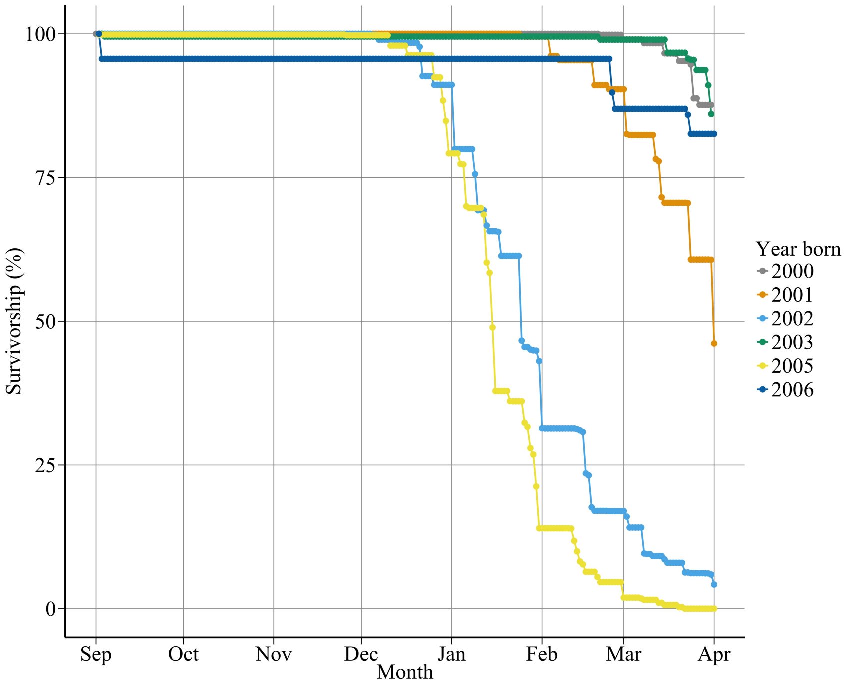


FIGURE 7.11: Cohort overwinter survival between 1st September and 1st April. Individuals born in 2002 and 2005 incurred far greater starvation mortality than those born in other years.

survivorship. Moreover, these cohorts incurred mortality much sooner than individuals born in other years. Overwinter survivorship declined to 50% in 24th and 14th January for those born in 2002, 2005, respectively.

There was a significant correlation between cohort mean length near the start of overwintering (1st September) and subsequent overwinter survival (Survival $= -2.1+0.37\,$Length, $n = 6$, $p< 0.01$, $R^2 = 0.9$).

Figure 7.14 shows changes in mean length and survivorship of sandeels born in 2005. Declines in survival were concurrent with increases in cohort mean length. This was due to smaller individuals incurring mortality before larger individuals.

Figure 7.13 shows changes in fat content of 0-group sandeels between June and April. The proportion of fat at which starvation occurs can be estimated by transforming length and weight into fat, protein, ash and water content (See section 7.6). Overwinter starvation occured once fat content decreased below 2.2%. This is in line with field estimates from the late 1980s which show an annual minimum fat content of 2% for *A. marinus* (Hislop et al., 1991). In addition, starvation occured once protein content in reserves dropped below 3.3%. Hence, starvation occured once the amount of 'mobilizable' protein and fat decreased below 6% of body weight.

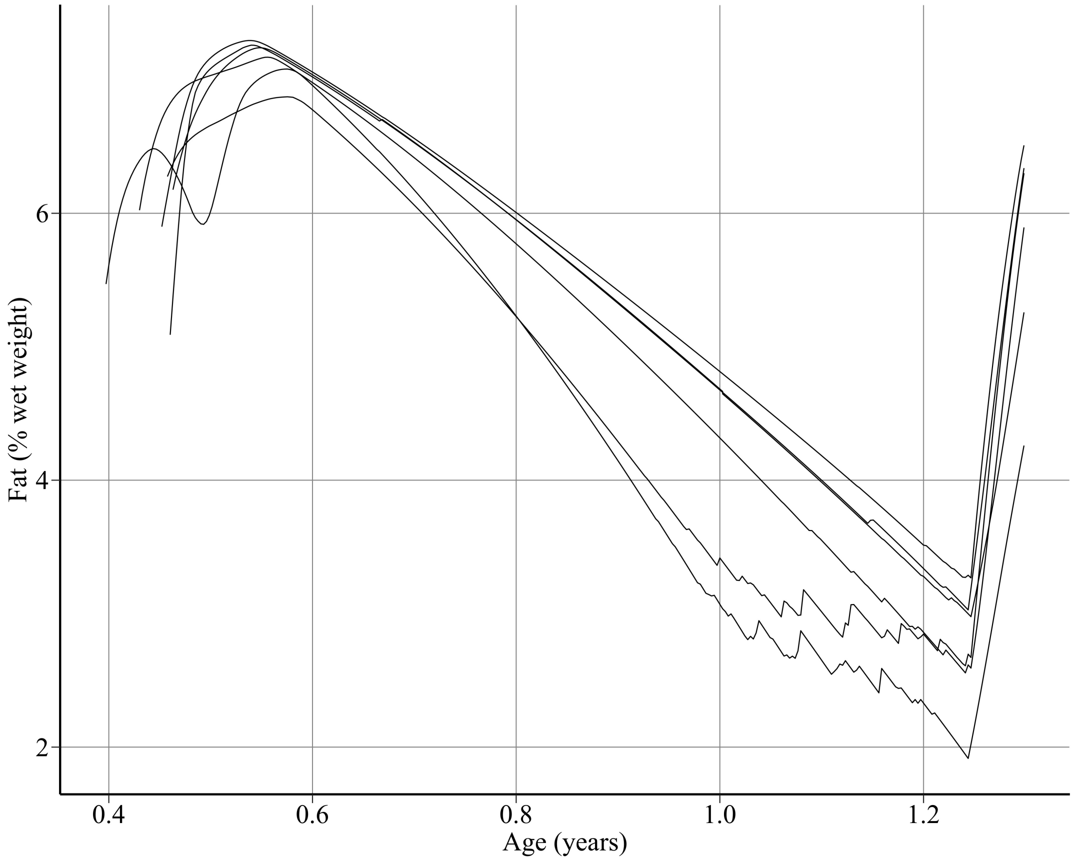


FIGURE 7.12: Changes in fat content (% wet weight) of 0-group sandeels between June and the following April. Starvation occurs when fat content drops below 2.2%.

Figure 7.15 shows modelled changes in cohort abundance assuming natural and starvation mortality. The constant mortality model with starvation performs reasonably well at reproducing changes in cohort abundance. Table 7.4 shows results of the AIC test used to compare a model of constant mortality with and without starvation. The starvation model outperformed the model without starvation for sandeels born in 2001, 2003, 2005 and 2006. A linear model performed better in 2000 and 2002. Abundance and biomass data showed that the largest mortality event between age 0 and age 1 occurred in 2005/06 (see Chapter 2, page 20). The model predicts a large overwinter mortality event for 0-group sandeels born in 2005, although the magnitude of starvation is overestimated.

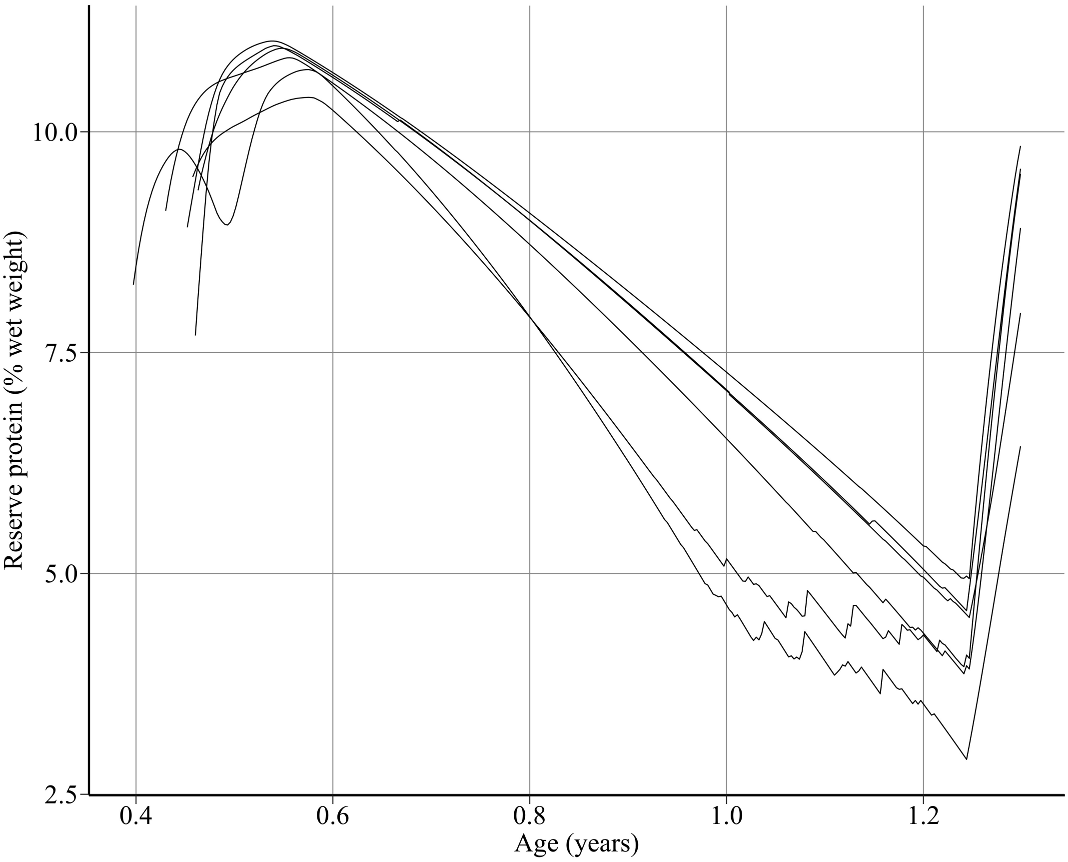


FIGURE 7.13: Changes in protein content in reserves (% wet weight) of 0-group sandeels between June and the following April. Starvation occurs when reserve protein content drops below 3.3%.

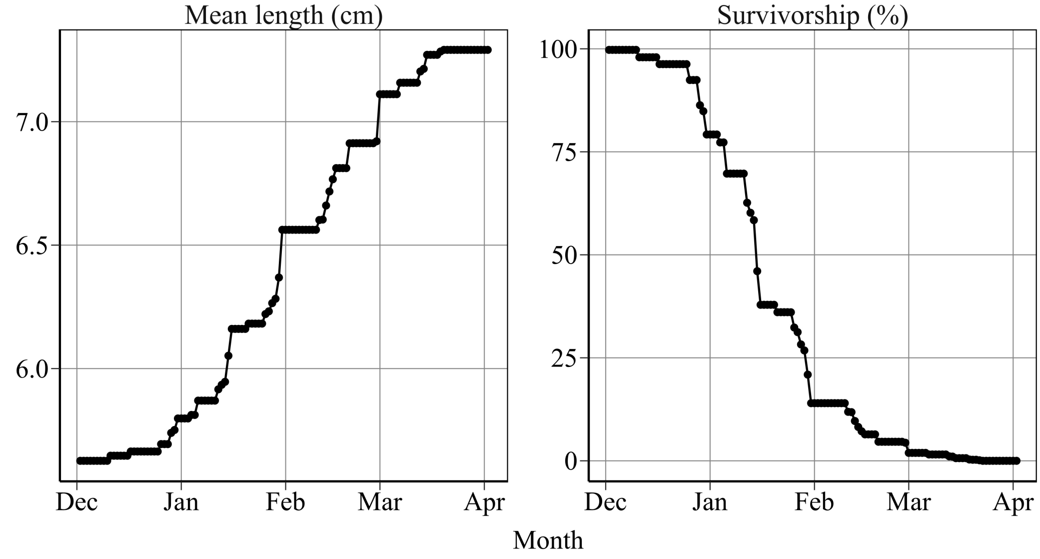


FIGURE 7.14: Overwinter survivorship in relation to mean length of 0-group sandeels born in 2005. Smaller individuals generally incur starvation mortality before older individuals, which is reflected in an increase in cohort mean length.

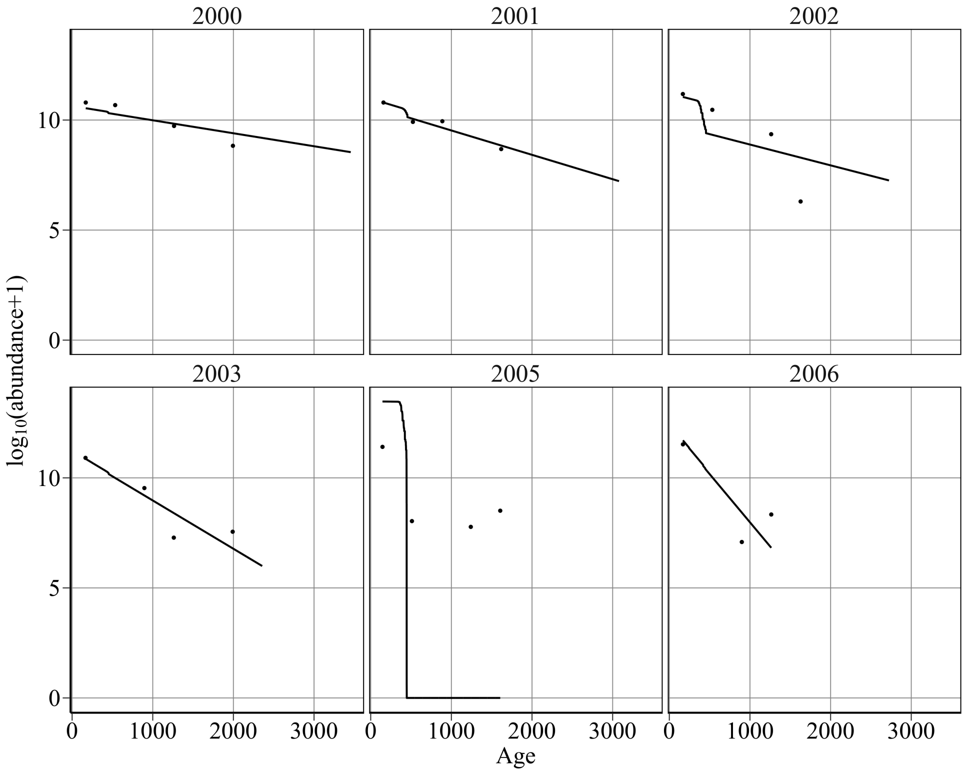


FIGURE 7.15: Starvation model fits to sandeel abundance data for individuals born in 2000, 2001, 2002, 2003, 2005 and 2006.

TABLE 7.4: Comparison of starvation mortality models and linear models using the Akaike Information Criterion (AIC).

Cohort	Observations	Starvation model			Linear model			Lower AIC
		p	R^2	AIC	*p*	R^2	AIC	
2000	4	0.01581	0.953	1.678791	0.009199	0.9725	-0.4731	Linear
2001	4	0.02898	0.9143	3.641205	0.03363	0.9008	4.2265	Starvation
2002	4	0.2035	0.4517	18.31006	0.07779	0.7757	14.7345	Linear
2003	4	0.1106	0.6866	14.26188	0.1124	0.6816	14.3251	Starvation
2005	4	0.0165	0.9509	6.66814	0.3408	0.1519	18.06644	Starvation
2006	3	0.3845	0.355	14.86838	0.3885	0.3432	14.92283	Starvation

7.7.3 Relative influence of food and temperature on sandeel physiology

There are two environmental factors that influence sandeel growth in the model, food and temperature. Year-to-year changes in sandeel growth are dependent on the amount of food available during the short feeding period and/or the effect of temperature on metabolism during the long overwintering period. The DEB model was used to unravel the relative influence of food and temperature on sandeel growth. This was done by running the baseline model using climatological average temperature and food separately, and comparing length, weight and energy predictions with estimates derived using observed food and temperature conditions (y-axis in Figure 7.10). Large deviations from these estimates would imply large sensitivity to temperature or food. Vice-versa, small deviations from the best model fit would imply robustness to temperature or food.

Figures 7.16 and 7.17 show climatalogical average food and temperature between 2000 and 2008, respectively. Large and small copepods showed marked seasonal cycles, characterised by distinct spring and autumn blooms (Figure 7.16). On average, energy concentration of large and small copepods was similar between January and late summer (Figure 7.16). The plankton community became increasingly dominated by large copepods in autumn. Temperature variation in the water column was negligible during the time of the year sandeels were buried in the sediment.

Figure 7.18 shows modelled length, weight and energy under climatological average food and temperature conditions in relation to modelled length, weight and energy under observed food and temperature conditions. The climatalogical average food model produced large changes in length, weight and energy, while the climatalogical average temperature model did not alter results demonstratively (Figure 7.18). Hence, fluctuations in food levels were the predominant influence on year-to-year changes in sandeel size.

Modelled survivorship was markedly higher when using a climatological average for food, and ranged from 74% in 2006/07 to 100% in 2000/01 and 2001/02 (figure 7.19, Table 7.5). Survivorship of sandeels born in 2002 and 2005 increased from 4% and 0% to 99% and 92%, respectively. Estimates of size significantly changed when using average food in the model. Using observed and climatalogical average food in the model resulted in mean lengths of 9 cm and 11.5 cm for age 1 sandeels at 1st June/July. Corresponding weights were $\sim$ 2.8 to $\sim$ 5.6 grams, respectively. Using a climatalogical average for temperature did not significantly alter model results.

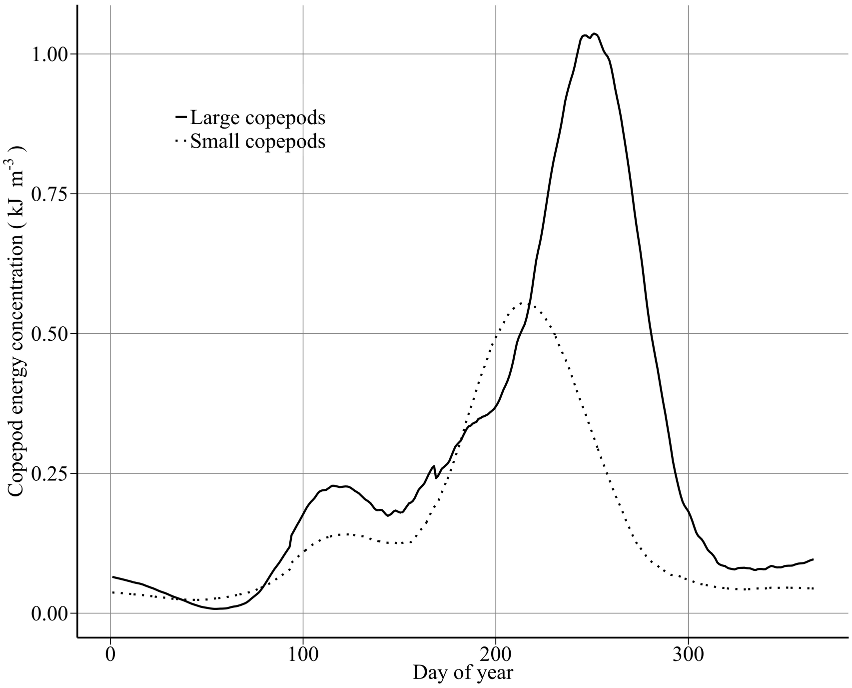


FIGURE 7.16: Climatological average food between 2000 and 2008. Large and small copepods comprised an equal amount of energy from spring until autumn. Both copepod size groups displayed spring and autumn blooms. Timing of the spring and autumn bloom for large copepods was 25th April and 8th September, respectively. Small copepods had spring and autumn blooms in 1st May and 2nd August, respectively.

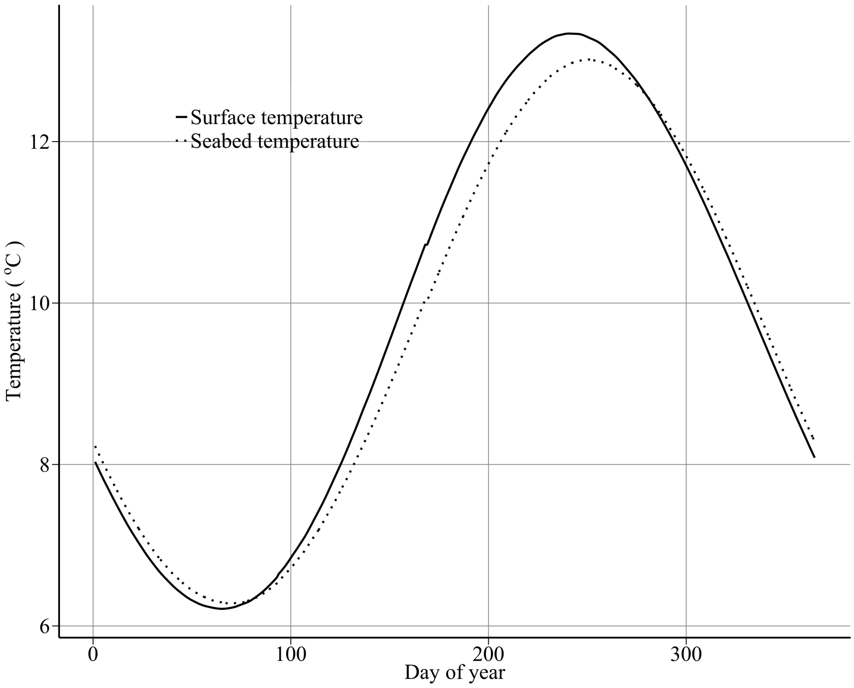


FIGURE 7.17: Climatological average temperature between 2000 and 2008. There was little difference in surface and seabed temperature towards the beginning and end of the year when sandeels overwinter. This is because the waters off the Scottish east coast are well mixed during this time of year.

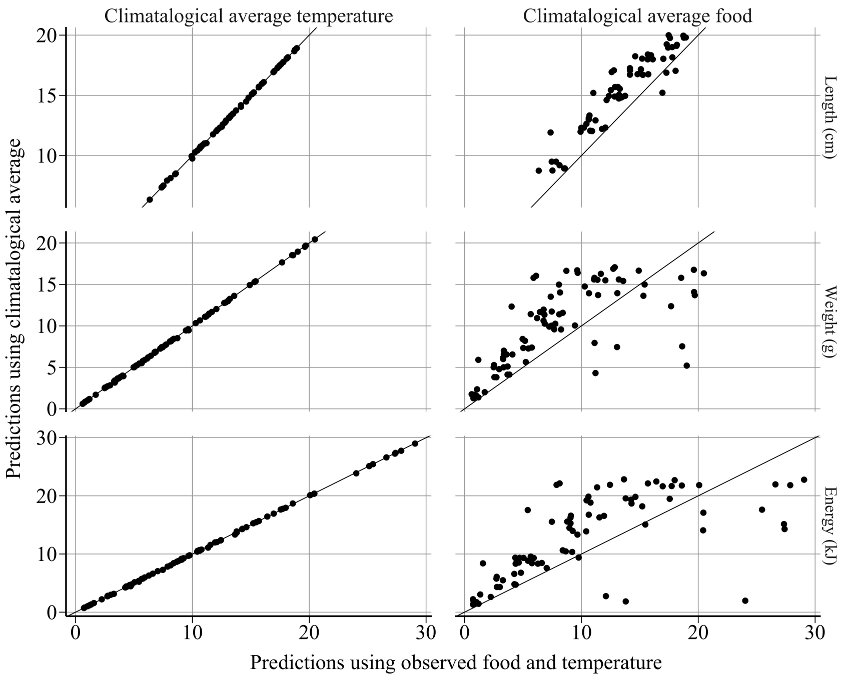


Figure 7.18: Model sensitivity of length, weight and energy to food and temperature. The x-axis represents the model predictions and the y-axis represents predictions using climatological averages. Year-to-year changes in sandeel size and energy are driven by variation in food, not temperature.

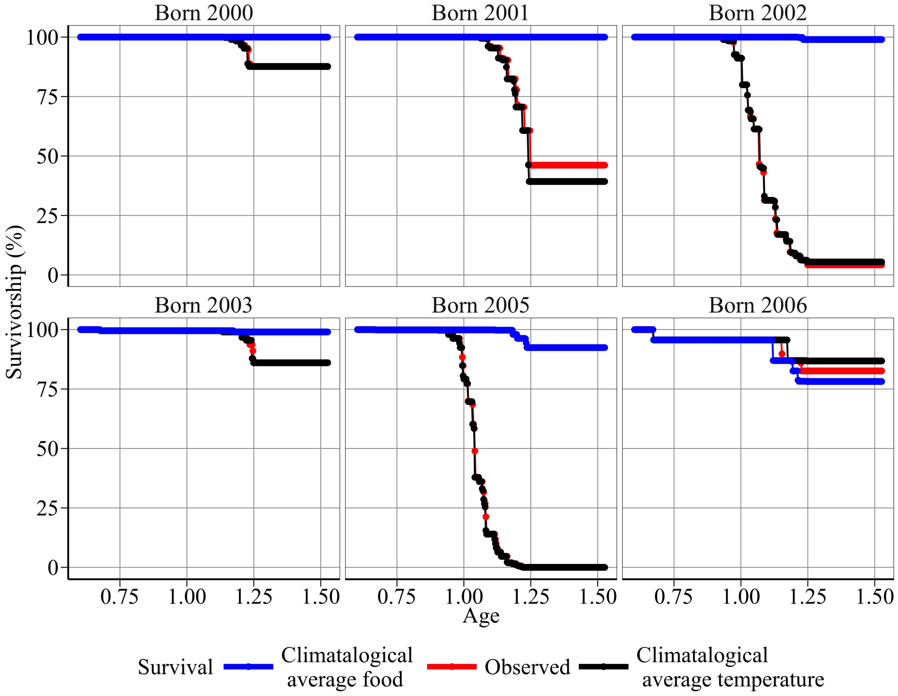


Figure 7.19: Sensitivity of survival to food and temperature. Red points denote results using the best model fit. Blue and black points denote results using climatological average food and temperature between 2000 and 2008, respectively.

Table 7.5: Sensitivity of modelled 0-group overwinter survivorship (%) to food and temperature. We run three models, one using observed food and temperature, one using climatological average temperature, and another using climatological average food. We then compare estimates of survivorship. The model is insensitive to year-to-year changes in temperature but is highly sensitive to year-to-year changes in food.

Winter	Food	Temperature	Survival
2000/01	Observed	Observed	88
2001/02	Observed	Observed	46
2002/03	Observed	Observed	4
2003/04	Observed	Observed	86
2005/06	Observed	Observed	0
2006/07	Observed	Observed	83
2000/01	Observed	Climatalogical average	88
2001/02	Observed	Climatalogical average	39
2002/03	Observed	Climatalogical average	5
2003/04	Observed	Climatalogical average	86
2005/06	Observed	Climatalogical average	0
2006/07	Observed	Climatalogical average	87
2000/01	Climatalogical average	Observed	100
2001/02	Climatalogical average	Observed	100
2002/03	Climatalogical average	Observed	99
2003/04	Climatalogical average	Observed	99
2005/06	Climatalogical average	Observed	92
2006/07	Climatalogical average	Observed	78

Figure 7.20 shows modelled 0-group survivorship in relation to food and temperature. Increasing food concentrations at a given temperature increase survival because individuals accumulate more reserves before overwintering. In contrast, a rise in temperature at a given food concentration decreases survival because reserves are depleted at a faster rate during winter. Differences in cohort survivorship are due to differences in initial length and weight conditions of modelled cohorts. For example, patterns of modelled survivorship notably varied between sandeels born in 2000 and 2006. This is because the initial lengths and weights of animals born in 2000 and 2001 were greater than those born in 2006. However, starvation estimates are not simply a consequence of initial conditions for length and weight. Modelled starvation is clearly a result of a combination of initial cohort length and weight, food and temperature.

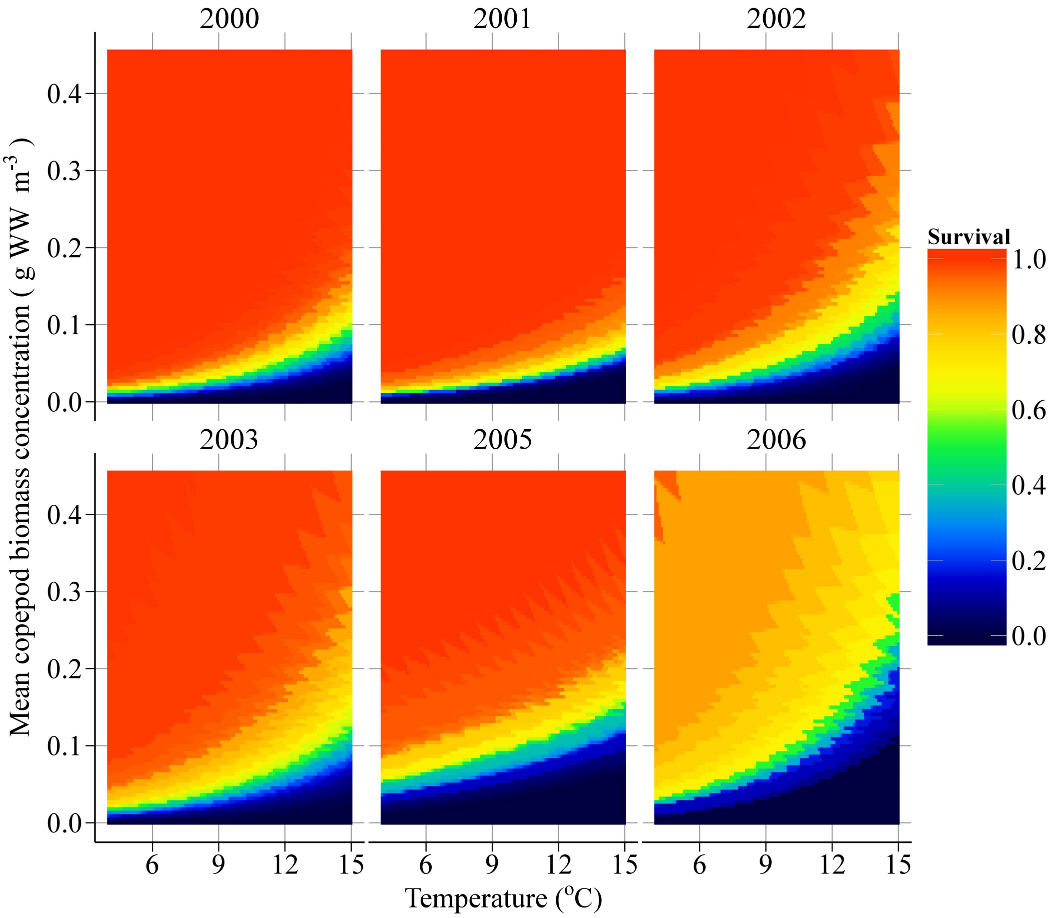


FIGURE 7.20: 0-group overwinter survivorship in relation to food and temperature for each cohort. The model was run using a constant daily temperature and food abundance between June and 1st April. Copepod biomass was assumed to consist of equal amounts of large and small copepods, e.g. 4 g WW m^{-3} denotes 2 g WW m^{-3} of small and large copepods. Seabed and surface temperature were assumed to be equal.

7.7.4 Modelled year-to-year changes in overwintering time

The model successfully reproduces size-dependent overwinter duration in sandeels. Shown in Table 7.6 are modelled overwinter start dates for different age classes. Modelled 0-group individuals rarely entered winter before mid-July, while those age 4 and older ceased feeding before June. Field studies show that larger individuals of the sandeel species have a shorter feeding season than smaller individuals (Reeves, 1994; Tomiyama and Yanagibashi, 2004). Differences in overwinter duration are ultimately related to differences in allometric scaling for ingestion and metabolism.

The amount of time spent feeding for a given age class varied considerably in the model. When food was relatively low between 2000 and 2005, most age 2 sandeels had started overwintering on 21st June. However, when food was relatively high between 2006 and 2008, most individuals in this age class had started overwintering by 21st May.

The model performs well in reproducing the actual timing of overwintering. Field data indicates the most common time to begin overwintering is July (Winslade, 1974; Reeves, 1994). Given that younger fish dominate the sandeel stock, this implies the 0-group and 1-group overwinter at this time. The model is consistent with this, showing that between 2000 and 2006, 0-group and 1-group sandeels overwintered in July (Table 7.6).

Table 7.6: Mean overwintering start dates of different age groups between 2000 and 2008. Older sandeels begin overwintering sooner than younger individuals. Overwintering start dates varied between 10th May and 31st July for sandeels aged between 0 and 5.

Age group	Year	Mean overwintering start date
0	2000	19th July
	2001	23rd July
	2002	31st July
	2003	17th July
	2005	31st July
	2006	18th July
1	2001	5th July
	2002	5th July
	2003	2nd July
	2004	5th July
	2006	10th July
	2007	23rd June
2	2002	19th June
	2003	20th June
	2004	26th June
	2005	12th June
	2007	19th June
	2008	20th May
3	2003	8th June
	2004	18th June
	2005	11th June
	2006	26th June
	2008	18th May
4	2004	1st June
	2005	2nd June
	2006	23rd June
	2007	5th June
5	2005	25th May
	2006	20th June
	2007	30th May
	2008	10th May

7.7.5 Modelled prey composition of sandeels

Individuals displayed a slight preference for large copepods (Figure 7.21). Mean biomass concentration of large and small copepods during the main foraging period (1^{st} April - 1^{st} August) between 2000 and 2008 was 0.05 and 0.07 g WW m^{-3}, respectively. Half-saturation constants were 0.075 and 0.166 g WW m^{-3} for animals feeding on large and small copepods, respectively. To assess the realism of these estimates, we can compare our modelled functional responses to the functional response of Pacific herring *Clupea pallasii*, a fish with a similar diet and foraging behaviour to sandeels. The estimated half-saturation value for herring feeding on very large calanoid copepods (>2.5 mm) is in the range $0.03 - 0.04$ g m^3 (Calcuated using digitized data from figure 4 in Willette et al. (1999)). Hence, our estimated half-saturation constant of 0.075 g WW m^{-3} for sandeels feeding on copepods larger than 1.3 mm does not appear unrealistic.

Ingestion rate showed considerable inter-annual variation. On average, animals only reached 27% of their maximum ingestion rate in 2002 during the main foraging period, but reached over 70% in 2008. Large copepods only accounted for $\sim$ 16% of sandeel energy intake in 2006, compared to $\sim$ 80% in 2008 (Figure 7.22).

To calculate biomass concentration of individual copepod prey species (see tables 7.2 and 7.1) on a given day, a smooth (LOESS, span = 0.04) was fitted to the time series of copepod measurements and the food on each day was extracted. Using this procedure, large and small copepod groups were further divided into individual copepod prey groups. The most important prey species between 2000 and 2008 were, in descending order, *Acartia*, *C. helgolandicus*, *C. finmarchicus*, *Pseudocalanus* and other large *Calanus* (Figure 7.23). In contrast, *Oithona*, *Temora*, *Small calanus* species, *Centropages*, *Paracalanus* and *Microcalanus* contributed significantly less energy between 2000 and 2008. That Acartia was an important prey item is consistent with recent field evidence off the Scottish east coast (Lynam et al., 2013).

7.7.6 Year-to-year changes in energy content

Given measurements of abundance at age, weight and length for each cohort, the model was used to reconstruct past changes in energy and condition (Figures 7.24 and 7.25). Figure 7.24 shows the ratio of reserve energy to structural energy. Reserve ratio shows a

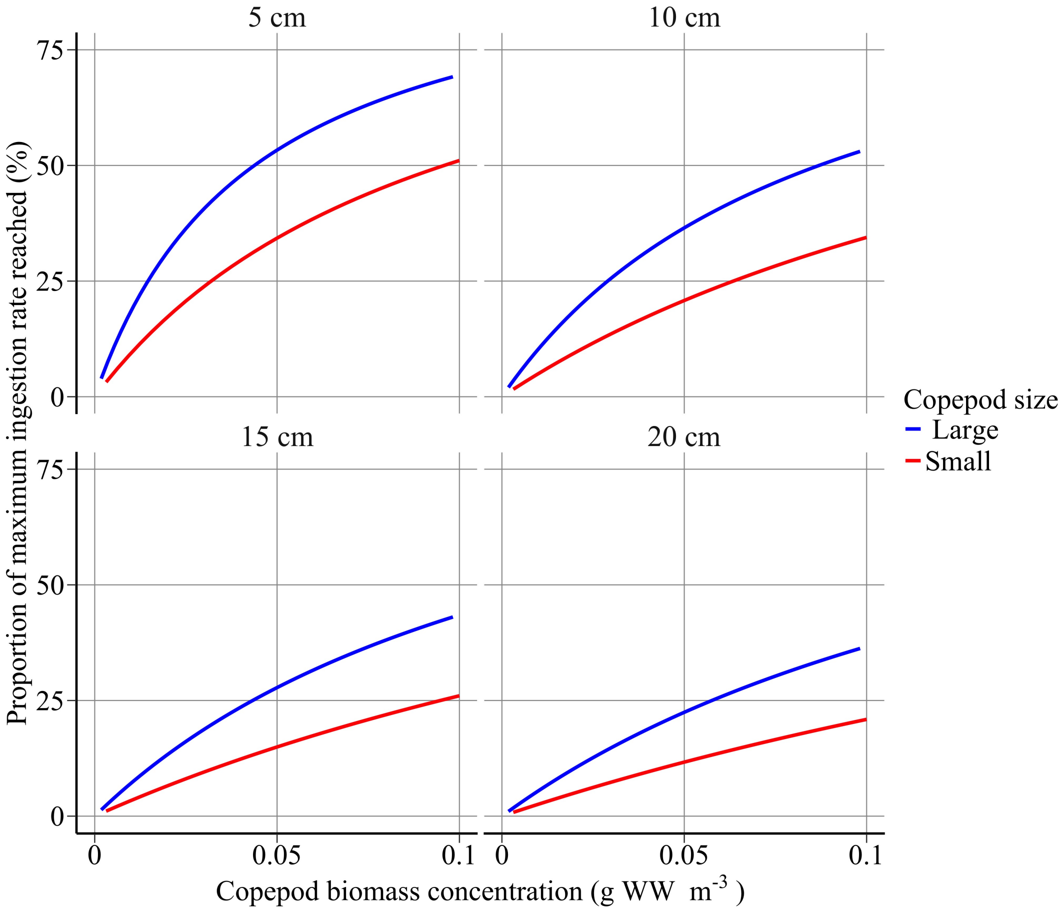


Figure 7.21: Best-fit functional response model for sandeels feeding exclusively on large (blue) or small (red) calanoid copepods.

strong seasonal pattern, especially for cohorts born in 2000, 2001, and 2002. Minimum and maximum reserve ratios occurred in March and June, respectively. This is expected since reserves should be at their minimum in March towards the end of the overwintering season, and peak in late summer shortly before the resumption of the overwintering period.

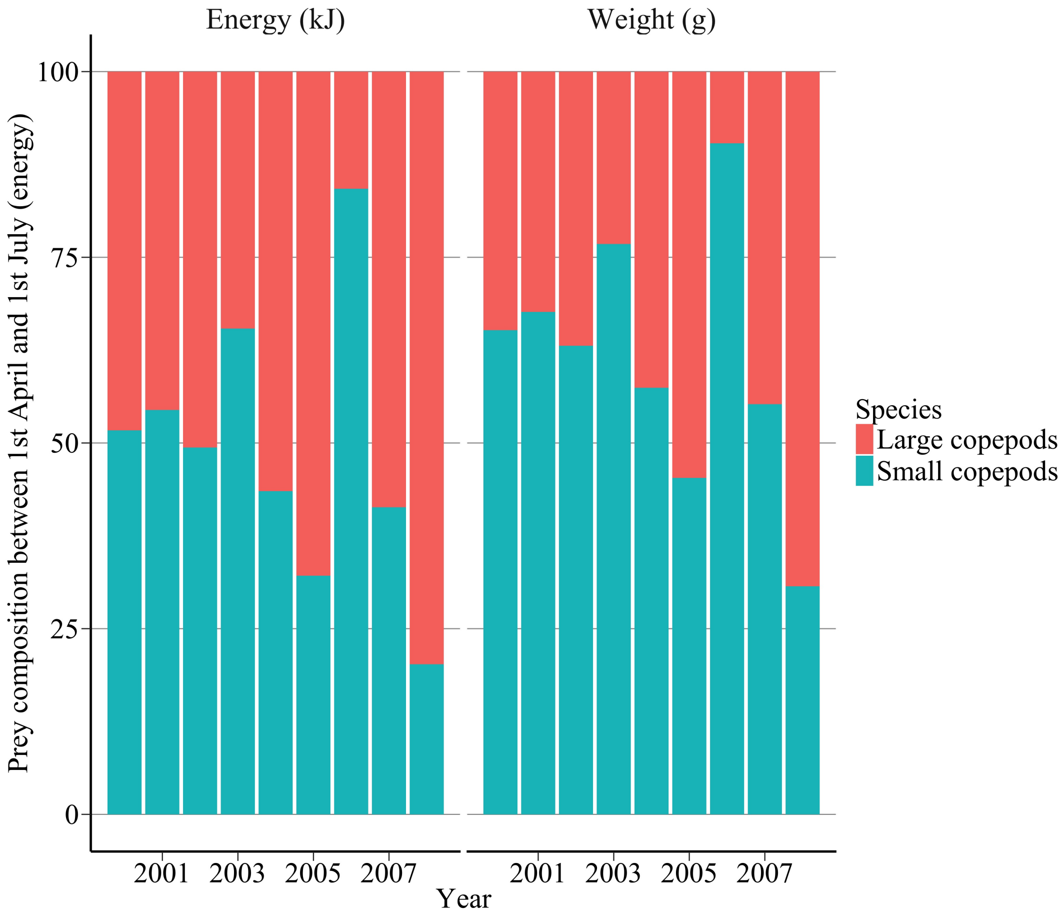


FIGURE 7.22: Modelled prey composition, grouped by copepod size.

Figure 7.25 shows year-to-year changes in sandeel energy content. There was considerable inter-annual variation in energy at age. 0-group energy content varied by a factor of 4 during the study period, ranging from $\sim$ 5.8 in 2000, to $\sim$ 1.2 in 2005 (Figure 7.25). A similar range was detected in age 1 fish, which had energy values of 16.7 and 73.2 kJ in 2002 and 2009, respectively.

A suite of gam models were used to determine the influence of different factors on cohort condition (Table 7.7). Gam models indicate that recent changes in the reserve ratio were influenced by age and Julian day, but not year. The best 2 variable model related the reserve ratio to age and Julian day.

$$\text{Reserve ratio} = 1.22 + 0.26\,\text{Age} + 0.0054\,\text{Julian day} \tag{7.20}$$

Combining all cohort data, a highly significant relationship was evident between wet

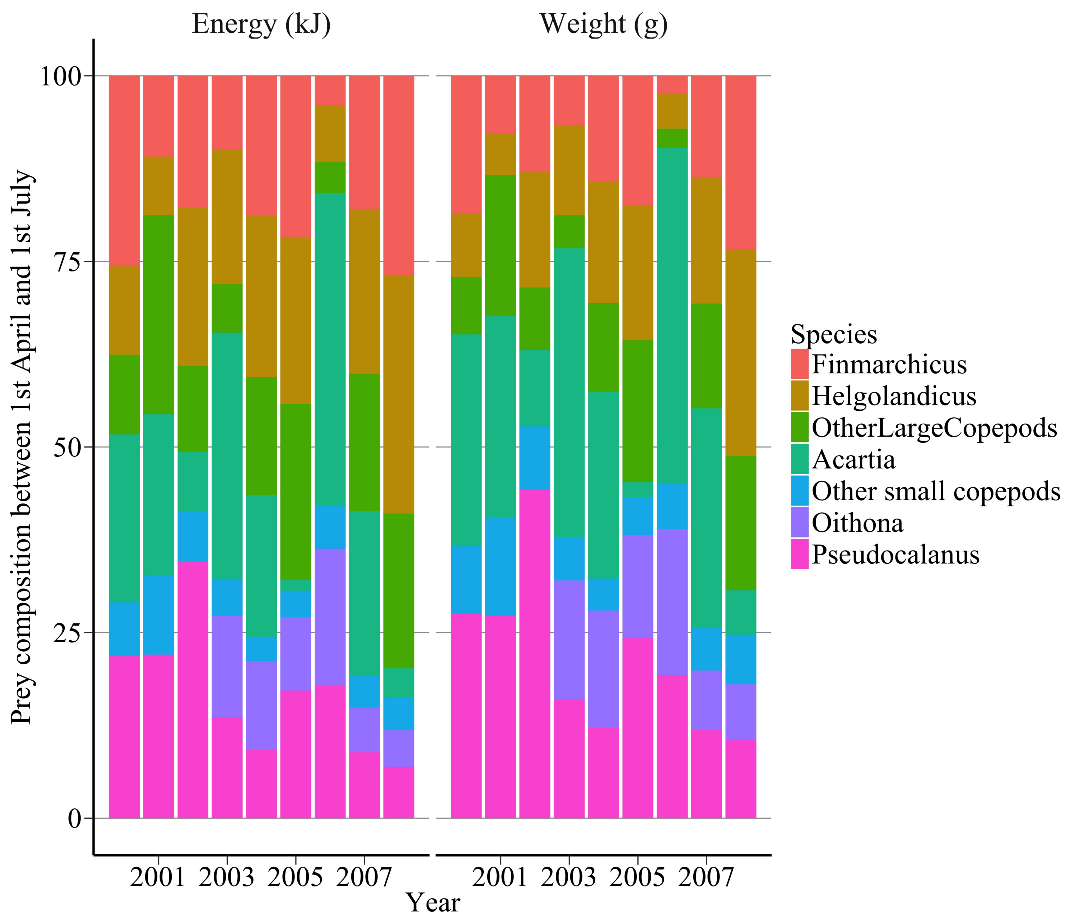


FIGURE 7.23: Modelled prey composition, grouped by copepod species.

TABLE 7.7: GAM models relating cohort mean reserve ratio to age, year and season. The reserve ratio, a proxy for condition, is dependent on age and time of year. This reflects both the seasonal variation in energy content of a sandeel, and the fact that condition generally increases with age.

Age	Julian Day	Year	R^2
▨	▨	▨	0.23
▨	▨		0.23
▨		▨	0.14
▨			0.14
	▨	▨	0.07
	▨		0.07
		▨	0

weight and the reserve ratio (Reserve ratio = 2.05 + 0.145 Wet weight, Figure 7.26). This means larger fish have a higher energy density, as corroborated by multiple studies on sandeel energy data and forage fish in general (Hislop et al., 1991; van Deurs et al., 2011; Anthony et al., 2000; Robards et al., 1999). Wet weight explains more variation in condition (reserve ratio) than length (R^2 =0.16), Julian day (R^2 = 0.09), or age (R^2 =0.03).

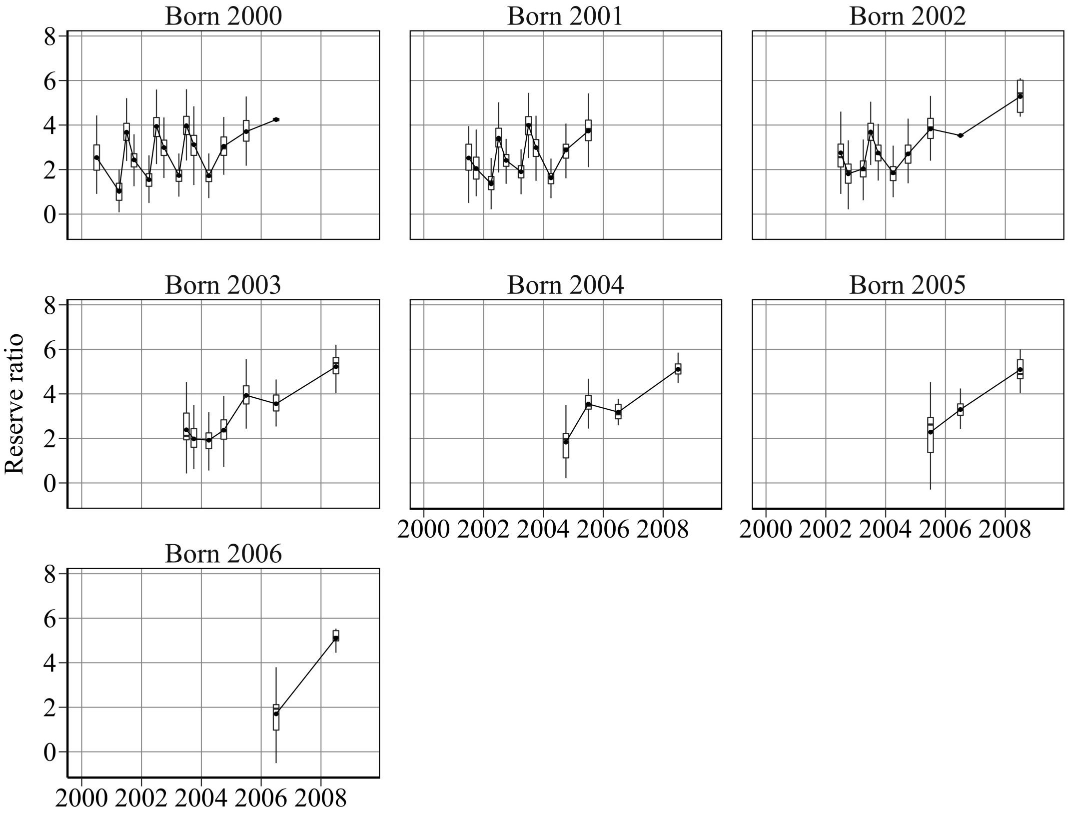


FIGURE 7.24: Year-to-year changes in cohort reserve ratio, the proxy for sandeel condition. Sandeel condition is highly seasonal, reaching a minimum in March and a maximum in June. Condition generally increases with age.

7.7.7 Using the model to project future changes in sandeel size, energy and survival

The model was used to predict the effects of expected temperature rises and declining food abundance on sandeel physiology. This was carried out using the following method: First, the abundance of each sandeel 0-group was normalised. Next, initial length and weight estimates for all cohorts were combined, producing abundance-at-length-and-weight for the average sandeel cohort between 2000 and 2008. Figure 7.27 shows length and weight estimates of the average 0-group during our study period. Changes in mean length, weight, energy content and overwinter survivorship of 0-group sandeels were tracked under different temperature and food conditions.

First, the influence of temperature rise on median length, weight, energy and survivorship was examined. To do this, the model was run under climatalogical average food and temperature conditions, but with an additional rise in temperature. Figure 7.28

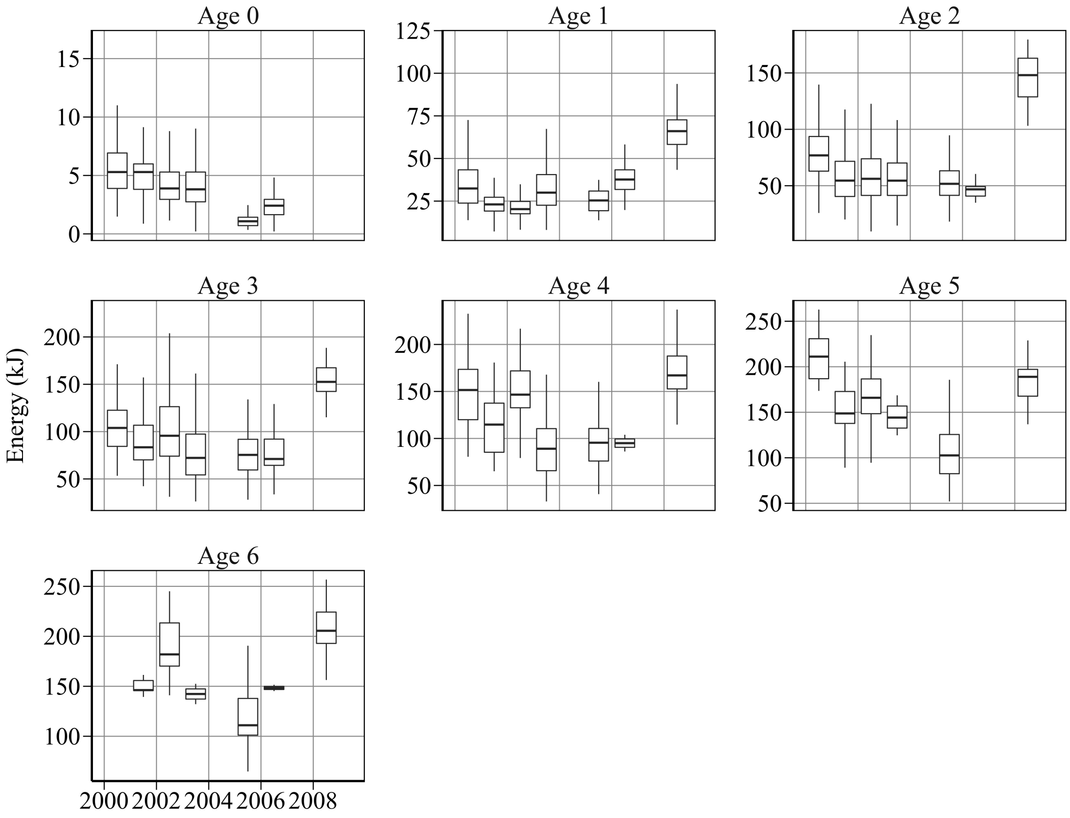


Figure 7.25: Year-to-year changes in energy content per sandeel. There was a general decline in energy content between 2000 and 2006 for most age groups. Energy per sandeel was relatively high in 2008.

shows changes in median length, weight, energy and survivorship between 15th June (average catch day of 0-group sandeels between 2000 and 2008) and 1st July under different temperatures. A temperature rise of 3 ^{o}C had little effect on sandeel length, weight, energy content and survivorship. Median length increased from 13.2 to 13.5 cm, median weight increased from 7.9 to 8.6 g, and energy content increased 56 to 60.6 kJ under a temperature rise of 3 ^{o}C. A temperature rise of 3 ^{o}C also had a minor effect on survivorship.

A second application of the model was to project the impact of simultaneous changes in food and temperature on sandeel survivorship. Using climatalogical average food and temperature between 2000 and 2008 as baseline environmental conditions, first year survivorship was tracked under varied temperature increases and food decreases. Figure 7.29 shows modelled survivorship of the average 0-group cohort under a reduction in food abundance and increase in temperature.

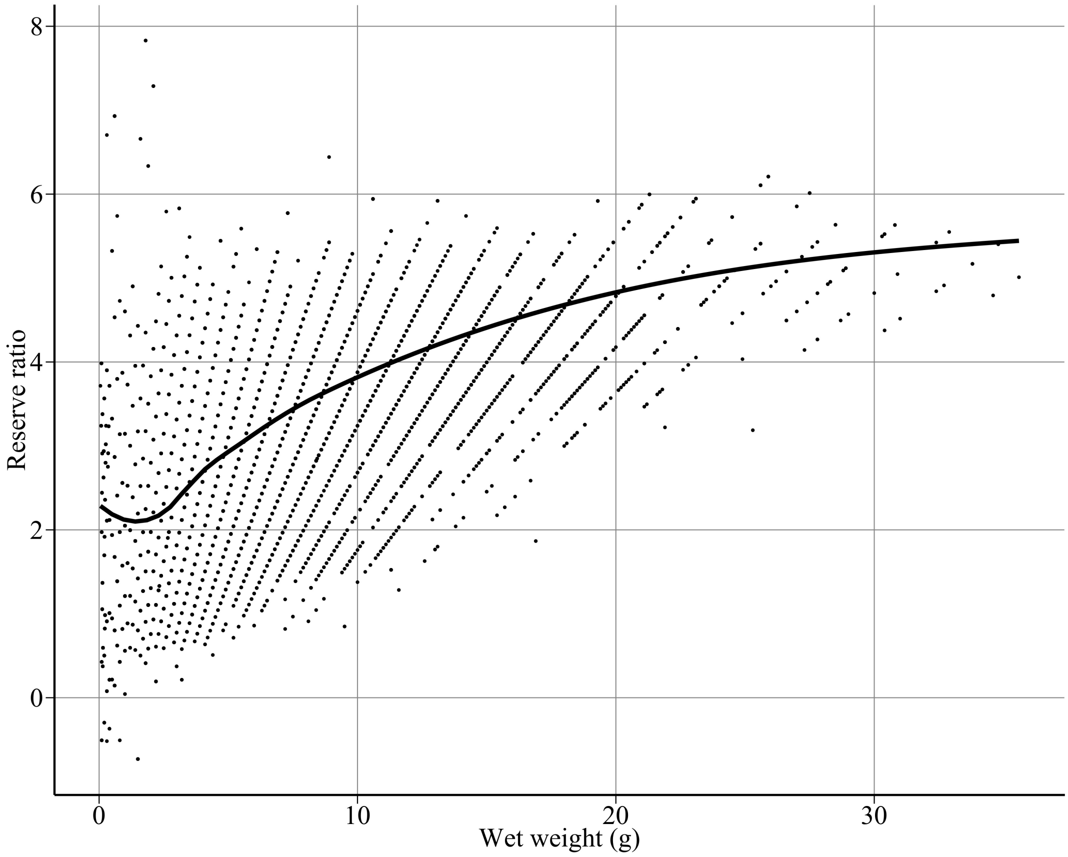


FIGURE 7.26: Relationship between wet weight (g) and reserve ratio. Reserve ratio = $2.05 + 0.145$Wet weight ($R^2 = 0.36$, $p < 0.0001$).

7.7.8 Parameter sensitivity

A one-at-a-time sensitivity analysis was performed to determine the sensitivity of model parameters. This was done to determine what parameters are sensitive and to check if model robustness to changes in parameter values. To do this, each parameter was varied by ±10% and changes in mean weight and starvation mortality of the 2000 cohort were tracked until immediately prior to spawning at age 4. Then, predicted cohort mean weight and starvation mortality was compared to modelled values at age 4. See table 7.3 for parameter details. Note that R_{dry}, S_{dry}, E_s and E_r are determined by γ, a, b, E_f, E_p, ash_x and ash_y and so are excluded from the sensitivity analysis.

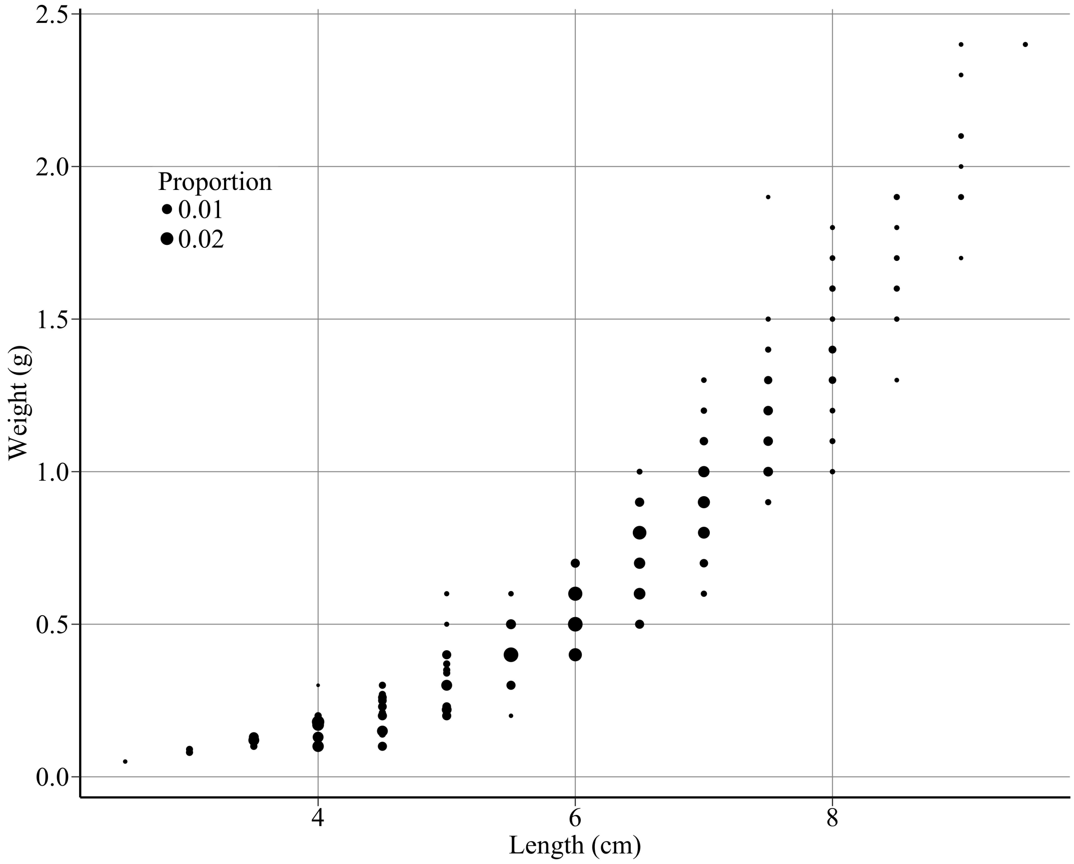


FIGURE 7.27: Length and weight of the average 0-group between 2000—2003 and 2005—2006 off the Firth of Forth. Abundance of each 0-group cohort between 2000—2003 and 2005—2006 was normalised. Then, we combined all length-weight data.

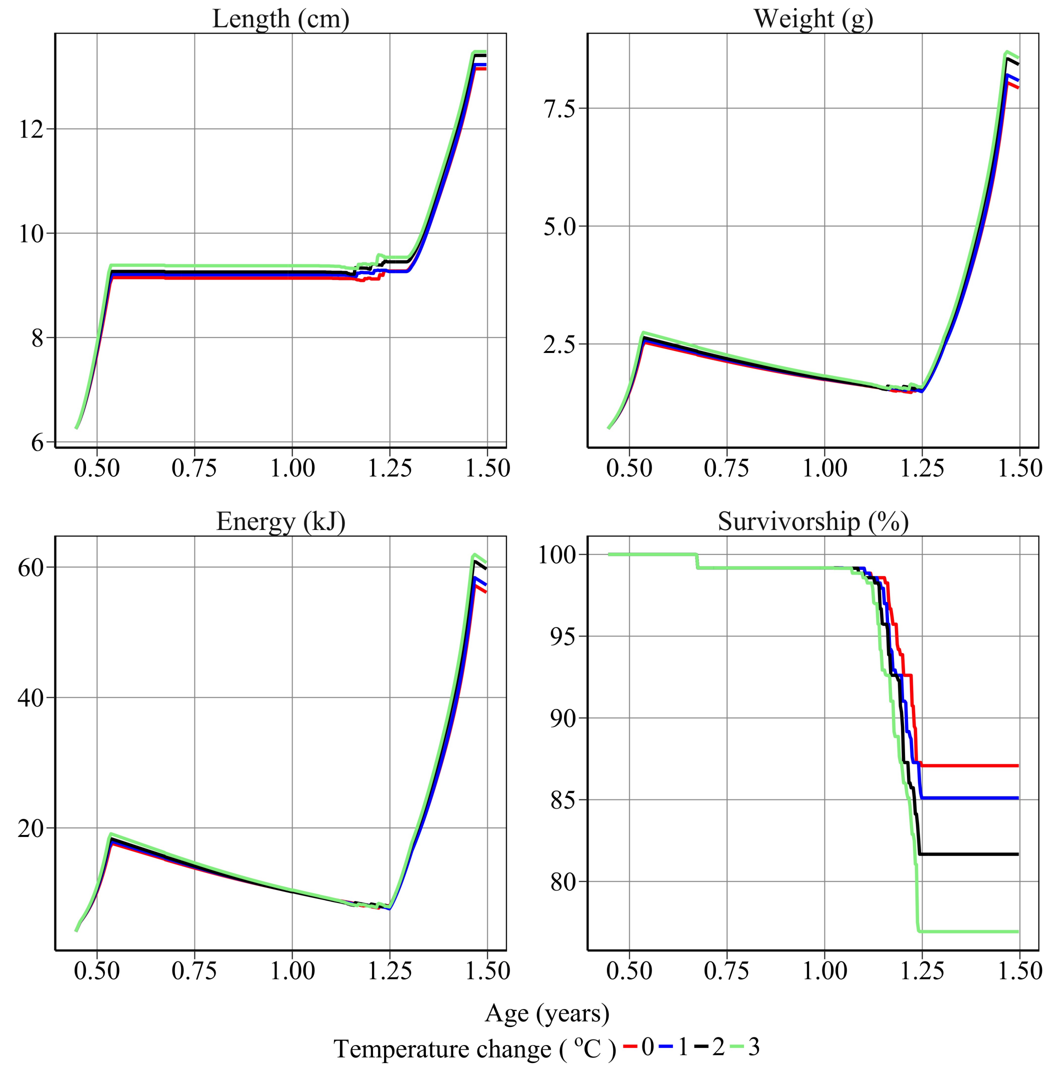


FIGURE 7.28: Changes in median length (cm), median weight (g), median energy content (kJ) and overwinter survivorship (%) of the average 0-group off the Firth of Forth under 1, 2 and 3 ^{o}C temperature rise.

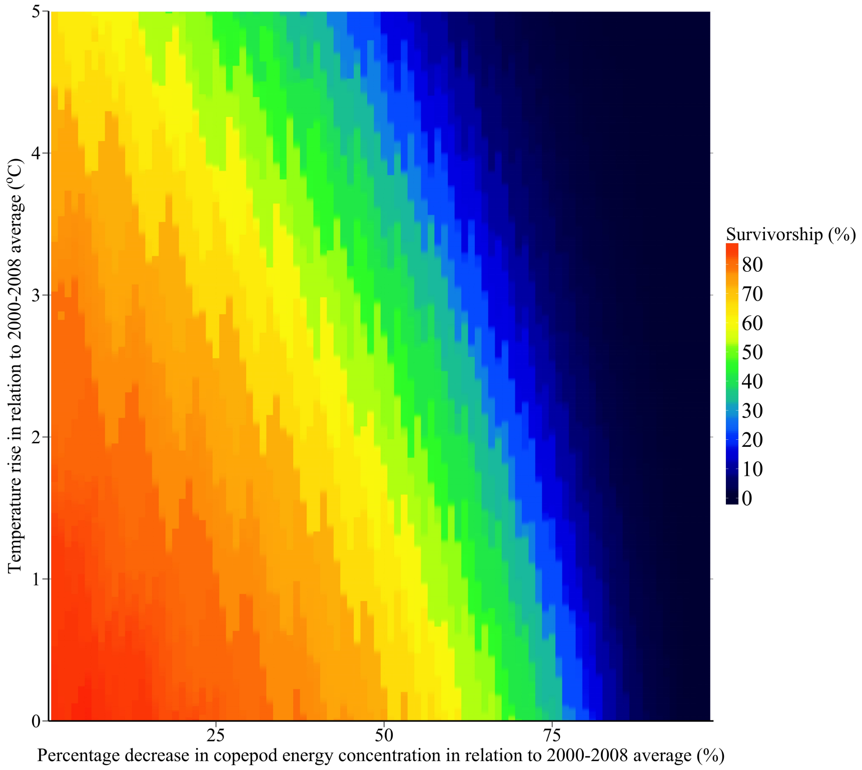


FIGURE 7.29: Modelled survivorship (%) of the average 0-group off the Firth of Forth under a simultaneous food reduction and temperature rise.

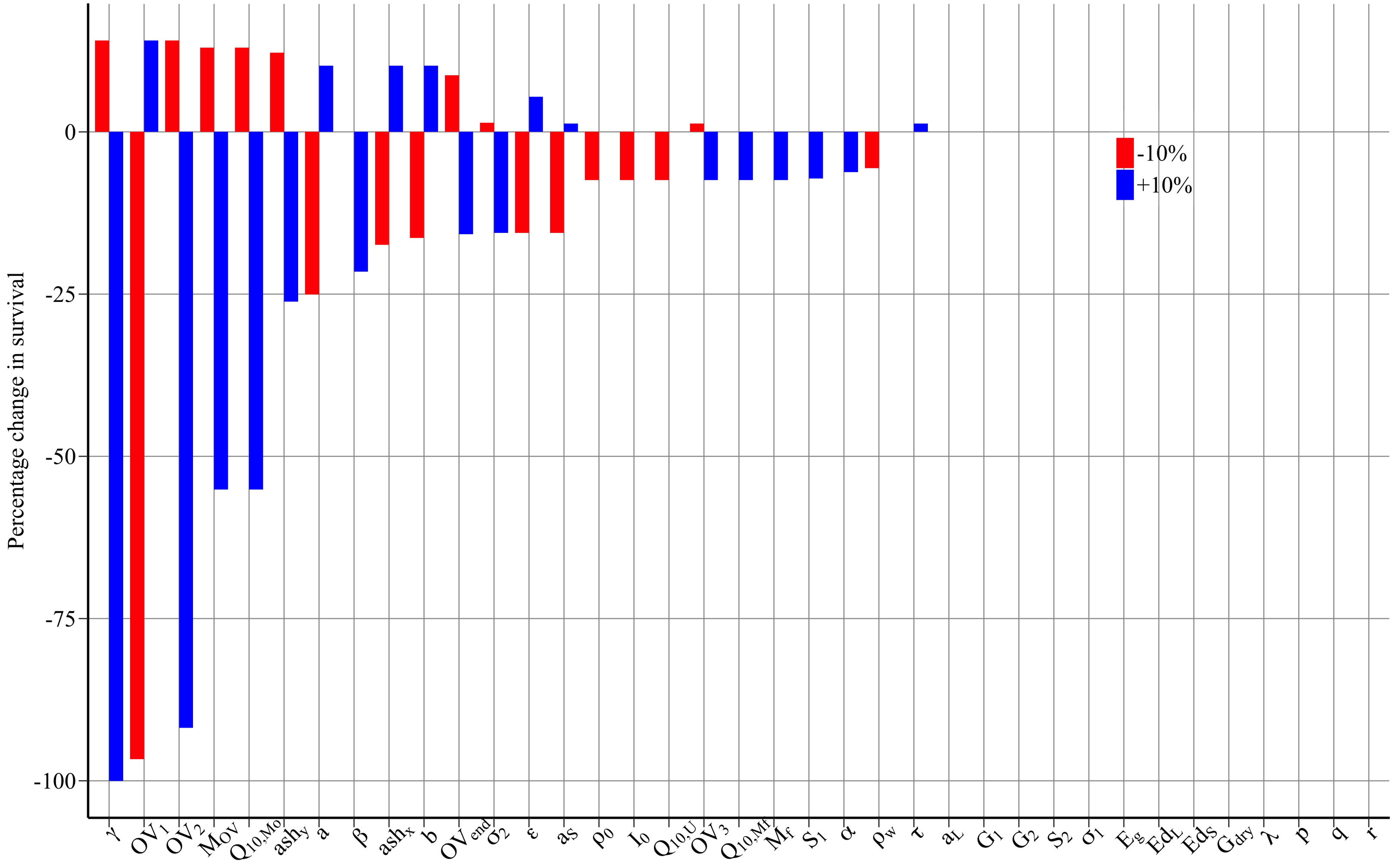


FIGURE 7.30: One-at-a-time sensitivity analysis of model parameters. Each parameter is adjusted ±10% and predicted starvation survival is compared to modelled starvation survival given by the baseline parameterisation.

Sensitivity analysis of fitted parameters (Figure 7.30) revealed that starvation is most sensitive to parameters representing the maximum proportion of water in a sandeel (γ), the overwintering threshold OV_1 and OV_2 (which control when sandeels begin overwintering) and overwintering metabolism (Q_{10,M_o} and M_o). A 10% decrease in OV_1 decreases survival by 97%. It is obvious why changes in this parameter value lead to great changes in survival. To illustrate, a 7 cm sandeel would require a reserve ratio threshold of 0.6 to begin overwintering on 1^{st} July, instead of the original value of 3.1. Hence, sandeels would have inadequate reserves to survive overwinter. A 10% increase in the Q_{10,M_o} leads to a decrease in survival of 50%, underlining the sensitivity of survival to overwinter metabolic rate. Increasing M_o by 10% results in similar changes in survival. Moderately sensitive parameters (10% $<$ change in survival $<$ 30%) are, in order of sensitivity, parameters determining the relationship between ash and water content (ash_x and ash_y), the proportion of fat in reserves (a), the length structure exponent (β), parameters determining the relationship between water and fat content (b), the date of overwintering exit (OV_{end}), the starvation threshold (σ_2), assimilation efficiency (ϵ) and small copepod encounter rate (a_S). Less sensitive parameters (1% $<$ change in survival $<$ 10%) are, in order of sensitivity, the defended reserve ratio (ρ_0), the ingestion scale (I_0), the effect of temperature on ingestion rate ($Q_{10,U}$), the effect of size on overwintering entry (OV_3), the effect of temperature on summer metabolism (Q_{10,M_f}), the metabolic cost scale (M_f), structural energy allocation parameter (S_1),the length structure scale (α), the allocation switch width (ρ_w) and the maximum ingestion rate reserve ratio threshold (τ). The least sensitive parameters (change in survival $<$ 1%) are, in order of sensitivity, the large copepod encounter rate (a_L), the gonad energy allocation parameters (G_1 and G_2), structural energy parameter (S_2), the shape of the starvation-reserve ratio curve (σ_1), energy densities for gonads (E_g), large and small copepods (Ed_S and Ed_S), the ratio of wet to dry gonad weight (G_{dry}), the maximum ingestion rate multiplier (λ), the effect of body size on maximum ingestion rate (p), search rate (q) and metabolism (r).

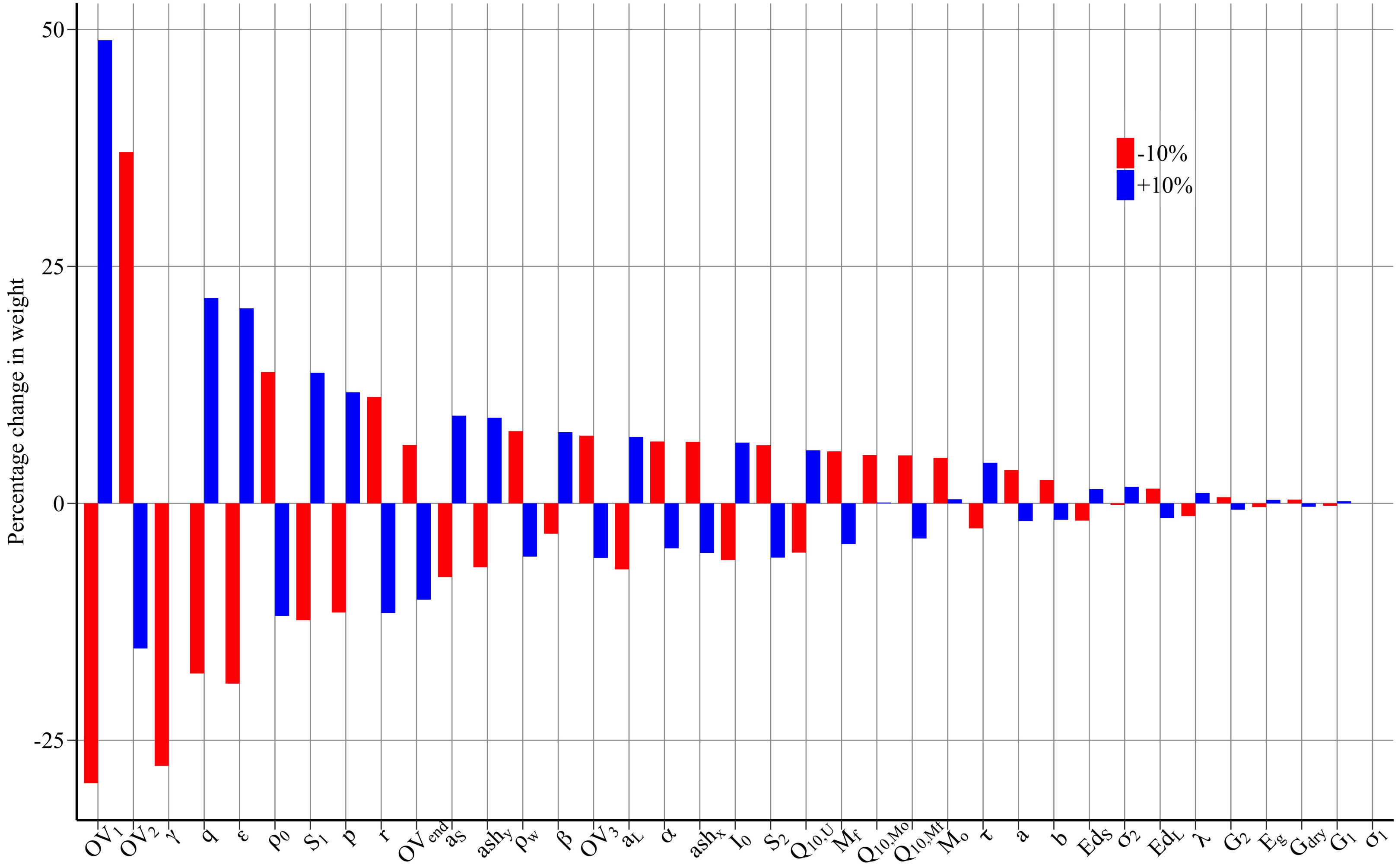


Figure 7.31: One-at-a-time sensitivity analysis of model parameters. Each parameter is adjusted ±10% and predicted mean weight is compared to modelled mean weight given by the baseline parameterisation. Note that there is no modelled mean weight for the case where γ is increased by 10%. This is due to 100% starvation mortality.

Sensitivity analysis of fitted parameters (Figure 7.31) revealed that weight is most sensitive to the overwintering threshold parameters (which control when sandeels begin overwintering). A 10% increase in OV_1 increases weight by 49%. Similarly, a 10% decrease in OV_2 increases weight by 37%. Moderately sensitive parameters (10% $<$ change in weight $<$ 30%) include the body size scaling parameters (p, q and r) and γ. Less sensitive parameters (1% $<$ change in weight $<$ 10%) include the copepod encounter rates (a_L and a_S) and other parameters related to ingestion. The least sensitive parameters (change in weight $<$ 1%) include the gonad allocation parameters (G_1 and G_2) and the shape of the starvation threshold (σ_2).

Figures 7.30 and 7.31 illustrate that modelled sandeel growth and survival is most sensitive to the maximum proportion of water in a sandeel, the timing of overwintering entry and overwinter metabolism. Other parameters that have a demonstrable effect on growth and survival are ash_y, ϵ, β and a. These parameters determine relationships between ash and water content, assimilation efficiency, length-structure exponent and the proportion of reserves that are fat, respectively. Note that an increase in weight does not necessarily translate to an increase in survival. For instance, a 10% decrease in the defended reserve ratio (ρ_0) increases weight but decreases survival. This is because when the reserve ratio threshold at which sandeels cease structural growth investment is lowered, individuals increase size but have inadequate reserves to survive winter.

7.8 Discussion

7.8.1 The role of starvation mortality in the sandeel decline

The model provides support for the hypothesis that a sudden decline of older sandeels was driven by starvation mortality. Analysis of stock abundance data shows that the steepest decline in 1+ group biomass recorded took place between 2005 and 2006, when the abundance of this group fell by 2 orders of magnitude (Greenstreet et al., 2010). To put this decline into context, the second largest decline over the study period occurred between 2006 and 2007, when 1+ group biomass fell by slightly less than 1 order of magnitude. Results suggests that the severity of the decline between 2005 and 2006 was because almost all sandeels born in 2005 incurred overwinter mortality. Modelled starvation mortality was almost 100% over this period. Therefore given that the stock is mostly comprised of fish younger than age 2, high starvation mortality was likely to blame for the decline in biomass at this time. The cause behind high overwinter mortality was a lack of food. Had the 2005 cohort experienced food conditions similar to the average over the study period, survival would have been markedly higher. This implication demonstrates that the degree of starvation mortality modelled in 2005/06 was not simply a consequence of the 2005 cohort being relatively small in size, and therefore the most vulnerable cohort to starvation.

The model hindcasts substantial overwinter mortality ($\sim$ 95%) for individuals born in 2002. This was despite the absence of a corresponding decline in 1+ group biomass between 2002 and 2003 in stock data gathered by Greenstreet (2010). However, stock abundance data yielded using different survey methods demonstrate a decline in 1+ group biomass during this time (Greenstreet et al., 2006). Indeed, grab surveys show a decline between 2002 and 2003, and such surveys may provide the most accurate estimates of stock abundance since it is guaranteed that the entire population is surveyed, and catchability is near 100% (Greenstreet et al., 2010).

More support for the starvation-triggered decline comes from the observed year-to-year estimates of 0-group energy content (Figure 7.25). The decline in 0-group energy between 2000 and 2005 reflects trends in stock abundance. The lowest 0-group energy occured in 2005, shortly before the steepest recored decline in 1+ group biomass.

Modelled juvenile sandeels incurred starvation mortality while older fish did not, which is consistent with size-selective starvation mortality. Smaller fish starve before larger fish, reflected by increases in mean length.

Sandeels on the east coast experienced far greater levels of natural mortality after 2005 than previously (Figure 7.15). In contrast to individuals born between 2000 and 2003, which incurred annual natural mortality rates ranging from 56-83%, those born in 2005 and 2006 incurred annual natural mortality rates of 95-100%, respectively.

7.8.2 Influence of rising temperatures on body size

Warming temperatures are expected to lead to smaller fish body size (Daufresne et al., 2009). However, large temperature rises do not lead to smaller body size in the model.

This is a result of the choice of Q10 for ingestion and metabolism, and the effect of temperature on assimilation efficiency. Animals were assumed to assimilate an extra 0.764% of ingested energy for every 1 ^{o}C degree temperature rise (Larimer, 1992). Moreover, Q10s for summer and winter metabolic rates were assumed to be 1.8 and 1.46, respectively (Quinn and Schneider, 1991). In addition, a Q10 of 1.72 for ingestion rate was derived using data from a similar species (derived from Van Deurs et al. (2010)).

In general, fish asymptotic length and growth rate are inversely related (Gislason et al., 2008). Off the Scottish east coast, sandeels grow slowly and reach asymptotic lengths exceeding 20 cm, however, sandeels which grow rapidly in Dogger Bank may only reach 15 cm in length (Rindorf et al., 2016). It is possible that after maturation further increases in length are sacrificed in favour of reserve accumulation for reproduction. Further increases in structure may be sacrificed in favour of reproductive investment once the difference between ingestion and metabolism is at a maximum (Jorgensen, 2008).

7.8.3 Direct temperature impacts on zooplankton

Direct temperature impacts on zooplankton have been hypothesised as the cause of a decrease in sandeel quality and availability (Frederiksen et al., 2013). Previous studies have shown a negative correlation between seabird breeding success off the Scottish east coast and SST in the previous year (Frederiksen et al., 2004, 2007). It is unclear why this is the case. If increases in winter temperature reduce *C. finmarchicus* abundance the following year then that may explain the negative association between sandeel recruitment and the winter index of the North Atlantic Oscillation (WNAO), since the WNAO influences winter temperature (Arnott and Ruxton, 2002). A lack of food for sandeel larvae could increase starvation mortality leading to poor recruitment. Alternatively, a reduction in recruitment could result from decreased larval growth rates, since slow growing larvae are more vulnerable to predation.

The direct impact of rising winter temperatures on zooplankton is likely driving reductions in seabird numbers. Indeed, seabird breeding success is negatively related to sea surface temperature the previous year (Frederiksen et al., 2004, 2007). Overall *Calanus* abundance has been declining since the 1980s (Reid et al., 2003). In consequence, the copepod community has shifted to one dominated by high energy density prey to low energy density prey.

An alternative hypothesis for a decline in sandeel quality and abundance could be that climate change is affecting primary production. Decreasing sandeel length in the North Sea could indicate parallel declines in phytoplankton abundance. Such a link between sandeel length and primary production has been demonstrated in another shelf sea (Eliasen et al., 2011).

Modelled prey composition favoured large copepods. This was despite small copepod energy concentration exceeding large copepod energy concentration between 2000 and 2006 during the main feeding season (1^{st} April - 1^{st} August). However, prey energy density may be more important than prey abundance. While the model shows an important contribution of small copepods (<1.3 mm) to the diet, large copepods (> 1.3 mm) were a better food item due to their substantially higher energy density. Handling time limitation may mean that sandeels sometimes ignore smaller copepods in favour of larger prey to maximize the energy reward per unit handling time (Werner and Hall, 1974). Few bioenergetics modelling studies have addressed the importance of variation in prey energy density, instead characterizing prey in terms of average energy density. However, this omission may be unwise since there is much evidence for particulate feeding in small pelagic fish (Northern Anchovy *Engraulis mordax*, (Leong and O'Connell, 1969); pilchard *Sardinops sagax*, (van der Lingen, 1994); Herring *Clupea harengus*, (Batty et al., 1986)).

Evidence suggests future reductions in copepod size will likely reduce sandeel growth rates (van Deurs et al., 2014). This is because sandeel ingestion rates may be positively correlated with copepod size (van Deurs et al., 2014). Unless decreasing copepod size is accompanied by a parallel increase in copepod abundance, sandeels energy uptake will decline. In fact, it is far more likely that the negative effect of decreasing copepod size on sandeel growth will be exacerbated by a decrease in copepod concentration. Indeed, ocean modelling predicts a decrease in primary production and zooplankton biomass in the North Sea by the end of the century (Chust et al., 2014).

Decreasing prey size may not be a problem unique to pelagic fish; it is possible that this could happen to zooplankton prey, phytoplankton. Morán et al. (2010) provides evidence that warming seas will lead to smaller primary producers. Shifts to smaller phytoplankton could increase food chain lengths, which can reduce trophic transfer efficiency. This is because assimilation losses to higher trophic levels will increase. In addition, if zooplankton ingestion rate decreases with smaller prey size, the net result will be declining copepod size.

7.8.4 Consequences of changes in copepod community composition on sandeels

Results provide further evidence that declines in *C. finmarchicus* abundance will be damaging to sandeels. Model results show that sandeels derived 17% of their energy from this copepod species on average between 2000 and 2008. An open research question is will there be an adequate replacement for *C. finmarchicus*? Currently, the most viable candidate is *C. helgolandicus* (Frederiksen et al., 2013; Wilson et al., 2015), the only other abundant calanoid copepod in the North Sea which reaches lengths exceeding 2 mm. The model suggests that *C. helgolandicus* was actually a more important food item for sandeels than *C. finmarchicus* between 2000 and 2008, with abundances of the former species far exceeding that of the latter species during sandeel feeding season (Figure 7.32). Since the 1960s, there has been a gradual shift in relative abundance between *C. finmarchicus* and *C. helgolandicus* (Reid et al., 2003). *C. helgolandicus* is forming an ever increasing proportion of total copepod abundance (Reid et al., 2003).

C. helgolandicus abundance is likely to increase in future, however, they may be an unsuitable replacement for *C. finmarchicus*. It has been suggested that *C. helgolandicus* is an inferior replacement to *C. finmarchicus* because it is smaller in size, and hence contains less energy (Frederiksen et al., 2013). However, there is currently no evidence to back up this assertion (Wilson et al., 2015). At a given latitude, all copepods will decrease in size (Reid et al., 1998, 2001; Beaugrand et al., 2002; Drinkwater et al., 2003; Reygondeau and Beaugrand, 2011). Therefore, since sandeels are unable to move northwards to track these changes in copepod size, they will progressively feed on smaller prey.

There are several lifecycle adaptations that sandeels could make to account for smaller prey abundances in spring. First, the duration of the foraging period could be extended. However, the current overwintering period duration is a result of a trade-off between growth and mortality (Van Deurs et al., 2010). Remaining longer in the water column,

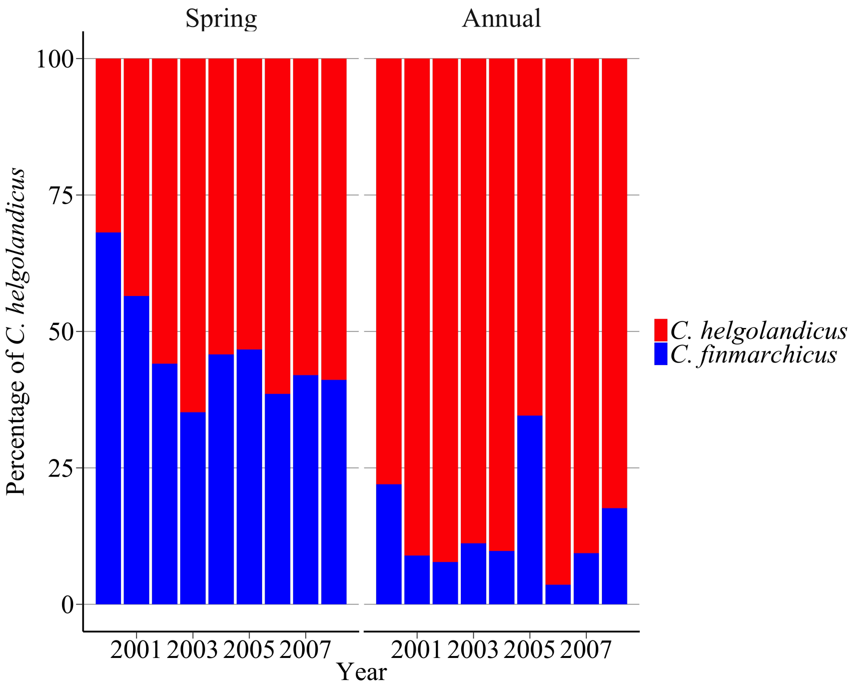


FIGURE 7.32: Relative percentage annual abundance of *C. finmarchicus* and *C. helgolandicus* off the Scottish east coast between 2000 and 2008. *C.helgolandicus* abundance was, on average, 5 times greater than *C.finmarchicus* abundance between 2000 and 2008.

where predation risk is higher than in the sediment, may therefore result in predation mortality that cannot be sustained.

7.8.5 Body size scaling

The body scaling exponent was estimated to be 0.645, which is within the common range of body scaling exponents found in fish (Clarke and Johnston, 1999). This is a similar scaling to Bay anchovy *Anchoa mitchilli* (0.65) (Jiangang Luo and Brandt, 1993) and Inland silverside *Menidia beryllina* (0.67) (Peck et al., 2003), which is likely not coincidental. These species share remarkably similar body shape and behaviour as sandeels, and both are probably stronger determinants of metabolic body scaling than taxonomic relationships (Clarke and Johnston, 1999). There is marked variation in the allometric scaling of forage fish metabolism, ranging from as low as 0.4 (Chizinski et al., 2008), to as high 1 (Karamushko and Christiansen, 2002; Meskendahl et al., 2010). Indeed, body scaling exponents for teleost species appear to lie within a range of 0.4 and 1 (Clarke and Johnston, 1999).

7.8.6 Energy allocation

The trade-off between allocating energy to reserves and structural growth has been largely overlooked in fish (Metcalfe et al., 2002). Sandeels require storage fat and protein to offset starvation risk and to fuel reproduction, respectively (Hislop et al., 1991; Robards et al., 1999). However, they also need to allocate energy towards growing structure. Predation mortality is generally large for small fish meaning selection may favour rapid growth to adult size (Calow and Townsend, 1981). Indeed, small sandeels appear to preferentially allocate energy to structural growth instead of lipid reserves (Robards et al., 1999). *A. hexapterus* appear to direct lipid reserves towards structural growth when between 5.5 and 8 cm. However, a dramatic change occurs around 8 cm. Lipid content, previously constant until this length, shows a marked rise. These changes suggest sandeels (Robards et al., 1999), in addition to many other fish species (Copeman et al., 2008; Kooka and Yamamura, 2012; Deegan, 1986; Luo et al., 2013; Post and Parkinson, 2001; Hurst and Conover, 2016; Biro et al., 2005), maximise energy allocation towards structural growth until a threshold size is reached.

Size-dependent starvation mortality can emerge from different energy allocation strategies employed by juvenile and adult fish. Juveniles use energy to grow rapidly to reduce predation pressure (Anthony et al., 2000). Some juvenile fish minimise predation by maintaining lipid levels just above the minimum required to survive, even though they are physiologically capable of allocating energy to reserves (Biro et al., 2005). Although this allocation strategy appears risky, it is employed during the feeding season, when the starvation risk is usually low. As winter approaches and food becomes scarce, young fish usually switch from preferentially allocating energy to structural growth to building energy reserves (Metcalfe et al., 2002; Hurst and Conover, 2016). However, some fish continue investing in structural growth before winter, possibly to minimise size-dependent predation (Hoeoek and Pothoven, 2009).

Since gonad size determines the amount of eggs produced, sandeels with larger reserves may have greater fecundity. This can account for variation in fecundity-at-length and fecundity-at-weight relationships (Boulcott and Wright, 2008, 2011). Figure 7.33 shows the regional and temporal variation in published fecundity-length relationships. Fecundity at the highest recorded length at maturation (~13 cm, Boulcott et al., 2007) shows considerable inter-annual and regional variation. For example, 13 cm animals in 2004 in the Firth of Forth produced approximately 3700 eggs, compared to 4400 in the Southern North Sea. Additionally, egg production of a 13 cm fish in the North-western North Sea was $\sim$ 50% higher than the same length class in 1999. It is possible that this variation reflects differences in animal condition; fatter fish at length invest more energy in gonad formation. Once the feeding season ends, the optimal strategy for these animals is to utilise energy in such a way to maximise egg production and ensure overwinter survival before the feeding season resumes.

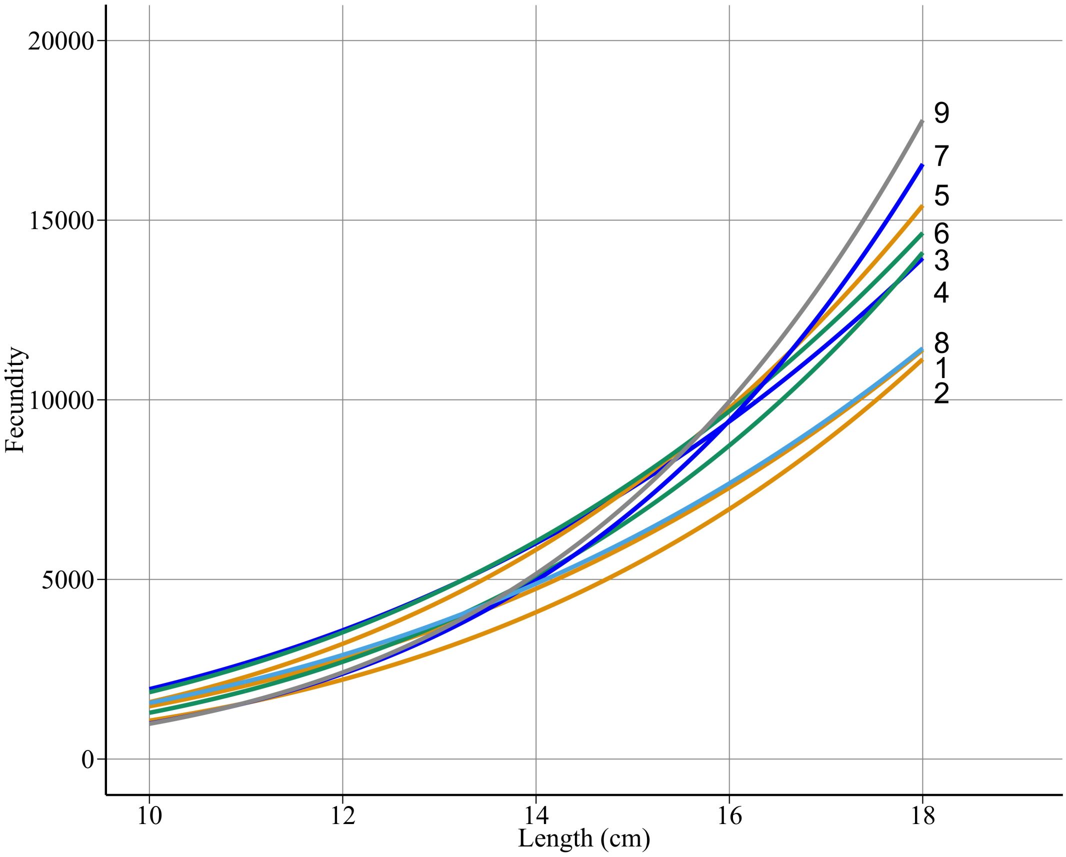


Figure 7.33: Temporal and spatial variation in *A. marinus* fecundity from experimental studies. Numbers represent the year and location: 1 Firth of Forth, 2004 (Boulcott and Wright, 2011); 2 Firth of Forth 1999 (Boulcott and Wright, 2011); 3 North-West Rough + Elbow Spit 2004 (Boulcott and Wright, 2011); 4 Fair Isle 1987 (Gauld and Hutcheon, 1990); 5 Moray Firth 1986 (Gauld and Hutcheon, 1990); 6 Shetland 1985 (Gauld and Hutcheon, 1990); 7 North-West Rough 2003 (Boulcott and Wright, 2011); 8 Norway Coast 1998 (Bergstad et al., 2001); 9 East central grounds 1998 (Bergstad et al., 2001).

Given the magnitude of energy expenditure into gonad formation it is possible that, in order to maximise fitness, sandeels may reproduce at the expense of mortality (Cole, 1954). It is unknown whether animals are semelparous (i.e. they spawn once before dying, e.g. capelin *Mallotus villosus*) or iteroparous animals (spawning multiple times during the lifecycle e.g. herring).

A further adaptation of the model could be the capability of reabsorbing gonad energy for maintenance purposes. This is a mechanism used by some fish to reduce starvation risk (Ma et al., 1998), and is a common assumption in DEB models (Kooijman, 2010). The process, which is the reabsorption of vitellogenic oocytes in the gonads, occurs when condition is poor and more energy is needed for somatic maintenance (Boulcott and Wright, 2011). This does happen in sandeels but it occurs at such low intensity that the effects are negligible. The implication is that fecundity does not decrease in response to condition.

Large spatial variation in age at maturity exists between populations. Since length is a strong determinant of maturity (Boulcott and Wright, 2011), differences in age-at-maturity reflect variation in growth rate. Hence, populations with high growth rates tend to mature at a younger age. Indeed, sandeels from the central North Sea, some of the largest and fastest-growing juveniles in the North Sea mature much earlier than sandeels elsewhere (Figure 7.34 ; Boulcott et al., 2007).

7.8.7 The importance of year-to-year changes in sandeel energy content for seabirds

Sandeel energy content at age varies markedly between years. For instance, seabirds feeding on 0-group sandeels in 2000 ingested almost 400% more energy per fish than in 2005 (Figure 7.25). Such extreme variation in prey energy content can negatively impact breeding success of single prey loading species (Wanless et al., 2005). This study is the first to provide a long-term account of variation in energy content. Energy content at age is likely to show pronounced spatial variation in addition to inter-annual variation. Large spatial differences in growth rate exist in the North Sea (Rindorf et al., 2016). By implication, the value of sandeel as prey to single-prey loaders will also show large spatial variation (Rindorf et al., 2016).

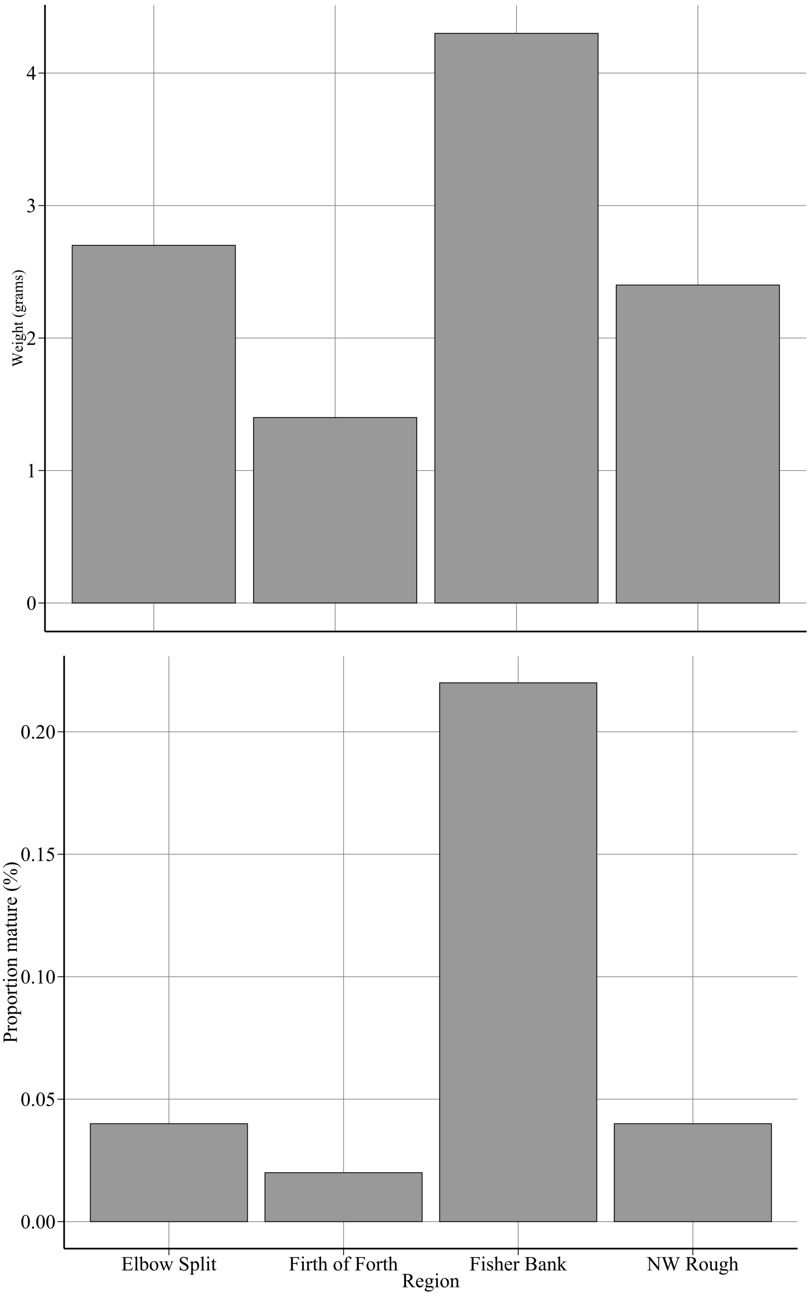


FIGURE 7.34: Mean weight and proportion mature at age 0 of sandeels from different regions (Boulcott et al., 2007). There is a low incidence of maturity at age 0 in the North Sea with the exception of individuals from Fisher Bank where over 20% mature in their first year.

7.8.8 Model caveats

Bioenergetic modelling often requires a number of assumptions to be made regarding species biology and lifecycle. This DEB model is no different in this respect. For example, a fixed overwintering end date and a condition and size dependent overwintering start date was assumed, body size and calendar day. This was based on the observation that variation in overwintering start dates appears to be substantially greater than variation in overwintering end dates (Reeves, 1994; Winslade, 1974).

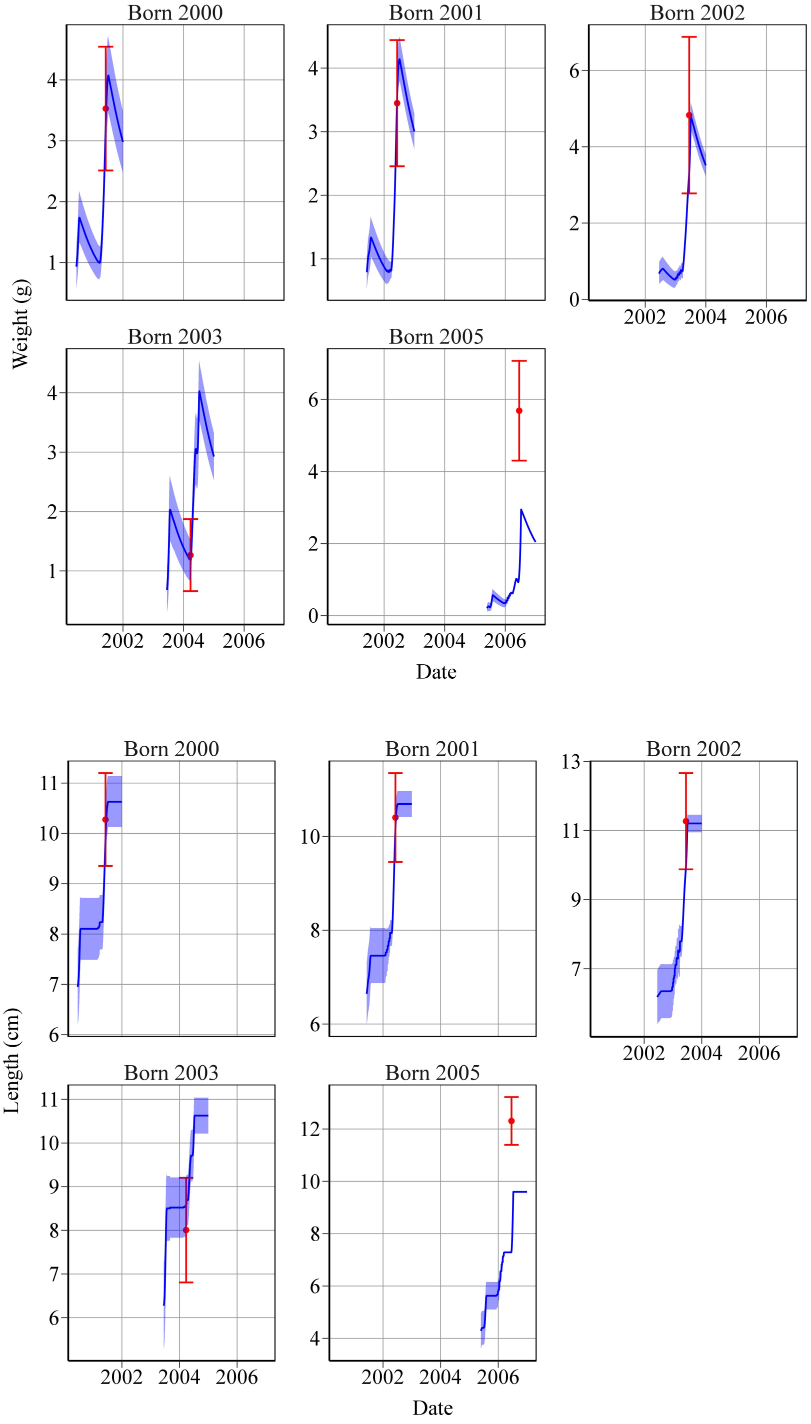


FIGURE 7.35: Modelled changes in weight and length (blue, mean ±1 s.d.) of 0-group sandeels in relation to observed length and weight of 1-group sandeels (red, mean ±1 s.d.).

Length and weight estimates of 0-group and 1-group sandeels were used as initial conditions for our model. The primary reason was that the dataset for 1-group sandeels was comparatively richer than the dataset for 0-group fish. However, if the model performs poorly at predicting length and weight at age 1, then including 1-group data as initial conditions is appropriate. Figure 7.35 shows the modelled changes in 0-group weight and length in relation to observed length and weight of 1-group sandeels the following year. Although the model performs well in predicting length and weight at age 1 for sandeels born in 2000, 2001, 2002 and 2003, it underestimates size for those born in 2005.

For model results to hold we must assume that density dependent effects on growth are negligible. Larger fish may supress growth of smaller fish by outcompeting them for prey, especially when population density is high. Further, the effect of density dependence can be exacerbated if small fish are common prey for larger fish. There are indications, however, that density dependent effects can be ignored for the purpose of the model. Density dependent effects should be limited to the egg and larval stages, while only post-metamorphic sandeels are modelled. There are two reasons why this should be true. First, cannibalism occurs primarily on medium size larvae, and declines for larger larvae (Ritzau Eigaard et al., 2014). Second, growth suppression of small fish by larger individuals is unlikely. Sandeels usually aggregate according to size (Johnsen et al., 2009; Jensen et al., 2011), therefore, conspecific food competition occurs between fish of similar size. This seems feasible since, for the most part, post-metamorphic 0-group sandeels are feeding when older sandeels have stopped feeding for winter.

Due to an absence of zooplankton abundance data from the Firth of Forth, a time series of weekly measurements of copepod concentration from another monitoring site was used. It is known that *C. finmarchicus* are transported into the North Sea from waters beyond the European shelf, so arrive later in Southern areas (Heath et al., 1999). The implication is that copepod phenology is earlier than it should be in the model. However, this effect is likely minimal due to the close proximity of the two monitoring sites. It was also assumed that copepod energy content remained fixed in time. Although large copepods show seasonal and inter-annual variation in energy content (Miller et al., 2000; McKinstry et al., 2013), this should not alter the results.

7.9 Appendix A. C code to fit model to survey data

```
/*
#=======================================#
     DEFINE CONSTANTS
#=======================================#
*/



/*~~~~~~~~~~~ Length structure scaling ~~~~~~~~~~~~*/


double LS_a  = 0.0002362601         ;            //   length-structure scale
double LS_b = 0.333333333333333333333;         //   length-structure exponent
double LS_c = 3 ;


double gam = 0.825 ;
double a =0.3709842767;
double b = 1.287 ;


/*~~~~~~~~~~~ Ash parameters ~~~~~~~~~~~~*/

double ashx = 0.4977837 ;
double ashy = 0.80780 ;


/*~~~~~~~~~~~ Energy density of fat and protein ~~~~~~~~~~~~*/

double Ef = 39.6 ;
double Ep = 23.7 ;


/*~~~~~~~~~~~ Energy density of structure  ~~~~~~~~~~~~*/

double Es = ( Ep + Ep*ashx - gam*Ep*ashy) ;
double Er = 27.98243 ;
double Eg = 23.7 ;


/*~~~~~~~~~~~ Dry to wet weight conversion factors ~~~~~~~~~~~~*/

double Gdw = 4.166667 ;
double Sdw = 1/(1 - gam)  ;

/*~~~~~~~~~~~ Ingestion ~~~~~~~~~~~~*/
```

```

double maxI = 3.696*0.0004359*( 1/ (LS_a*Es)); // maximum ingestion rate scale



/*~~~~~~~~~~~ Metabolism ~~~~~~~~~~~~*/


double M_OV = 0.01722;            //  overwinter metabolic rate scale
double M_FEED = 0.02025882 ;            //  feeding metabolic rate scale (have to multiply by activity multiplier)

double Q10_MF = 1.8 ;                    //  metabolism Q10
double Q10_MO = 1.46 ;                   //  metabolism Q10



/*~~~~~~~~~~~ Ingestion ~~~~~~~~~~~~*/
double H_U = 2;                                // hungry uptake scaling factor
double Q10_U = 1.72;                           // ingestion Q10



/*~~~~~~~~~~~ Energy density of small and large copepods ~~~~~~~~~~~~*/

double Elargecop = 5.6 ;
double Esmallcop = 3.2 ;




/* ~~~~ CHRONOLOGICALS ~~~~ */

#define NoDays 3210                        // total number of days in run

/* ~~~~ INDIVIDUALS  ~~~~ */

#define IndNum 949                         // total number of individuals to track

/* ~~~~ OBSERVED DATES  ~~~~ */

#define NumDates 14                           // total number of dates where we compare observed and modelled data

#define NumMeanLengths 83                     // number of rows in MEAN_WL

#define HalfNumMeanLengths 40                  // roughly number of rows in MEAN_WL divided by 2 (no rows in MEAN_WLO)
```

```

#define IndNumAllDates NumDates*IndNum      //  for DRUN, ABUNDANCE

#define NoParameters 14    // total number of parameters
```

CONSTANTS.h

```
/*
#=======================================#
     DEFINE FUNCTIONS
#=======================================#
*/



/*
#=======================================#
         STARVATION RESPONSE
#=======================================#
*/


double LAMBDA_F(float rho, float tau_1)
{
   return((rho>tau_1) + (rho<= tau_1)*H_U);
}

/*
#=======================================================#
 PROPORTION OF EXCESS ASSIMILATE DIRECTED TOWARDS LENGTH
#=======================================================#
*/

double k_0 ;
double StructuralAllocation ;


double kappa(  float rho, float S,  float rho_0,  float rho_w , float  S1 ,float S2)
{
k_0 = S1 -S2*log(S) ;
StructuralAllocation =  ((rho > (rho_0+rho_w) )*k_0 +  (rho <= (rho_0+rho_w) ) *(  k_0 * ( (rho> rho_0)*(rho-rho_0) ) /rho_w ) );
StructuralAllocation =   (StructuralAllocation>=1) + (StructuralAllocation>0)*(StructuralAllocation<1)*StructuralAllocation ;
return(StructuralAllocation) ;
}

```

```


/*
#==========================================================#
 DAILY PROPORTION OF RESERVES DIRECTED TOWARDS GONADS
#==========================================================#
*/



double GonadAllocation ;
double G_0 ;

double GONAD(  float rho,float  S,  float rho_0,   float rho_w ,  float G1 , float  G2)
{
  G_0 = G1 +G2*log(S) ;
GonadAllocation =  ((rho > (rho_0+rho_w) )*G_0 +  (rho <= (rho_0+rho_w) ) *( G_0 * ( (rho> rho_0)*(rho-rho_0) ) /rho_w ) );
GonadAllocation =   (GonadAllocation>=1) + (GonadAllocation>0)*(GonadAllocation<1)*GonadAllocation ;
return(GonadAllocation) ;
}
```

FUNCTIONS.h

```
/*
#========================================#
   FUNCTION TO MINIMISE MODEL ERROR
#========================================#
*/

#include <R.h>
#include <Rmath.h>


#include<stdio.h>
#include <stdlib.h>
#include <string.h>
#include <math.h>
#include <time.h>

#include "CONSTANTS.h"
#include "FUNCTIONS.h"




```

```


double MODEL_ERROR(double X[NoParameters] ,
       double TT_FEED[NoDays] , double TT_OV[NoDays] ,
       int JulianDayV[NoDays],
       double FL[NoDays] , double FS[NoDays],
       double DF_R[IndNum] ,double DF_S[IndNum], double DF_G[IndNum],
       int DF_STATE[IndNum] ,int DF_DATE_ADDED[IndNum], int DF_DATE_FINISH[IndNum] ,
       double DF_LENGTH[IndNum] , double DF_WEIGHT[IndNum]  , int DRUN[IndNumAllDates]  , int DATE_CHECK[NumDates]  ,
       double MEAN_WL_LENGTH[NumMeanLengths] , double MEAN_WL_WEIGHT[NumMeanLengths]  ,
       int MEAN_WL_DATE_ADDED[NumMeanLengths]  , int MEAN_WL_DRUN[NumMeanLengths] , double ABUNDANCE_DAILY[IndNum], int Age[IndNum], int AGE[IndNumAllDates],
       double FINAL_DATE_ADDED[IndNumAllDates], double FINAL_DATE_FINISH[IndNumAllDates], double ACT_MET[NoDays], double ACT_CONS[NoDays],
       double ProteinPROP[IndNum], double FatPROP[IndNum], double Rdw2[IndNum], double Er2[IndNum],
       double *result)
{





/*~~~~~~~~~~~ SET MODEL ERROR TO ZERO (LEAST SQUARE ERROR) ... ~~~~~~~~~~~*/





if(X[0] <= X[1]){*result = *result + 1E10 ; }  // parameter constraints
if(X[0] > X[1])  // parameter constraints
{



/*~~~~~~~~~~~ ENVIRONMENTAL DATA VECTORS ~~~~~~~~~~~~*/

double aL = X[0] ;
double aS = X[1] ;

double CopepodEnergyDensityV[NoDays]; // This is  (1/E)
    for( int i = 0; i < NoDays; i++)
```

```
        CopepodEnergyDensityV[i] =   (FL[i]*aL + FS[i]*aS) /(Elargecop* FL[i]*aL + Esmallcop*FS[i]*aS)    ;

double ConsumptionTerm1V[NoDays]; // This is  assimilation eff. * (U0/E)*Q10 * (aL Fl + aS Fs)
    for( int i = 0; i < NoDays; i++)
      ConsumptionTerm1V[i] =  ACT_CONS[i]*(0.8241 + 0.00764*TT_FEED[i])*(maxI*CopepodEnergyDensityV[i])* pow(Q10_U , TT_FEED[i] / 10 ) *( aL*FL[i] + aS*FS[i] ) ;

double ConsumptionTerm2V[NoDays]; // This is (U0/E)*Q10
    for( int i = 0; i < NoDays; i++)
        ConsumptionTerm2V[i] =  (maxI*CopepodEnergyDensityV[i])* pow(Q10_U , TT_FEED[i] / 10 ) ;

double ConsumptionTerm3V[NoDays]; // This is (aL Fl + aS Fs)
    for( int i = 0; i < NoDays; i++)
        ConsumptionTerm3V[i] =    ( (aL*FL[i])/Elargecop + (aS*FS[i])/Esmallcop ) ;

double METABOLISM_Q10_FEEDV[NoDays];
 for( int i = 0; i < NoDays; i++)
   METABOLISM_Q10_FEEDV[i] =  ACT_MET[i]*M_FEED*pow(Q10_MF , TT_FEED[i] / 10) ;

double METABOLISM_Q10_OVV[NoDays];
 for( int i = 0; i < NoDays; i++)
   METABOLISM_Q10_OVV[i] = M_OV*pow(Q10_MO , TT_OV[i] / 10 )  ;


double X3 = X[2], X4 = X[3]  , X5 = X[4], X6 = X[5] , X7 = X[6] ,  X8 = X[7] , X9 = X[8]  ,  X10 = X[9] , X11 = X[10] , X12 = X[11] , X13 = X[12] , X14 = X[13] ;





/*~~~~~~~~~~~ ADJUST RESERVE AND STRUCTURE ~~~~~~~~~~~~*/

for( int i = 0; i < IndNum; i++) // checked
   DF_S[i] =  Es*LS_a*pow(DF_LENGTH[i],LS_c) ;


for( int i = 0; i < IndNum; i++)  // checked
   DF_R[i] = Er*(((1-gam)*DF_WEIGHT[i] - (DF_S[i]/Es)) / (1-a*b)) ;


/*
```

```
#=======================================#
           MAIN LOOP
#=======================================#
*/


static double NET_A[IndNum*NoDays];
static double    dS[IndNum*NoDays];


int JulianDay  ;

double ConsumptionTerm1;
double ConsumptionTerm2;
double ConsumptionTerm3;


double METABOLISM_Q10_FEED  ;
double METABOLISM_Q10_OV;

double DF_R_RESULT[IndNumAllDates] ;
double DF_S_RESULT[IndNumAllDates] ;
double DF_G_RESULT[IndNumAllDates] ;
double Er2_RESULT[IndNumAllDates] ;
double Rdw2_RESULT[IndNumAllDates] ;


double ABUNDANCE_RESULT[IndNumAllDates] ;


int tracker ;
tracker = 0 ;




double Rmass = 0 ;

double dgdt ;

double Rdwold ;
double Gold ;
double Rold ;
double Erold ;
double ProteinReserve ;
double FatReserve ;


```

```
for( int t = 0; t < NoDays; t++)
{
  JulianDay =  JulianDayV[t];

  ConsumptionTerm1  = ConsumptionTerm1V[t] ;
  ConsumptionTerm2 =  ConsumptionTerm2V[t] ;
  ConsumptionTerm3 =  ConsumptionTerm3V[t] ;

  METABOLISM_Q10_FEED = METABOLISM_Q10_FEEDV[t];
  METABOLISM_Q10_OV = METABOLISM_Q10_OVV[t];



  for( int i = 0; i < IndNum; i++)
  {
    if(t >= DF_DATE_ADDED[i])
    {
      if( DF_STATE[i])
      {




  DF_STATE[i] = !(  ( (DF_R[i] / (DF_S[i])) > (X4 - JulianDay*X5)/pow(DF_S[i],X12)) && (JulianDay > 120)) ;  // overwintering entry



      }
      else
      {

  DF_STATE[i] =  (JulianDay == 92) ;  // overwintering exit

      }

    }

    if( (t >= DF_DATE_ADDED[i])*(JulianDay ==360)*(DF_STATE[i]) )  //forcing overwinter by late december (day 360)
    {
     DF_STATE[i] = 0;

    }



```

```
  NET_A[i+t*IndNum] = (DF_R[i] > 0) * ((DF_STATE[i]) * ((LAMBDA_F(DF_R[i] / (DF_S[i]), X3)*ConsumptionTerm1*DF_S[i]) / (LAMBDA_F(DF_R[i] / (DF_S[i]), X3)*ConsumptionTerm2*pow(DF_S[i],0.33)+ConsumptionTerm3)      )  -
                                   (  pow(DF_WEIGHT[i],.645) ) * ((!DF_STATE[i]) * METABOLISM_Q10_OV  + (DF_STATE[i]) * METABOLISM_Q10_FEED )) ;



          // Allocation towards structure


    dS[i+t*IndNum] =  (NET_A[i+t*IndNum] > 0) * (NET_A[i+t*IndNum] * kappa(DF_R[i]/(DF_S[i]),  DF_S[i],  X8 ,   X9 ,   X10, X11)) ;

    DF_S[i] =  DF_S[i] + dS[i+t*IndNum] * (t >=  DF_DATE_ADDED[i]) * (t <= DF_DATE_FINISH[i]) ;

    DF_R[i] = DF_R[i] + (t >= DF_DATE_ADDED[i]) * (t <= DF_DATE_FINISH[i]) * (NET_A[i+t*IndNum] -dS[i+t*IndNum] ) ;




  // Gonad production
  if( (JulianDay > 273 || JulianDay < 21 )*(t >= DF_DATE_ADDED[i]) * (t <= DF_DATE_FINISH[i]))
  {

    dgdt = (DF_R[i]*GONAD(  DF_R[i]/(DF_G[i]+DF_S[i]),  DF_S[i],  X8, X9,X13,X14)) ;



   //*** This is for mass and energy conservation
    if( Age[i] && dgdt >0 ){
      // Age 1+
Rdwold = Rdw2[i] ;
Gold = DF_G[i];
DF_G[i] = DF_G[i] + dgdt ;
Rold = DF_R[i] ;
Erold = Er2[i] ;
ProteinReserve = ProteinPROP[i]*DF_R[i]  - dgdt ;
FatReserve = FatPROP[i]*DF_R[i] ;
DF_R[i] = DF_R[i] - dgdt ;
FatPROP[i] = FatReserve/(ProteinReserve + FatReserve) ;
ProteinPROP[i] = 1-FatPROP[i] ;
```

```
 Er2[i] = FatPROP[i]*39.6 + ProteinPROP[i]*23.7 ;
 Rdw2[i] = (Rdwold*(Rold/Erold) + Gdw*(Gold/Eg) -
  Gdw*(DF_G[i]/Eg))*(Er2[i]/DF_R[i]) ;

   }
   if( !Age[i] && ( (t-300) > DF_DATE_ADDED[i] ) && dgdt >0){
 // Age 0
 Rdwold = Rdw2[i] ;
 Gold = DF_G[i];
 DF_G[i] = DF_G[i] + dgdt ;
 Rold = DF_R[i] ;
 Erold = Er2[i] ;
 ProteinReserve = ProteinPROP[i]*DF_R[i]  - dgdt ;
 FatReserve = FatPROP[i]*DF_R[i] ;
 DF_R[i] = DF_R[i] - dgdt ;
 FatPROP[i] = FatReserve/(ProteinReserve + FatReserve) ;
 ProteinPROP[i] = 1-FatPROP[i] ;
 Er2[i] = FatPROP[i]*39.6 + ProteinPROP[i]*23.7 ;
 Rdw2[i] = (Rdwold*(Rold/Erold) + Gdw*(Gold/Eg) -
  Gdw*(DF_G[i]/Eg))*(Er2[i]/DF_R[i]) ;

   }

  }

    // Spawning occurs on 21st January
  DF_G[i] = !(JulianDay ==21)*DF_G[i] ;

  DF_WEIGHT[i] = Rdw2[i]*(DF_R[i]/Er2[i] ) + Gdw*(DF_G[i]/Eg) +  Sdw*(DF_S[i]
  /Es) ;




      // Starvation mortality
   if(!DF_STATE[i]){
  if( (t >=  DF_DATE_ADDED[i])  && (t <=  DF_DATE_FINISH[i]) )
  {
   ABUNDANCE_DAILY[i] = ABUNDANCE_DAILY[i] /  (1+
  exp(-X6*(DF_R[i]/DF_S[i]-X7)))  ;  // SURVIVAL PROBABILITY

  }
}





```

```
// Store model results at each survey date
    if( ( t == DATE_CHECK[0] || t== DATE_CHECK[1] || t == DATE_CHECK[2] || t == DATE_CHECK[3] || t == DATE_CHECK[4] || t ==  DATE_CHECK[5] || t == DATE_CHECK[6] || t == DATE_CHECK[7] || t == DATE_CHECK[8] || t == DATE_CHECK[9] || t == DATE_CHECK[10] || t == DATE_CHECK[11]  || t == DATE_CHECK[12] || t ==  DATE_CHECK[13]) ) // messy but best option...
    {
      DF_R_RESULT[i + tracker*IndNum] = DF_R[i] ; // STORE RESERVES
      Er2_RESULT[i + tracker*IndNum] = Er2[i] ; // STORE RESERVES
      Rdw2_RESULT[i + tracker*IndNum] = Rdw2[i] ; // STORE RESERVES
      DF_S_RESULT[i + tracker*IndNum] = DF_S[i] ; // STORE STRUCTURE
      DF_G_RESULT[i + tracker*IndNum] = DF_G[i] ; // STORE GONAD


      ABUNDANCE_RESULT[i + tracker*IndNum] = ABUNDANCE_DAILY[i] ; // STORE ABUNDANCE



     if( i==IndNum - 1) // another IndNum individual reserves and structure added to RESULT
       tracker = tracker + 1 ;

    }

  }

} // end of main loop





 /*
#==========================================#
  Compute mean length and weight at survey
#==========================================#
*/

double ModelledReserves0[HalfNumMeanLengths] = { 0 };    // array of mean weights
double ModelledStructure0[HalfNumMeanLengths] = { 0 };    // array of mean weights
double ModelledWeight0[HalfNumMeanLengths] = { 0 };    // array of mean weights
double ModelledLength0[HalfNumMeanLengths] = { 0 }; // array of mean lengths

double ModelledDenominator0[HalfNumMeanLengths] = { 0 };


```

```
double ModelledReserves1[HalfNumMeanLengths+3] = { 0 };   // array of mean weights
double ModelledStructure1[HalfNumMeanLengths+3] = { 0 };   // array of mean weights
double ModelledWeight1[HalfNumMeanLengths+3] = { 0 };   // array of mean weights
double ModelledLength1[HalfNumMeanLengths+3] = { 0 }; // array of mean lengths

double ModelledDenominator1[HalfNumMeanLengths+3] = { 0 };





for( int i = 0; i < IndNumAllDates ; i++)
{



Rmass =DF_R_RESULT[i]/Er2_RESULT[i];


  if(FINAL_DATE_ADDED[i] <  DRUN[i] && FINAL_DATE_FINISH[i] >= DRUN[i] && DF_R_RESULT[i] > 0) // remove dead sandeels
    {
      for( int j = 0; j < (HalfNumMeanLengths) ; j++)
      {

  if(FINAL_DATE_ADDED[i] == MEAN_WL_DATE_ADDED[j] && DRUN[i] == MEAN_WL_DRUN[j] && !AGE[i])
  {

  ModelledReserves0[j] = ModelledReserves0[j] + ABUNDANCE_RESULT[i] *DF_R_RESULT[i] ;
  ModelledStructure0[j] = ModelledStructure0[j] + ABUNDANCE_RESULT[i] *DF_S_RESULT[i] ;

        ModelledWeight0[j] = ModelledWeight0[j] + ABUNDANCE_RESULT[i] * ( Rdw2_RESULT[i]*(Rmass) + Gdw*(DF_G_RESULT[i]/Eg) +  Sdw*(DF_S_RESULT[i] /Es)) ;
  ModelledLength0[j] = ModelledLength0[j] + ABUNDANCE_RESULT[i] *pow( DF_S_RESULT[i] / (LS_a*Es) , LS_b) ;
  ModelledDenominator0[j] = ModelledDenominator0[j] + ABUNDANCE_RESULT[i] ; // keep track of abundance so we can divide at end...

  }

      }

```

```
      for( int j = 0; j < (HalfNumMeanLengths+3) ; j++)
      {
  if(FINAL_DATE_ADDED[i] == MEAN_WL_DATE_ADDED[j+HalfNumMeanLengths] && DRUN[i] == MEAN_WL_DRUN[j+HalfNumMeanLengths] && AGE[i])
  {

  ModelledReserves1[j] = ModelledReserves1[j] + ABUNDANCE_RESULT[i]*DF_R_RESULT[i] ;
  ModelledStructure1[j] = ModelledStructure1[j] + ABUNDANCE_RESULT[i]*DF_S_RESULT[i] ;


  ModelledWeight1[j] = ModelledWeight1[j] + ABUNDANCE_RESULT[i] * (Rdw2_RESULT[i]*(Rmass) + Gdw*(DF_G_RESULT[i]/Eg) +  Sdw*(DF_S_RESULT[i]/Es)) ;
  ModelledLength1[j] = ModelledLength1[j] + ABUNDANCE_RESULT[i] *  pow(DF_S_RESULT[i] / (LS_a*Es) , LS_b) ;
  ModelledDenominator1[j] = ModelledDenominator1[j] + ABUNDANCE_RESULT[i] ; // keep track of abundance so we can divide at end...


  }
      }
    }
}





double ModelledWeight[NumMeanLengths] = { 0 };
double ModelledLength[NumMeanLengths] = { 0 };
double ModelledReserves[NumMeanLengths] = { 0 };
double ModelledStructure[NumMeanLengths] = { 0 };


double ModelledDenominator[NumMeanLengths] = { 0 };

  for( int i = 0; i < HalfNumMeanLengths ; i++)
  {
    ModelledWeight[i] = ModelledWeight0[i] ;
    ModelledLength[i] = ModelledLength0[i] ;
    ModelledReserves[i] = ModelledReserves0[i] ;
    ModelledStructure[i] = ModelledStructure0[i] ;

    ModelledDenominator[i] = ModelledDenominator0[i] ;
  }

```

```
  for( int i = 0; i < (HalfNumMeanLengths+3) ; i++)
  {
    ModelledWeight[i+HalfNumMeanLengths] = ModelledWeight1[i] ;
    ModelledLength[i+HalfNumMeanLengths] = ModelledLength1[i] ;
    ModelledReserves[i+HalfNumMeanLengths] = ModelledReserves1[i] ;
    ModelledStructure[i+HalfNumMeanLengths] = ModelledStructure1[i] ;

    ModelledDenominator[i+HalfNumMeanLengths] = ModelledDenominator1[i]    ;
  }



 /*
#==================================================================================#
   Finally, compute difference between observed and modelled length and weight
    ...
#==================================================================================#
*/


// FIT WEIGHT , LENGTH , RESERVE RATIO


double modelledSenergy = 0 , realSenergy = 0 , modelledRenergy = 0, realRenergy
    = 0 ,  modelledRS = 0 ,  realRS= 0  ;




// Age 1 data given x times weight of age 0


if( *result ==0)
{
  for( int i = 0; i < HalfNumMeanLengths ; i++)
  {




      // for age 0

    modelledSenergy = ModelledStructure[i]/ModelledDenominator[i] ;
    realSenergy  =    LS_a*Es*pow(MEAN_WL_LENGTH[i], LS_c) ;

    modelledRenergy = ModelledReserves[i]/ModelledDenominator[i] ;

    realRenergy = Er*(((1-gam)*MEAN_WL_WEIGHT[i] - (realSenergy/Es)) / (1-a*b)) ;
```

```

    modelledRS =modelledRenergy / modelledSenergy ;

    realRS = realRenergy / realSenergy ;







            *result = *result +
          1*((modelledRS - realRS)/realRS)*((modelledRS - realRS)/realRS) +  // LEAST SQUARES FOR RS
        1*((MEAN_WL_LENGTH[i] - ModelledLength[i]/ModelledDenominator[i])/MEAN_WL_LENGTH[i]  )*   ( (MEAN_WL_LENGTH[i] - ModelledLength[i]/ModelledDenominator[i])/MEAN_WL_LENGTH[i] ) + // LEAST SQUARES FOR LENGTH
      1*( (MEAN_WL_WEIGHT[i] - ModelledWeight[i]/ModelledDenominator[i])/MEAN_WL_WEIGHT[i]  ) *( (MEAN_WL_WEIGHT[i] - ModelledWeight[i]/ModelledDenominator[i])/MEAN_WL_WEIGHT[i]  ) ; // LEAST SQUARES FOR WEIGHT





  }



    for( int i = HalfNumMeanLengths; i < NumMeanLengths ; i++)
    {

  // for age 1

    modelledSenergy = ModelledStructure[i]/ModelledDenominator[i] ;
    realSenergy  =    LS_a*Es*pow(MEAN_WL_LENGTH[i], LS_c) ;

    modelledRenergy = ModelledReserves[i]/ModelledDenominator[i] ;


    realRenergy = Er*(((1-gam)*MEAN_WL_WEIGHT[i] - (realSenergy/Es)) / (1-a*b)) ;



    modelledRS =modelledRenergy / modelledSenergy ;
```

```

    realRS = realRenergy / realSenergy ;




      *result = *result +
      1*((modelledRS - realRS) /realRS)*((modelledRS - realRS)/realRS) +  // LEAST SQUARES FOR RS
      1*((MEAN_WL_LENGTH[i] - ModelledLength[i]/ModelledDenominator[i])/MEAN_WL_LENGTH[i]  )*   ( (MEAN_WL_LENGTH[i] - ModelledLength[i]/ModelledDenominator[i])/MEAN_WL_LENGTH[i] ) + // LEAST SQUARES FOR LENGTH
      1*( (MEAN_WL_WEIGHT[i] - ModelledWeight[i]/ModelledDenominator[i])/MEAN_WL_WEIGHT[i]  ) *( (MEAN_WL_WEIGHT[i] - ModelledWeight[i]/ModelledDenominator[i])/MEAN_WL_WEIGHT[i]  ) ; // LEAST SQUARES FOR WEIGHT



    }
}




}




return( *result) ;

}
```

Model.c

```
################################################################################################
#~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~  DEB MODEL ~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~#
################################################################################################


# SET WORKING DIRECTORY

rm(list = ls())
```

```

if (as.data.frame(Sys.info()["sysname"]) == "Linux")
  DBdir <- ("/home/qrb12181/Dropbox") else
  DBdir <- ("/Users/Alan/Dropbox")
setwd(paste0(DBdir, "/PhD/DEBmodel5"))

#~~~~~~~~ NOTES ~~~~~~~~#

# day 169 means 169 days on from 1/1/2000

#~~~~~~~~~~~ REQUIRED PACKAGES ~~~~~~~~~~#

library(GenSA)
library(plyr)
library(dplyr)
library(geosphere)

#~~~~~~~~ READ IN TEMPERATURE DATA ~~~~~~~~#

# surface temperature
TT_FEED <- read.csv("Temperature/TT_FEED.csv")
TT_FEED$jd = rep(1:365, 11)
TT_FEED = TT_FEED[534:(534 + 3209), 4]

# seabed temperature
TT_OV <- read.csv("Temperature/TT_OV.csv")
TT_OV$jd = rep(1:365, 11)
TT_OV = TT_OV[534:(534 + 3209), 3]

#~~~~~~~~ READ IN TIME DATA ~~~~~~~~#

JulianDayV <-
  read.table("IndividualData/JulianDay.txt",
             quote = "\"",
             comment.char = "")[, 1]
JulianDayV = c(JulianDayV, c(231:365), c(1:93))

#~~~~~~~~ READ IN FOOD DATA ~~~~~~~~#

# large copepods
FL <- read.csv("Food/SmoothInterpolation/FL_smooth.txt")[, 2] * 1E-3
FL = FL[1:3210]

# small copepods
FS <- read.csv("Food/SmoothInterpolation/FS_smooth.txt")[, 2] * 1E-3
FS = FS[1:3210]

#~~~~~~~~ READ IN SANDEEL INDIVIDUALS DATA ~~~~~~~~#
```

```

# individuals are overwintering (0) or feeding (1), age 1
DF_STATE1 <-
  read.table("IndividualData/DF_STATE.txt",
             quote = "\"",
             comment.char = "")[, 1]

# individuals are overwintering (0) or feeding (1), age 0
DF_STATE0 <- read.table("Age0Stuff/DF_STATE0.txt", quote = "\"")[, 1]

# times when age 1 sandeels are added to model
DF_DATE_ADDED1 <-
  read.table("IndividualData/DF_DATE_ADDED.txt",
             quote = "\"",
             comment.char = "")[, 1]

# final times when age 1 sandeels are modelled
DF_DATE_FINISH1 = 3210

# initial lengths of age 1 sandeels
DF_LENGTH1 <-
  read.table("IndividualData/DF_LENGTH.txt",
             quote = "\"",
             comment.char = "")[, 1]

# initial weights of age 1 sandeels
DF_WEIGHT1 <-
  read.table("IndividualData/DF_WEIGHT.txt",
             quote = "\"",
             comment.char = "")[, 1]

DRUN1 <-
  read.table("IndividualData/DRUN.txt",
             quote = "\"",
             comment.char = "")[, 1]

DATE_CHECK1 <-
  read.table("IndividualData/DATE_CHECK.txt",
             quote = "\"",
             comment.char = "")[, 1]

# initial abundance of age 1 sandeels
ABUNDANCE1 <-
  read.table("IndividualData/ABUNDANCE.txt",
             quote = "\"",
             comment.char = "")[, 1]

# times when age 0 sandeels are added to model
```

```
DF_DATE_ADDED0 <-
  read.table("Age0Stuff/DF_DATE_ADDED0.txt", quote = "\"")[, 1]

# final times when age 0 sandeels are modelled
DF_DATE_FINISH0 <- 3210

# initial lengths of age 0 sandeels
DF_LENGTH0 <-
  read.table("Age0Stuff/DF_LENGTH0.txt", quote = "\"")[, 1]

# initial weights of age 0 sandeels
DF_WEIGHT0 <-
  read.table("Age0Stuff/DF_WEIGHT0.txt", quote = "\"")[, 1]

DRUN0 <- read.table("Age0Stuff/DRUN0.txt", quote = "\"")[, 1]

DATE_CHECK0 <-
  read.table("Age0Stuff/DATE_CHECK0.txt", quote = "\"")[, 1]

# initial abundance of age 0 sandeels
ABUNDANCE0 <-
  read.table("Age0Stuff/ABUNDANCE0.txt", quote = "\"")[, 1]

#~~~~~~~~ FITTING DATA ~~~~~~~~#

# mean lengths of age 1 sandeels at different survey dates
MEAN_WL_LENGTH1 <-
  read.table("IndividualData/MEAN_WL_LENGTH.txt",
             quote = "\"",
             comment.char = "")[, 1]

# mean weights of age 1 sandeels at different survey dates
MEAN_WL_WEIGHT1 <-
  read.table("IndividualData/MEAN_WL_WEIGHT.txt",
             quote = "\"",
             comment.char = "")[, 1]

MEAN_WL_DATE_ADDED1 <-
  read.table(
    "IndividualData/MEAN_WL_DATE_ADDED.txt",
    quote = "\"",
    comment.char = ""
  )[, 1]

MEAN_WL_DRUN1 <-
  read.table("IndividualData/MEAN_WL_DRUN.txt",
             quote = "\"",
             comment.char = "")[, 1]
```

```

ABUNDANCE_DAILY1 <- ABUNDANCE1[1:740]

# mean lengths of age 0 sandeels at different survey dates
MEAN_WL_LENGTH0 <-
  read.table("Age0Stuff/MEAN_WL_LENGTH0.txt", quote = "\"")[, 1]

# mean weights of age 0 sandeels at different survey dates
MEAN_WL_WEIGHT0 <-
  read.table("Age0Stuff/MEAN_WL_WEIGHT0.txt", quote = "\"")[, 1]

MEAN_WL_DATE_ADDED0 <-
  read.table("Age0Stuff/MEAN_WL_DATE_ADDED0.txt", quote = "\"")[, 1]

MEAN_WL_DRUN0 <-
  read.table("Age0Stuff/MEAN_WL_DRUN0.txt", quote = "\"")[, 1]

ABUNDANCE_DAILY0 <- ABUNDANCE0[1:209]

#~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~#
#~~~~~~~ Now combine age 0 and 1 data ~~~~~~~#
#~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~#

DF_STATE <- c(DF_STATE0, DF_STATE1)

DF_DATE_ADDED <- c(DF_DATE_ADDED0, DF_DATE_ADDED1)
DF_FINAL_DATE_ADDED = rep(DF_DATE_ADDED, 14)
DF_DATE_FINISH <- c(DF_DATE_FINISH0, DF_DATE_FINISH1)
DF_FINAL_DATE_FINISH = rep(DF_DATE_FINISH, 14)
DF_LENGTH <- c(DF_LENGTH0, DF_LENGTH1)
DF_WEIGHT <- c(DF_WEIGHT0, DF_WEIGHT1)

DATE_CHECK <- c(DATE_CHECK0, DATE_CHECK1)
DATE_CHECK = sort(unique(DATE_CHECK))

DRUN <- c(DRUN0, DRUN1)
DRUN = rep(DATE_CHECK, each = 949)

ABUNDANCE <- c(ABUNDANCE0, ABUNDANCE1)

MEAN_WL_LENGTH <- c(MEAN_WL_LENGTH0, MEAN_WL_LENGTH1)
MEAN_WL_WEIGHT <- c(MEAN_WL_WEIGHT0, MEAN_WL_WEIGHT1)
MEAN_WL_DATE_ADDED <- c(MEAN_WL_DATE_ADDED0, MEAN_WL_DATE_ADDED1)
MEAN_WL_DRUN <- c(MEAN_WL_DRUN0, MEAN_WL_DRUN1)
MEAN_AGE = c(rep(0, 40), rep(1, 43))
ABUNDANCE_DAILY <- c(ABUNDANCE_DAILY0, ABUNDANCE_DAILY1)

Age <- c(rep(0, 209), rep(1, 740))
```

```

AGE = rep(Age, 14)

#~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~#
#~~~~~~~ ACTIVITY MULTIPLIERS ~~~~~~~#
#~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~#

# hours of daylight
hrs.daylight = daylength(lat = 56.25, JulianDayV)

# activity multiplier
ACT.MET = 1 + (1 / 24) * hrs.daylight

# fraction of day spent feeding
ACT.CONS = hrs.daylight / 24


#~~~~~~~~~~~ ADJUST RESERVE AND STRUCTURE ~~~~~~~~~~~#

a = 0.3709842767
alpha = 0.0002362601

# length-structure exponent
Length_structure_exponent = 3
gamma = 0.825
b =  1.287
Ef = 39.6 # energy density of fat
Ep = 23.7 # energy density of protein

ashx = 0.4977837
ashy = 0.80780

DF_Sdryweight = alpha * DF_LENGTH ^ Length_structure_exponent # structural dry weight



DF_Rdryweight = ((1 - gamma) * DF_WEIGHT - DF_Sdryweight) / (1 - a * b) # reserve dry weight

ReserveEnergy = DF_Rdryweight * (Ef * a + Ep * (1 - a) + Ep * ashx - Ep *
                                   gamma * ashy + (Ep * ashy * a * b * (DF_Rdryweight + DF_Sdryweight)) / DF_WEIGHT) # reserve energy

StructuralEnergy = DF_Sdryweight * (Ep + Ep * ashx - gamma * Ep * ashy) # structural energy

DF_R = ReserveEnergy # reserve energy
```

```

DF_S = StructuralEnergy # structural energy

DF_G = rep(0, length(DF_R)) # gonad energy

# to conserve sandeel mass we must track energy densities...

ProteinPROP = rep(1 - a, length(DF_R))

FatPROP = rep(a, length(DF_R))

Rdw = rep(((1 - a * b) / (1 - gamma)) , length(DF_R))

Er = rep(27.98243, length(DF_R))

X =  ((1 - a * b) / (1 - gamma))
Y =  (1 / (1 - gamma))

A = Ef * a + Ep * (1 - a) + Ep * ashx - Ep * gamma * ashy
B = Ep * ashy * a * b

W = X * DF_Rdryweight + Y * DF_Sdryweight

ReserveEnergy = (1 / W) * ((A * X + B) * DF_Rdryweight ^ 2 + (A * Y + B) *
    DF_Rdryweight * DF_Sdryweight)



#~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~#
#~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~ BOUNDS ~~~~~~~~~~~~~~~~~~~~~~~~~~~#
#~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~#

ci <- c(
  0,-30, # aL
  0,-30, # aS
  0,-3.5, # tau
  20,-40 , # OVTHRESH 1
  0.01, -0.2, # OVTHRESH 2
  0,-2000, # sigma 1
  0, -1.5, # sigma 2
  0, -4, # rho_01
  0, -1000, # rho_w1
  0, -50, # S_1
  0, -50, # S_2
  0.1, -0.8,# OVthresh 3
  -40, -40, # G_1
  0, -40 # G_2
  )
```

```

# lower bound
lb <-
  c(ci[1] , ci[3], ci[5] , ci[7] , ci[9] , ci[11] , ci[13], ci[15] ,
    ci[17], ci[19], ci[21], ci[23], ci[25], ci[27])

# upper bound
ub <- -c(ci[2] , ci[4], ci[6] , ci[8] , ci[10] , ci[12] , ci[14],
          ci[16] , ci[18], ci[20], ci[22], ci[24], ci[26] , ci[28])

#~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
#~~~~~~~~~~~~~~~~~~~~~~~~ FUNCTION TO CALL C CODE 'MODEL.c' TO COMPUTE MODEL
    ERROR ~~~~~~~~~~~~~~~~~~~~~~~~#
#~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~

A = function(X)
{
  {
    RunModel =  .C(
      "MODEL_ERROR",
      as.double(X) ,
      as.double(TT_FEED) ,
      as.double(TT_OV),
      as.integer(JulianDayV),
      as.double(FL),
      as.double(FS) ,
      as.double(DF_R),
      as.double(DF_S) ,
      as.double(DF_G),
      as.integer(DF_STATE) ,
      as.integer(DF_DATE_ADDED),
      as.integer(DF_DATE_FINISH) ,
      as.double(DF_LENGTH) ,
      as.double(DF_WEIGHT)  ,
      as.integer(DRUN)  ,
      as.integer(DATE_CHECK)  ,
      as.double(MEAN_WL_LENGTH) ,
      as.double(MEAN_WL_WEIGHT)  ,
      as.integer(MEAN_WL_DATE_ADDED)  ,
      as.integer(MEAN_WL_DRUN) ,
      as.double(ABUNDANCE_DAILY),
      as.integer(Age),
      as.integer(AGE),
      as.double(DF_FINAL_DATE_ADDED),
      as.double(DF_FINAL_DATE_FINISH),
      as.double(ACT.MET),
      as.double(ACT.CONS),
      as.double(ProteinPROP),
```

```
      as.double(FatPROP),
      as.double(Rdw),
      as.double(Er),
      result = double(length(1))
    )
  }
  RunModel[["result"]]
}

#~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
#~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~ SIMUALTED ANNEALING FUNCTION
    ~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~#
#~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~

# choose random parameters
no.para = 14
X = vector(length = no.para)
index = 1
for (para in 1:no.para)
{
  X[para] = runif(1, ci[index], -ci[index + 1])
  index = index  + 2
}

SANNr = function()
{
  RunSANN <-
    GenSA(
      par = X,
      lower = lb,
      upper = ub,
      fn = A,
      control = list(maxit = 1e8, temperature = Temp)
    )
  print(RunSANN)
}
```

ParameterisationLatex.R

Chapter 8

Discussion

8.1 The sandeel stock decline off the Scottish east coast

In the beginning of this thesis potential factors which may have contributed to a decline in sandeels were highlighted (Table 1.1 in Chapter 1). We return to this table with the aim of highlighting the most likely factors (Table 8.1).

TABLE 8.1: Potential factors which can lead to a reduction in sandeel abundance.

Factor	Reasons	Likelihood	Paper
Declining fecundity	Reduction in energy stores required for reproduction	Low	Wright et al. (2017)
Increasing overwinter mortality	Elevated metabolism due to temperature,	Low	This work
	insufficient energy reserves due to poor food availability in summer	High	This work
Increasing juvenile mortality	Predation, lack of food	High	This work
Egg mortality	Temperature, predation	Further research required	
Larval mortality	Predation, poor food availability	Low	Heath et al. (2012)
Changes in larval drift patterns e.g. being swept to unsuitable areas.	Hydrodynamic changes	Low	Christensen et al. (2008)

The original hypothesis was that temperature driven increases in overwinter mortality was the cause of the sandeel stock decline. Consequent work demonstrated that this hypothesis was half true. Instead, the conclusion is that food-driven overwinter starvation of 0-group sandeels was a major contributor of the decline. In other words, it is not the increase in metabolic costs associated with increased temperature, which uses up sandeel energy reserves faster, that casuses the overwinter mortality, it is the fact that these reserves are smaller because of the poorer feeding conditions. Notably, the dynamic energy model hindcasts almost 100% overwinter mortality for the 2005 cohort, corresponding to the time period when 0-group mortality was highest (Figure 7.15, page 122). Abundance-at-age estimates showed that of those born in 2005, only 0.04% survived. For comparison, the second highest incidence of 0-group mortality occured in 2001/02 when 13% survived. Analysis showed that modelled starvation mortality was primarily influenced by food, not temperature.

Many of the results in this thesis point to the conclusion that recent year-to-year variations in food have had a considerably larger impact on sandeels than temperature. For instance, by showing that spawning and hatch dates were relatively fixed between 2000 and 2009, and robust to recent changes in temperature, the cause of declining post-metamorphic 0-group length was narrowed down to changes in differential larval mortality or growth rate. However, there are several reasons why declines in larval growth rate appear more likely than larval mortality. First, the survival of young larvae increased between 2000 and 2009 (Heath et al., 2012). Second, one would expect to observe a reduction in 0-group abundance if larval mortality increased, especially given that sandeel spawning stock biomass declined, but this was not the case. Further, a significant relationship was found between post-metamorphic 0-group length and larval growth rate between 2000 and 2002.

Results demonstrate that current temperature effects on sandeels are secondary in importance to observed changes in their copepod prey. This is consistent with the lack of evidence of negative effects of rising temperature on fish physiology in UK waters (Heath et al., 2012). This could explain why sandeel populations in areas that have undergone most warming have not declined. For instance, the southern north sea (Area 1 and 2) and Kattegat (Area 6) have warmed the most since the 1970s, and yet sandeel stocks in these areas have fared better than stocks in northern areas (Figure 8.1). Mean temperature in Area 4 (the Scottish east coast) between 2000—2013 was 0.58^oC higher than in 1980—1999, with only sandeel populations north of 59^o showing less warming.

The direct effect of temperature is unlikely to negatively impact sandeel size, and possibly physiology. It is possible that climate warming effects on physiology can be ignored completely. According to the dynamic energy budget model, a 3^oC rise alone will have a slight effect on length and weight. By inference, energy content will not change markedly.

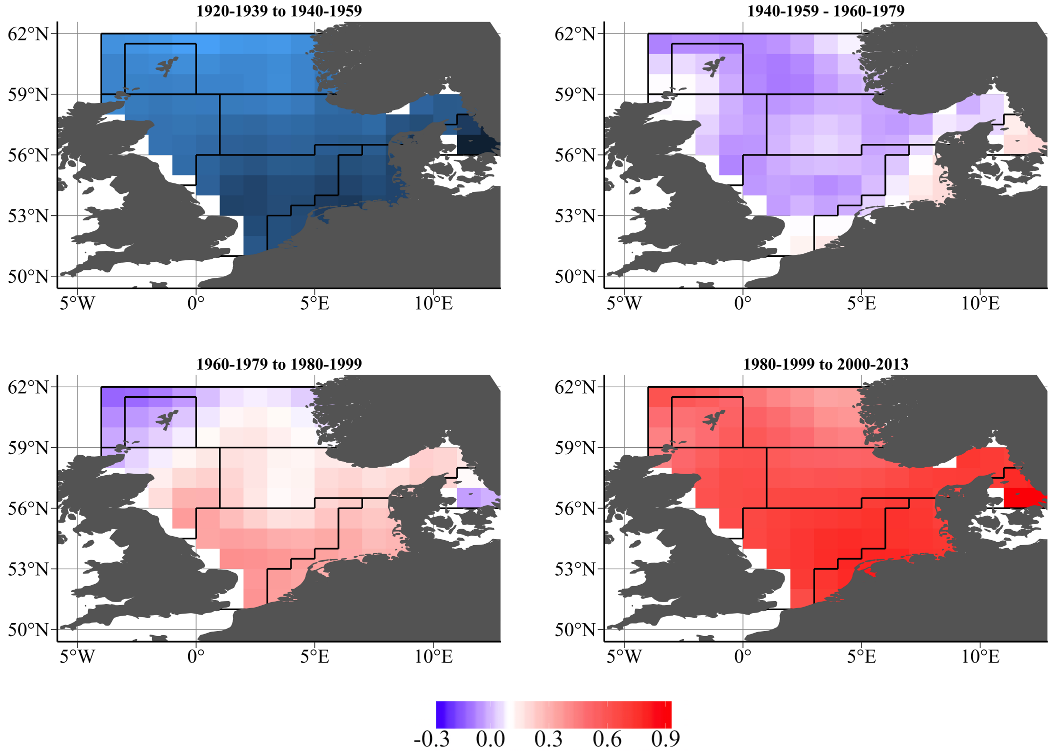


FIGURE 8.1: Changes in sea surface temperature in the North Sea between 1940 and 2013. Temperature data from the Met Office Hadley Centre's sea ice and sea surface temperature (SST) data set, HadISST1.

This is consistent with recent experimental work which showed that *A.marinus* somatic energy content will not be significantly affected by future temperature rises (Wright et al., 2017a).

Recent labortatory studies do, however, suggest a negative effect of temperature on *A.marinus* reproduction (Wright et al., 2017a,b). For example, a 5^oC temperature rise will diminish reproductive energy and delay spawning by more than two months, increasing the possibility of a mismatch between larval emergence and food availability (Wright et al., 2017a,b). In contrast, if the contribution of a hatch cue is ignored, the egg development relationship in equation 4.3, chapter 4 implies that mean hatch duration would only decrease by approximately 20 days under a 5^oC temperature rise. Therefore, a 5^oC temperature rise would delay hatching by at least a month. However, these experimental studies provide precautionary estimates of temperature effects on physiology, since temperature projections forecast temperature rises of less than 3^o C in the northern North Sea by the end of this century (Dye et al., 2013). Moreover, such laboratory studies do not account for gradual adaptations to temperature.

Dynamic energy budget model results (Chapter 7) indicates that year-to-year changes in growth and mortality reflect changes in copepod biomass concentration. This is diagnostic of a bottom-up trophic cascade effect on sandeel (Heath et al., 2014). Evidence of bottom-up limitation by phytoplankton (Frederiksen et al., 2006; Eliasen et al., 2011) and zooplankton (Frederiksen et al., 2006) on sandeels has been demonstrated before. Frederiksen et al. (2006) showed that North Sea larval biomass was related to phytoplankton and zooplankton abundance during their feeding period. On the Faroe shelf, a link has been established between juvenile sandeel abundance and length and primary production (Eliasen et al., 2011). Certainly, it appears that spatial variation in sandeel productivity mirrors regional differences in copepod abundance (Heath et al., 2012; OBrien et al., 2013). For instance, Fransz et al. (1991) found that the spring bloom in the Firth of Forth was shorter than elsewhere in the North Sea, potentially limiting the foraging window of copepods. Also, copepods off the Scottish east coast are typically less abundant than in central and southern areas (Edwards et al., 2010).

While the importance of direct temperature effects on sandeel population dynamics cannot be conclusively ruled out, this work is not the first to suggest they are negligible. Studies investigating the relative influence of direct and indirect factors on larval abundance have found weak temperature effects, but significant food effects (Pitois et al., 2012). This relative influence of food and temperature on physiology is also apparent in a study on larval *A. americanus* mortality (Buckley et al., 1984). *A. americanus* survival is highly sensitive to variation in prey abundance but insensitive to variation in temperature (Buckley et al., 1984).

8.2 Other potential contributing factors to sandeel stock decline

8.2.1 Changes in predator abundance

The cause of the sandeel stock decline on the Scottish east coast was addressed by considering only direct physiological and lifecycle changes to the sandeel. The central conclusion is that food, not temperature, is the dominant driver of physiology. Climate warming appears to affect sandeels through negative effects on lower trophic levels. Low copepod abundance can severely limit energy and growth, causing substantial overwinter size-dependent mortality. The role of predation mortality was not analysed, and this is undoubtedly an important driver of stock dynamics.

Cod, haddock and whiting consume a high percentage of sandeels in their diets, and could potentially reduce the sandeel stock (Greenstreet et al., 1998; Hislop, 1997). Sandeels consumed by piscivorous fish are primarily juveniles, while older sandeels, which are less abundant and important in the context of the stock, are less likely to be targeted. While mortality by piscivorous fish cannot be definitively ruled out as the cause of the stock decline, there has been no significant increase in the abundance of these fish off the Firth of Forth (Greenstreet et al., 2010).

Few studies have been carried out on fish predation on sandeels, even though this is the dominant source of predation mortality. Removals of sandeels and pelagic fish by fish predators are far higher than the combined removals by fisheries and other marine predators (Heath et al., 2009). For example, between 1983 and 1986, the annual consumption of pelagic fish and sandeels by piscivorous fish was 7.4 million tonnes, compared to less than 2 million tonnes for seabirds, marine mammals and the fisheries combined (Heath et al., 2009). The fact that sandeel abundance was depressed by the fishery that operated off the Scottish east coast suggests fish predators may have a similar negative effect. For example, if haddock biomass were to reach three times the level seen in 1997 as a result of stricter stock management, then the amount of sandeels this species would consume between May and June would be roughly 36,000 tonnes off the Firth of Forth (Reilly et al., 2014). Average landings in this area at the height of the Danish sandeel fishery (1991-1998) are only slightly above this, amounting to 47,550 tonnes. Clearly, more work is required to quantify the effect of predation on sandeel population dynamics.

Sandeel abundance may be supressed by changes in forage fish. In contrast to large piscivorous fish which predominately prey upon the post-larval stages (Greenstreet et al., 1998), forage fish are more likely to consume eggs and larvae. The intensity of interspecific egg predation in pelagic fish can be remarkably high (Szeinfeld, 1991; Bachiller et al., 2015). For example, in the Bay of Biscay, sardines *Sardina pilchardus* alone account for up to 33% of total egg predation on anchovy *Engraulis encrasicolus* (Bachiller et al., 2015). However, there has been no significant increase in a single forage fish species off the Scottish east coast.

Since the turn of the century, the sandeel predator mackerel (Engelhard et al., 2008) has increased markedly in abundance on the scale of the North Sea. During the 1960s, a significant decline in mackerel spawning biomass was proposed as contributing to an increase in sandeels, apparently due to less food competition or predation (Jones, 1983). Since 2000, there has been a reversal in the trajectories of these species; sandeel spawning stock biomass has declined while mackerel spawning stock biomass has increased (Figure 8.2).

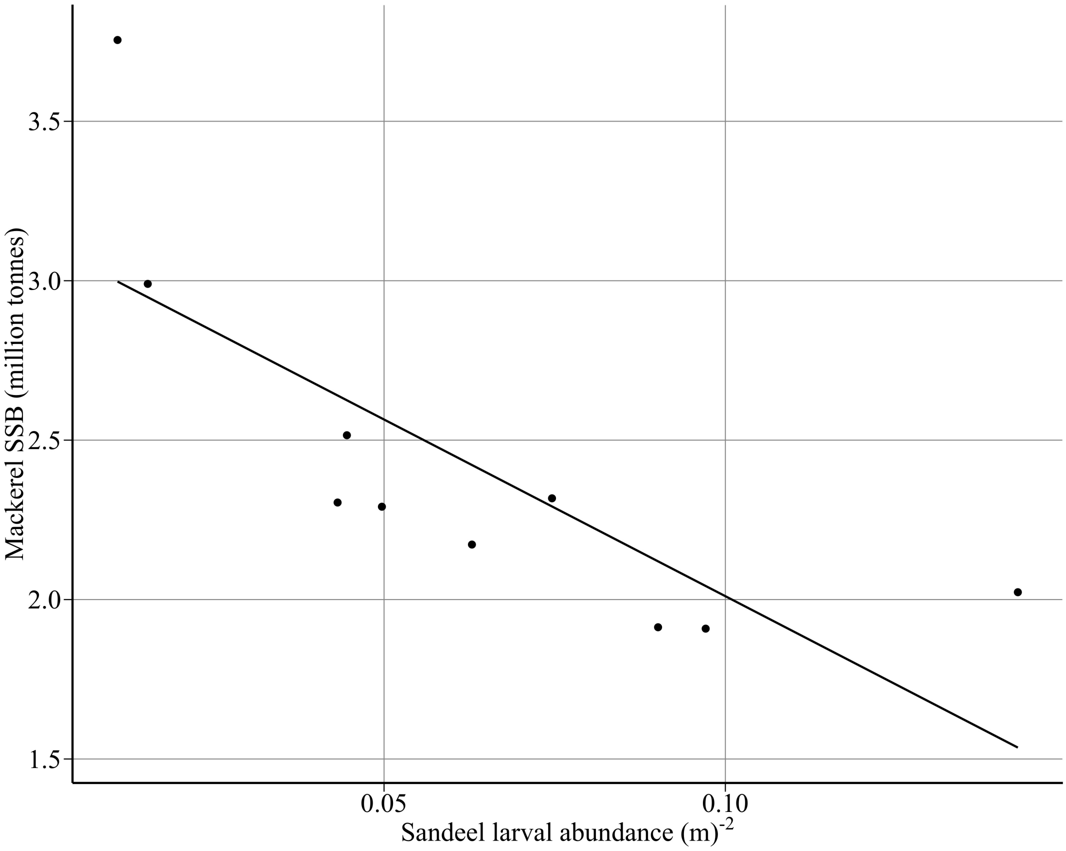


FIGURE 8.2: Statistically significant relationship between sandeel larval abundance and mackerel spawning stock biomass (SSB) between 2000 and 2009 ($p< 0.01$,$R^2 = 0.56$). The relationship suggests a possible top-down predation effect on sandeel abundance by mackerel. The black points represent observed data and the black line represents the best linear model fitted to data. Mackerel SSB taken from Jansen (2016).

There is a precedent to climate driven increases in pelagic fish predators. An example is North Pacific pink salmon *Oncorhynchus gorbuscha*, which have increased in recent decades due to rising temperature (Springer and van Vliet, 2014). Through food competition and predation, these fish appear to have caused a reduction in pelagic fish (Springer and van Vliet, 2014).

Other pelagic fish are known to exert a negative influence on sandeels. When abundant, herring supress sandeel abundance through predation on larvae (Frederiksen et al., 2007). However, there is one reason why the sandeel decline is unlikely to have resulted from herring predation. The decrease in sandeel abundance is matched by a concurrent decline in herring recruitment (Figures 8.3 and 8.4).

Cannibalism has been proposed as the driver of the post 2000s decrease in herring recruitment (Corten, 2013). Sandeels are highly cannibalistic and represent a large proportion of total larval mortality (Yamada et al., 1998; Ritzau Eigaard et al., 2014). This may explain why the usually positive relationship between spawning stock biomass (SSB) and recruitment is offset in years of high 1+ group abundance (Arnott and Ruxton, 2002; van Deurs et al., 2009). A similar situation exists in Japanese waters, where *A. personatus* may be responsible for over a third of larval mortality (Yamada et al., 1998). In addition to consuming larval conspecifics, adults may also cannibalise eggs. Evidence suggests that larval cannibalism was not responsible for the sandeel stock decline. Sandeel larval survival in Scottish waters has increased in the past decade suggesting the effect of cannibalism on larvae is negligible (Ritzau Eigaard et al., 2014). However, the intensity of egg cannibalism is unknown, and this could be important. Juveniles that approach the end of winter (January—April) in poor condition may be more likely to consume eggs. This provides a mechanism by which low copepod availability in summer could not only decrease survival of overwintering juveniles, but also reduce the following year class.

8.2.2 Decreasing oxygen concentrations in the sediment

Future climate change is expected to substantially reduce dissolved oxygen concentration (Bopp et al., 2013). Exposure to low 0_2 levels raises activity and overwintering fish may leave the sediment, increasing the possibility of predation. An increase in predation may also occur because low 0_2 levels force fish to raise their head above the sediment in order to respire properly, making them more visible to predators (Behrens et al., 2010). In Danish waters, $\sim$ 10% of suitable habitat are affected by oxygen deficiency during an average year.

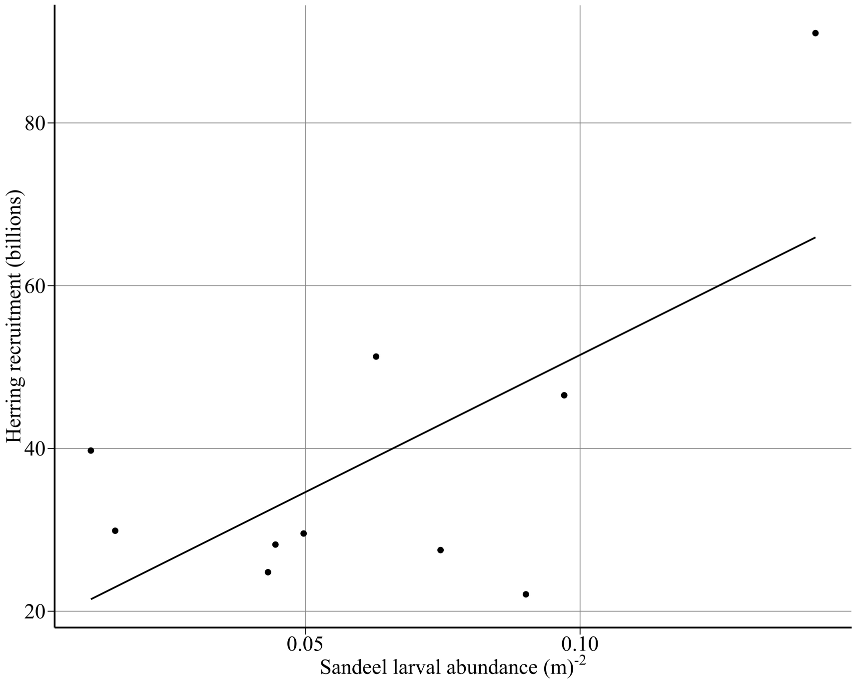


Figure 8.3: Statistically significant relationship between sandeel larval abundance and herring recruitment between 2000 and 2009 ($p< 0.05$,$R^2 = 0.353$). The relationship suggests a common environmental factor is affecting herring recruitment and sandeel larval abundance. Herring recruitment data was taken from ICES (2014).

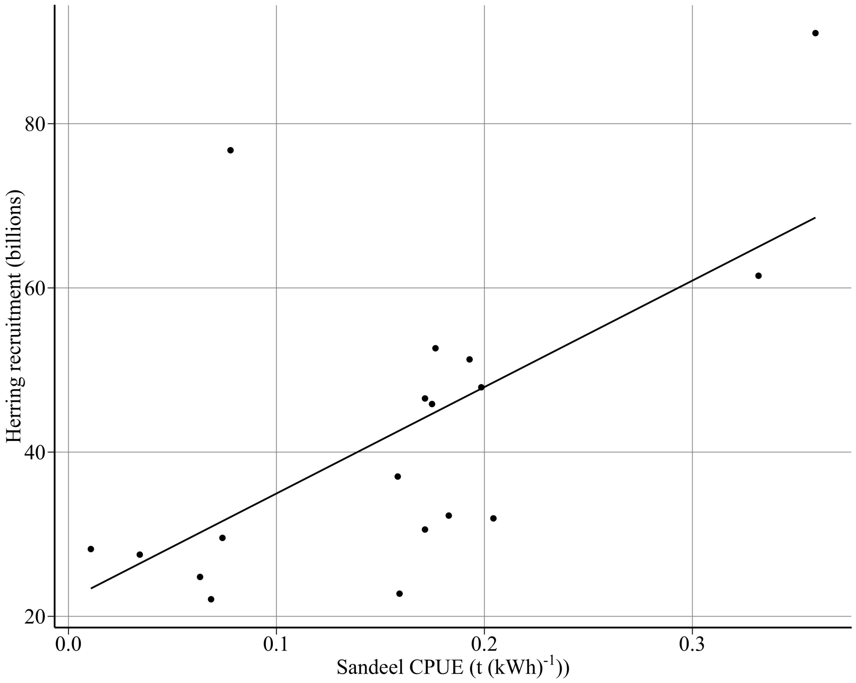


Figure 8.4: Relationship between sandeel catch per unit effort (CPUE) and herring recruitment. CPUE and herring recruitment were significantly related ($p<0.01$,$R^2 = 0.35$). No relationship was apparent when the sandeel fishery was active between 1990 and 1999 ($p<0.935$, $R^2 = 0.124$). However, a strong relationship was apparent during the period when the fishery was not operational ($p < 0.0001$, $R^2 = 0.928$).

8.3 Future changes in the North Sea ecosystem

It is unclear whether other species can fill the void left by sandeels. Within the North Sea pelagic community, sprat, herring, sandeels, and Norway pout *Trisopterus esmarki* are likely functionally interchangeable (Heath, 2005). Hence, any one of these species is suitable for transferring energy up the food web, although each may differ in terms of suitability as seabird prey.

Projected future rises in temperature are expected to cause a northward shift in distribution patterns for many fish species (Lenoir et al., 2011; Chen et al., 2011), and dramatically alter the forage fish community composition. Polewards shifts in distribution will lead to decreases in abundance at the southern edge of the geographic range of a species and increases at the northern edge. Temperature-associated species-level changes in abundance that may be accounted for in this way have been identified in 39 of 50 of the most common fish species in the North Sea (Simpson et al., 2011). Catches of warm-water species such as European anchovy *Engraulis encrasicolus* and sardine *Sardina pilchardus* all increased in the North Sea, coinciding with increased temperatures after 1995 (Solomon, 2007). Moreover, statistical modelling shows a northwards distribution movement for Atlantic horse mackerel *Trachurus trachurus*, European anchovy, European sprat *Sprattus sprattus*, pollack *Pollachius pollachius*, common sole *Solea solea*, saithe *Pollachius virens*, and turbot *Scophthalmus maximus* between the 1960s and the period 2000—2005 (Lenoir et al., 2011). Northwards movements in the geographical range of these species, with the exception of pollack, are predicted to increase substantially under changes in SST projected by the IPCC (Intergovernmental Panel on Climate Change) (Solomon, 2007). Some fish species now inhabit areas where they were absent prior to the 1980s. Examples include anchovy and sardine (Beare et al., 2004), striped red mullet (Beare et al., 2005), and bluemouth *Helicolenus dactylopterus* (Mamie et al., 2007). Warm-water species such as anchovies may replace sandeels in future (Lenoir et al., 2011), and there are signs that this is already happening. In the aftermath of the North Sea regime shift, the abundance and distribution of sprat expanded rapidly (ICES, Álvarez Fernandez et al., 2012).

Temperature changes can drive the replacement of one forage fish by another. As a consequence of a regime shift from a cool to warm phase in the 1970s, the Pacific anchovy was gradually replaced by the sardine (Chavez et al., 2003). However, while new species will occupy the ecological niche of a sandeel, they might not be sufficient in quality and abundance during seabird breeding season. The sandeel lifecycle appears to facilitate seabird breeding success and survival.

Breeding season of sandeel specialist seabirds coincides with the time of year when young sandeels begin feeding in the pelagic zone (Lewis et al., 2001) During this time, no other fish species are both high in lipid and protein content and hugely abundant. 0-group sandeels are unique in this respect. Regime shifts in shelf ecosystems usually have a profound effect on the population dynamics of the fish community. In particular, pelagic and demersal species display marked differences in population trajectories (Litzow et al., 2006). This is likely driven by changes in prey necessary for lipid accumulation, which fuels growth and reproduction of many pelagic species. In the 1980s the North Sea underwent a regime shift characterised by a sudden large change in plankton community composition (Beaugrand, 2004). Since then, sandeel size-at-age has decreased on the scale of the North Sea (van Deurs et al., 2014; Wanless et al., 2004).

8.4 The need for more empirical data on *A. marinus*

Due to a lack of empirical data on *A.marinus* we had to rely on experimental data on closely related species. This decision is justified by similarilty in length-weight relationships of sandeel species (Figure 8.5, Table 8.2).

Future work should focus on how sandeel ingestion rate responds to food, the functional response. Previous work provides evidence that sandeels ingestion rate is strongly dependent on prey size (van Deurs et al., 2014). This response can only be accurately determined from field data. This is because it is difficult to fully recreate the conditions experienced by a sandeel under laboratory setting. Sampling of sandeel stomach content, zooplankton size and concentration are necessary to formulate a functional response.

There is marked variation in physiological responses to temperature between sandeel species. For instance, *A. tobianus* metabolism is approximately 2 times more sensitive to temperature than *A. hexapterus* (Quinn and Schneider, 1991; van Deurs et al., 2011). However, we note that the metabolic response to temperature in *A. tobianus* is inconsistent with other pelagic fish. Further, the Q10 for metabolism found for *A. hexapterus* is far more common in pelagic fish, and teleost species in general (Clarke and Johnston, 1999). Clearly, future modelling of *A. marinus* metabolism would benefit from a species specific laboratory study in this area.

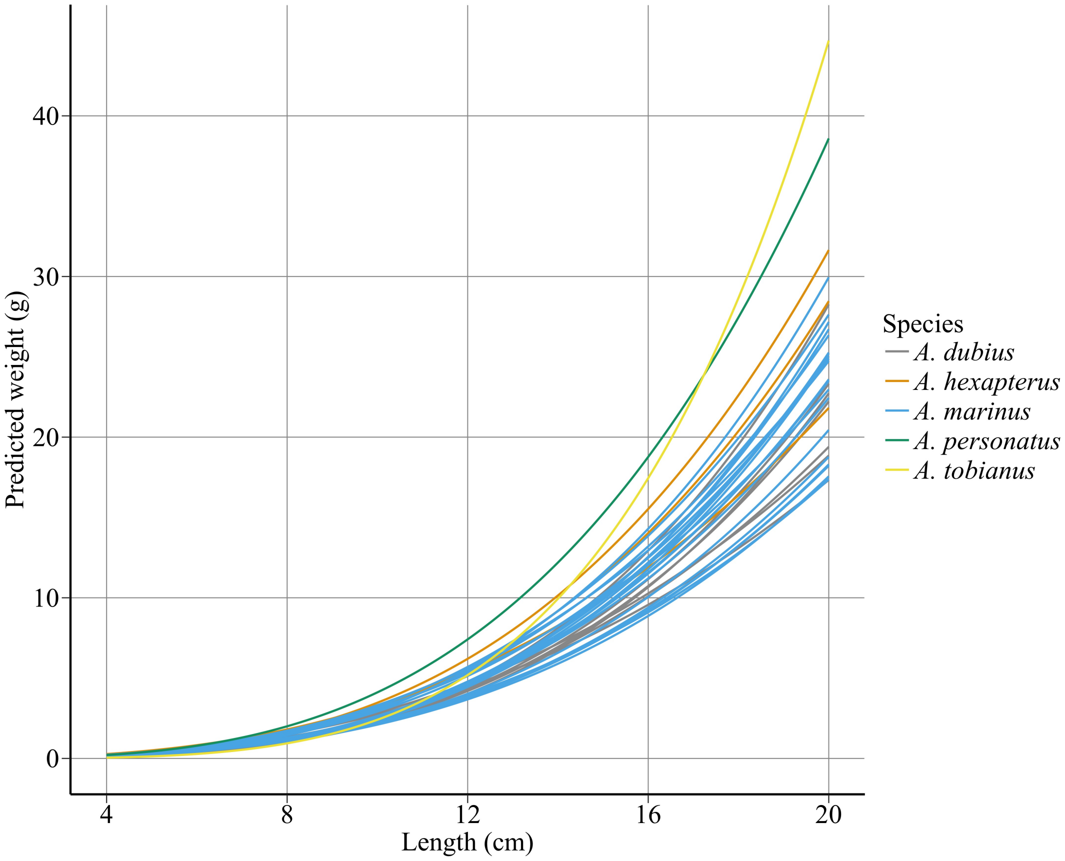


FIGURE 8.5: Length-weight relationships for *A. dubius*, *A. hexapterus*, *A. marinus*, *A. personatus* and *A.tobianus* of the form $W = aL^b$. Values for a and b are given in Table 8.2.

More information is needed on maturation drivers. The model assumes maturity at age 1 which was based on the observation that 2% and 79% of east coast sandeels mature at age 0 and 1 (Boulcott et al., 2007).

8.5 Closing thoughts

It is expected that two thirds of the global fish supply will be provided by fish farming by 2030 (World Bank, 2013). This is primarily because of the emerging market in China, which is likely to account for 57% of the global aquaculture industry at this time. This will place more strain on stocks of small pelagic fish, which form the bulk of the aquaculture catch (FAO, 1999).

Landings in the North Sea have shifted from large piscivourous fish to smaller invertabrates and planktivourous fishes over the last century. In the 1950s, the main target species were young herring and mackerel, however, after these stocks collapsed, Norway pout and sandeels were primarily targeted (Furness, 2000). 'Fishing down the food web' has been linked with a reduction in fish landings in numerous ecosystems, possibly due to negative food web effects arising from intensive fishing of small pelagic fish (Pauly et al., 1998). For example, excessive landings of Norway pout *Trisopterus esmarkii* could be damaging for two reasons. First, they are vital prey for important commercial fish such as cod, and second, they exert predation control on krill, which in turn consume copepods, the preferred prey of small pelagic fish and gadoid larvae (Pauly et al., 1998). The North Sea may be sensitive to fishery-driven food web effects due to its wasp-waist structure i.e. there are relatively few species capable of transferring zooplankton energy onto higher trophic levels (Fauchald et al., 2011).

The 1980s regime shift which was characterised by dramatic changes in fish and plankton distributions, abundance and community composition is well documented (Beaugrand, 2004; Beaugrand and Ibanez, 2004; Beaugrand et al., 2009; Lenoir et al., 2011). Less documented is the apparent regime shift that took place between 1998—2000 (Edwards et al., 2007; Álvarez Fernandez et al., 2012). During this time, changes in the plankton community were characterised by an increased dominance of warm-water copepods (Edwards et al., 2007). Prior to this regime shift, average sandeel biomass was double the level it currently stands (Christensen et al., 2013). Interestingly, this shift also coincided with a decrease in herring larvae survival (Payne et al., 2009).

Elucidating bottom-up climate impacts on pelagic fish is challenging and may require development of complex process-based models incorporating all lower trophic levels - nutrients, phytoplankton, zooplankton and pelagic fish. Coupling existing process-based zooplankton mathematical models (Banas et al., 2016; Wilson, 2015; Wilson et al., 2016) with models of pelagic fish (van Deurs et al., 2015, this thesis) would provide a suitable framework to analyse climate impacts.

TABLE 8.2: Length-weight relationships for *A. dubius*, *A. hexapterus*, *A. marinus*, *A. personatus* and *tobianus* of the form $W = aL^b$.

Species	a (g cm^{-b})	b	Month	Year	Location	5 cm	10 cm	15 cm	20 cm	Source
A. dubius	0.00542	2.72	—		Gulf of Maine	0.43	2.86	8.62	18.85	Nelson and Ross (1991)
	0.003	2.93	—	—	Georges bank (spring)	0.33	2.55	8.35	19.40	
	0.00088	3.39	—	—	Georges bank (summer)	0.21	2.17	8.57	22.72	
	0.00127	3.26	—	—	Georges bank (autumn)	0.24	2.32	8.69	22.22	
	0.00593	2.66	—	—	Southern New England (spring)	0.43	2.74	8.06	17.34	
	0.00118	3.30	—	—	Middle Atlantic (spring)	0.24	2.37	9.02	23.32	
	0.00079	3.50	—	—	Middle Atlantic (autumn)	0.22	2.49	10.32	28.26	
A. hexapterus	0.00214	3.17	June	—	Alaska	0.35	3.16	11.43	28.46	Robards et al. (1999)
	0.00224	3.19	August	—		0.38	3.47	12.64	31.64	
	0.00631	2.72	October	—		0.50	3.31	9.98	21.82	
A. marinus	0.00263	3.09	June	2000	Firth of Forth	0.38	3.24	11.35	27.63	This work
	0.00188	3.07	March	2001		0.26	2.19	7.57	18.29	
	0.00416	2.90	June	2001		0.44	3.31	10.74	24.74	
	0.00086	3.46	October	2001		0.22	2.47	10.04	27.17	
	0.00183	3.06	March	2002		0.25	2.11	7.28	17.56	
	0.00146	3.31	June	2002		0.30	3.01	11.54	29.95	
	0.00106	3.38	October	2002		0.25	2.56	10.09	26.71	
	0.00173	3.10	March	2003		0.25	2.19	7.69	18.77	
	0.00247	3.10	June	2003		0.36	3.08	10.81	26.35	
	0.00148	3.25	October	2003		0.28	2.65	9.89	25.20	
	0.002	3.04	March	2004		0.27	2.21	7.59	18.22	
	0.00174	3.17	September	2004		0.29	2.60	9.43	23.51	
	0.001	3.38	November	2010		0.23	2.40	9.46	25.03	
	0.00295	2.90	March	2011		0.31	2.33	7.55	17.37	
	0.0042	2.87	—	—	Shetland	0.43	3.14	10.05	22.97	Baistrocchi (2003)
	0.0012	3.32	—	—	SpeyBay	0.25	2.52	9.71	25.26	
	0.00149	3.18	April	2007	Faroe Islands	0.25	2.25	8.19	20.45	Eliasen (2013)
	0.00238	3.09		2008		0.34	2.92	10.23	24.89	
	0.00154	3.22		2009		0.27	2.54	9.35	23.60	
	0.00177	3.09		2010		0.25	2.16	7.53	18.30	
A. personatus	0.00242	3.23	—	—	Ise Bay	0.44	4.11	15.24	38.59	Tomiyama and Yanagibashi (2004)
A. tobianus	0.00015	4.21	—	—	Laboratory	0.13	2.41	13.30	44.69	

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