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**The Effects of Changes in Climate and Food Supply on the
Timing of Reproduction in Great Skuas (*Stercorarius skua*)
and Arctic Skuas (*Stercorarius parasiticus*)**

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University of Glasgow, MVLS 2010/2011

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Introduction: Biomonitoring and Marine Ecosystems

For much of history, marine ecosystems have remained unexplored and largely unmonitored, in spite of their importance as a source of food and other natural services such as nutrient cycling, due to their large size and inaccessibility relative to terrestrial ecosystems (Safina 1997). Because of this, monitoring changes in ecological health can prove difficult, even in important commercial fisheries (Safina 1997, Watson *et al.* 2005). One way to gather ecological information is to use one species as a proxy—termed a biomonitor. Ideally this species is a wide-ranging predator, which can provide information about the health of lower trophic levels (Tataruch and Kierdorf 2003). Even without the challenge of monitoring organisms that dwell out of visual range, ocean ecosystems are larger than their terrestrial counterparts, making it more difficult to locate study species, let alone study their interactions. Because of this vast size, marine ecosystems have often been regarded as inexhaustible resources, especially for fish extraction. However, the radical decline in worldwide fish stocks has prompted more interest in management, which necessitates monitoring of the marine food web (De Jonge *et al.* 2006, Safina 1997, Watson *et al.* 2005).

One way to accomplish this is to use individual species, termed *bioindicators* or *biomonitors*, to assess the health of the ecosystem as a whole. A variety of small marine species have been used, including invertebrates such as barnacles, crustaceans and bivalves (Rainbow 2002). Tataruch and Kierdorf (2003) note, however, that carnivores, particularly highly motile species with large home ranges, provide a broader view of their ecosystem, as their success can be indicative of events in lower trophic levels.

Seabirds as Biomonitors

The Shetland Island breeding populations of Great Skua (*Stercorarius skua*) and Arctic Skua (*Stercorarius parasiticus*) provide an accessible set of widely foraging predators, with several decades of data on their ecology and behavior (Hamer *et al.* 1991, Furness and Camphuysen 1997).

Seabirds present several advantages as bellweathers of ocean and fishery health, including relatively easy access for researchers, sensitivity to environmental changes, longevity, and status as piscivorous marine predators (Hamer *et al.* 1991, Mallory 2006, Mallory *et al.* 2006). Springer *et al.* (1996) further conclude that some seabirds can also provide indications of the benthic ecosystem structure, as many species feed preferentially in particular ecosystems, which allows avian species distribution to serve as a proxy for benthic ecosystem types.

Many of these seabird species nest at predictable times and locations, returning repeatedly to the same site, making the task of tagging offspring and monitoring the survival rate of adults relatively straightforward. Colonial nesting behavior makes nests relatively easy to locate, and allows a single expedition to mark and monitor a large number of individual birds. Furthermore, data on bird populations, migration and breeding have been recorded both by professional scientists and by the public, and kept for many decades, allowing retrospective investigations of many seabird colonies (Furness and Camphuysen 1997).

Seabirds, like other predators, have proven sensitive to environmental pollutants, such as mercury, and blood or tissue samples collected from them can provide a good indication of chemical levels in the ecosystem at large, both long and short-term (Goodale *et al.* 2009, Thompson *et al.* 1998). Seabirds are also highly sensitive to changes in the food supply (Frederiksen *et al.* 2002, Frederiksen *et al.* 2004, Hamer *et al.* 1991, Le Corre and Jaquemet

2005, Mallory 2006, Mallory *et al.* 2006). In many species, breeding success—and in some cases adult survival—is closely tied to the availability of food during that season (Frederiksen *et al.* 2004, Furness 2007, LeCorre and Jaquemet 2000, Mallory 2006, Phillips *et al.* 1997). Study of a Black-legged Kittiwake (*Rissa tridactyla*) colony in Newfoundland revealed a close relationship between food availability and breeding success in a given season, which has been observed in other larid species (Regehr and Montevecchi 1997).

Skuas and other larids also offer another source of information about their food supply in the form of cast pellets. Collection and dissection of pellets can reveal the content of the birds' diets and in what proportions different food types are consumed. As pellets are cast each day, dietary information can be monitored over the course of a season (Votier *et al.* 2003, Votier *et al.* 2004). The Great Skua and Arctic Skua populations in the Shetland Islands have been monitored since the 1970s, and can provide information about the North Sea fish stocks on which they feed during the nesting season. This long data set, combined with the aforementioned advantages of studying larid species, makes the Shetland Island skuas suitable biomonitor species.

Seabird Phenology as Biomonitor

The effects of low food availability Great and Arctic Skua populations in Shetland have already been studied, and decreased fishery biomass is known to decrease both the number of nesting pairs and the number of chicks raised per pair by the remaining birds (Phillips *et al.*

1997). Part of the decrease in numbers of breeding pairs during these years may be due partially to lowered adult survival in years with limited food supply (Cam *et al.* 1998), and partially to less experienced birds choosing not to attempt nesting (Catry *et al.* 1998, Davis *et al.* 2005).

Although the effects of food supply on seabird breeding success and adult survival has been widely studied, there is little known about the effect of food supply and climate change on the timing of breeding in seabirds. Climate change in terrestrial systems has been shown to advance the date of breeding for songbirds, with some species breeding up to thirteen days before their previous average laying date, as breeding date is mediated at least in part by ambient temperature and climate-related cues (Butler 2003). In seabirds, by contrast, breeding date appears to be mediated by food resources (Perrins 1996, Meijer and Drent 1999). However, studies of Black-legged Kittiwakes, European Shags, and Common Guillemots by Frederiksen *et al.* (2004) found evidence of nesting pattern in these seabird colonies similar to that of terrestrial species, where higher sea surface temperatures correlated with earlier laying dates. However, there was no evidence as to the underlying mechanism. Furthermore, the climate systems which showed correlations with breeding patterns varied between species, indicating that foraging and migratory ranges were a factor in this effect (Frederiksen *et al.* 2004). Examination of long-term trends in Great Skua phenology may give insight into these mechanisms as they act on the Shetland and Southern North Sea ecosystem.

To gain a more complete understanding of the interaction between marine predators and ecological disturbances, particularly anthropogenic climate change, it is important to examine the ecology of lower trophic levels. In the southern North Sea, the preferred food fish for breeding skuas is the sand eel *Ammodytes marinus* (Votier *et al.* 2004). The recruitment success of sand

eels, in turn, depends on the number and species composition of North Sea plankton populations (Arnott and Ruxton 2002).

This paper will examine the relationship between marine predators and disruptions of the Shetland and North Sea fishery due to anthropogenic climate change. The first chapter will give an overview of localized climate patterns in Shetland and the wider ocean areas, with some original analysis of raw climate data from the region. Climate models specific area will be used to determine if statistically significant trends in ocean temperature exist in the southern North Sea outside of the normal cyclic climate patterns known as the North Atlantic Oscillation and the Arctic Oscillation. Winter sea surface temperature will be used throughout as a proxy for climate variation, as this is more stable an indicator than air temperature, and more relevant to the life cycles of pelagic organisms. Confirming the presence of climate change in the study area is necessary to posit a causal link between climate change and alterations in the region's ecosystem.

The Shetland plankton community is the topic of the second chapter, with statistical analysis of relationships between plankton types and climate change, as well as interactions within the plankton community. The first focus of the chapter is to determine if a significant relationship exists between variation in climate and the life cycle of phytoplankton, specifically diatoms, which are the most abundant species. The second is to determine the nature of the relationship, if any, between diatom life cycle and productivity and the success of zooplankton—specifically copepods,

Chapter Three examines the relationship between sandeels and copepods, which are their preferred food species. Both copepod population and the timing of the population peak are considered as possible drivers of sandeel population success. Furthermore, the possibility of a

direct link between sea surface temperature and sandeel numbers is explored using regression analysis.

Finally, we examine the relationship between seabird phenology, sandeel biomass by using the Great and Arctic Skuas nesting on Foula as study populations. Regression analysis will be used to study the significant relationship, if any, between sandeel population on skua breeding success and the timing of nesting.

The implications of these relationships will then be discussed on an ecosystem scale. This will allow the creation of an overall model of the southern North Sea ecosystem's response to anthropogenic climate change by modeling the mechanisms at each level of the food web.

Chapter One: Climate Patterns in the North Sea

1.1: Introduction

1.1.1: The North Atlantic Oscillation

Three non-anthropogenic temperature variations affect the North Sea on a cyclic basis: the path and northern extremity of the Gulf Stream, the Arctic Oscillation, and the North Atlantic Oscillation (Frid and Huliselan 1996, Planque and Taylor 1998). The North Atlantic Oscillation Index (NAO) is measured as the difference in air pressure between the Icelandic coast and the Azores. A 'positive' phase, indicated by a high NAO Index, brings warmer weather to Central Europe and the North Atlantic, while a 'negative' phase, indicated by a low NAO Index, brings cold air into the same area (Trigo *et al.* 2002). Although cyclic, the NAO can persist in a particular phase for years or even decades, setting weather patterns throughout entire regions of

Europe and the Atlantic Ocean (Hurrell and VanLoon 1997, Otterman *et al.* 2000). Latif *et al.* (2004) propose that thermohaline circulation in the North Sea, and consequently sea surface temperatures, actually move through a multi-decadal warming and cooling cycle mediated predominantly by the NAO.

This climatic cycle has a widespread influence on the distribution, survival, relative populations, and ecological roles of many North Sea organisms, particularly plankton communities (Otterman *et al.* 2000). However, there appears to be a delay between a climatic anomaly and a change in the plankton bloom timing or variety of species. Abnormally warm autumnal temperatures, for example, do not have a significant effect on the autumn plankton bloom, but are correlated with an earlier plankton bloom the following spring (Wiltshire *et al.* 2008). That effect will be examined in greater detail in the next chapter.

1.1.2: The Gulf Stream

The path of the Gulf Stream is also variable year to year, particularly in the latitude of the northern edge, called the Northern Gulf Stream Wall (NGSW). The NGSW has a strong interaction with the NAO: a high NAO Index caused the NGSW to favour a more northerly route. There is a time delay of approximately two years in this relationship, which reflects the slow readjustment rate of ocean currents. However, if the speed of ocean water masses is controlled for, the NAO is responsible for about half of the interannual variation in the location of the NGSW (Taylor and Stevens 1998).

The position of the NGSW shows a strong correlation with variability in plankton population, with temperature anomalies in the North Sea linked to anomalous changes in zooplankton and phytoplankton populations in the region (Edwards *et al.* 2002, Planque and

Taylor 1998). Planque and Taylor (1998) argue that plankton population fluctuations are tied to these variations, with temperature changes accounting for as much as forty-five percent of variability in plankton population. Edwards *et al.* (2002) observe that lowered sea surface temperatures, consistent with a negative-phase NAO or the NGSW at a lower latitude, caused a drop in both phytoplankton and zooplankton populations. Furthermore, the spring plankton bloom following such a temperature was delayed, consequently delaying the population increase in zooplankton which feed on diatoms (Edwards *et al.* 2002).

1.1.3: The Arctic Oscillation

Much like the NAO, the Arctic Oscillation is the result of cyclic changes in air pressure. However, it crosses the pole, effecting weather in the northern regions of both the Atlantic and Pacific Oceans. This pattern is thought to explain between fourteen and twenty-five percent of climate variation in the North Sea (Ambaum *et al.* 2001). Wang and Ikeda's (2000) models indicate that the AO is also responsible for about forty percent of the variation in sea ice distribution.

Unlike the NAO, however, the AO is more prominently affected by terrestrial temperature changes on the northern Eurasian continent and may be partially driven by the contrast between marine and terrestrial temperatures (Thompson and Wallace 1998). The major mechanism behind the AO is variation in air currents in the stratosphere and troposphere, as the air movements that characterize the AO start in the stratosphere and propagate downwards (Baldwin and Dunkerton 1999).

A positive AO index indicates strengthened polar jet stream over the region, while a negative one indicates a slackening of that air current. Because of the nature of the AO, a positive index in the Atlantic means a negative index in the Pacific, and vice versa (Ambaum *et al.* 2001, Deser 2000).

1.1.4: Local Effects in Shetland

As the Shetland Islands are bounded by a large shelf area of relatively shallow water, near shore current patterns would be expected to have a strong effect on local sea surface temperature. Because the edge of this shelf runs north to south, currents were once thought to be guided exclusively along this line. However, more detailed mapping of localized water movement shows that relatively swift currents also move west to east, bringing water from the North Atlantic to the west coast of Shetland (Dooley *et al.* 1976).

A large volume of water also moves from the North Atlantic into the North Sea through the Faroe-Shetland Channel, during which it is subjected to heavy turbulence due to moving rapidly over seafloor ridge formations. This turbulence leads to a more homogenized influx of North Atlantic water to the North Sea (Sherwin *et al.* 2006). Although there is evidence of some local upwellings, these appear to be relatively scattered events and do not constitute a regular part of sea surface temperature variation in the region (Dooley *et al.* 1976).

Furthermore, the specific patterns of current flow and temperature around Shetland appear to be linked to the larger oscillation cycles of the North Atlantic and North Sea. Because of this large-scale cyclic water movement, the climate patterns of the North Atlantic, the southern North Sea and the region surrounding Shetland can be described as a single large system subject to similar salinity and temperature variation (Turrell *et al.* 1996). For the purposes

of this paper, the Shetland region in which the data were gathered will be viewed as part of this greater body of water.

1.1.5: Effects of Anthropogenic Climate Change

Anthropogenic increases in global temperatures have altered the phase and magnitude of the NAO in recent decades, resulting in increased wind and storm wave activity in the North Sea (Ulbrich and Cristoph 1999). Climate models predict a trend towards a positive NAO Index if anthropogenic global warming continues at the current rate (Fyfe *et al.* 1999), and a study of sea surface temperatures and high temperature anomalies in the Northern Hemisphere indicate an average warming of the North Sea (Beauregard *et al.* 2002).

In spite of the association between a high NAO Index and warmer sea temperatures, some climate models predict a cooling trend in the region, possibly induced by an influx of fresh water from melting ice caps, which would change the density and temperature of the ocean surface (Vellinga and Wood 2002). There may also be a decrease in the strength of thermohaline circulation, including the Gulf Stream, which could potentially alter the latitude of the GSNW (Joos *et al.* 1999).

The AO and the associated stratospheric temperature anomalies appear to behave episodically independent of warming trends, despite strong linear effects on other Arctic oceanographic and atmospheric processes, such as sea ice formation, in response to temperature increases (Overland and Wang 2005). Gillett *et al.* (2002) suggest that this unpredictability is driven by the stratospheric variation itself, as models which exclude stratosphere effects predict a strong linear relationship between greenhouse gasses and increases in the AO, which does not match climate observations from the field. However, another model hypothesizes that radiation

will be increasingly deflected towards the equator, leading to a cooled and strengthened Arctic vortex, which would in turn have an increased effect on sea surface temperatures in the northern hemisphere (Gillett *et al.* 2002).

This chapter will attempt to separate the effects of anthropogenic climate change in the southern North Sea from the cyclic climate variation mediated by the NAO and AO. This will be achieved by statistical modeling of the system, starting with the relationship between the NAO and AO, then by removing these effects from the analysis in order to detect unrelated trends in climate, described by using sea surface temperature as a proxy.

1.2: Methods

1.2.1: SST Data

Data were initially gathered by the International Council for the Exploration of the Sea (ICES) in a single sector of the North Sea. The latitudinal boundaries of this sector are 60°N and 65°N, and the longitudinal boundaries are 0°E and 5°W. This sector encompasses the Shetland Island study sites and includes 304,269 sample sites. As sandeel populations are highly localized to sandbanks close to the islands, there was no need to use temperature data from locations further offshore.

Sea surface readings are collected year-round at depths of ten meters or less, using collection bottles or continuous readings from a research vessel. To calculate average winter SST for the region, readings taken between November 1 and February 28 of each year were extracted from the data set and the mean value calculated for every winter between 1953 and 2009. The part of the year used as 'winter' corresponds with the time when North Sea plankton species are inactive.

1.2.2 : Climate Patterns in the North Atlantic

Data on the average annual AO and NAO indexes come from the National Center for Atmospheric Research (NCAR) via Jim Hurrell's Climate Analysis Sector (CAS) of the NCAR's Climate and Global Dynamics (CGD) department. These data sets were collected in the North Sea and processed at the NCAR main lab in Boulder, Colorado.

The NAO index is calculated from air pressures recorded at fixed buoy stations in the North Atlantic. To eliminate noise from local weather patterns, principal component analysis (PCA) was used to determine the relative significance of atmospheric anomalies (Hurrell and Deser 2009). These same techniques are used to calculate the AO index. Both of these data sets are available for research use via Hurrell's research site (<http://www.cgd.ucar.edu/cas/jhurrell/indices.html>), having already been run through PCA.

1.2.3: Statistical Analysis Techniques

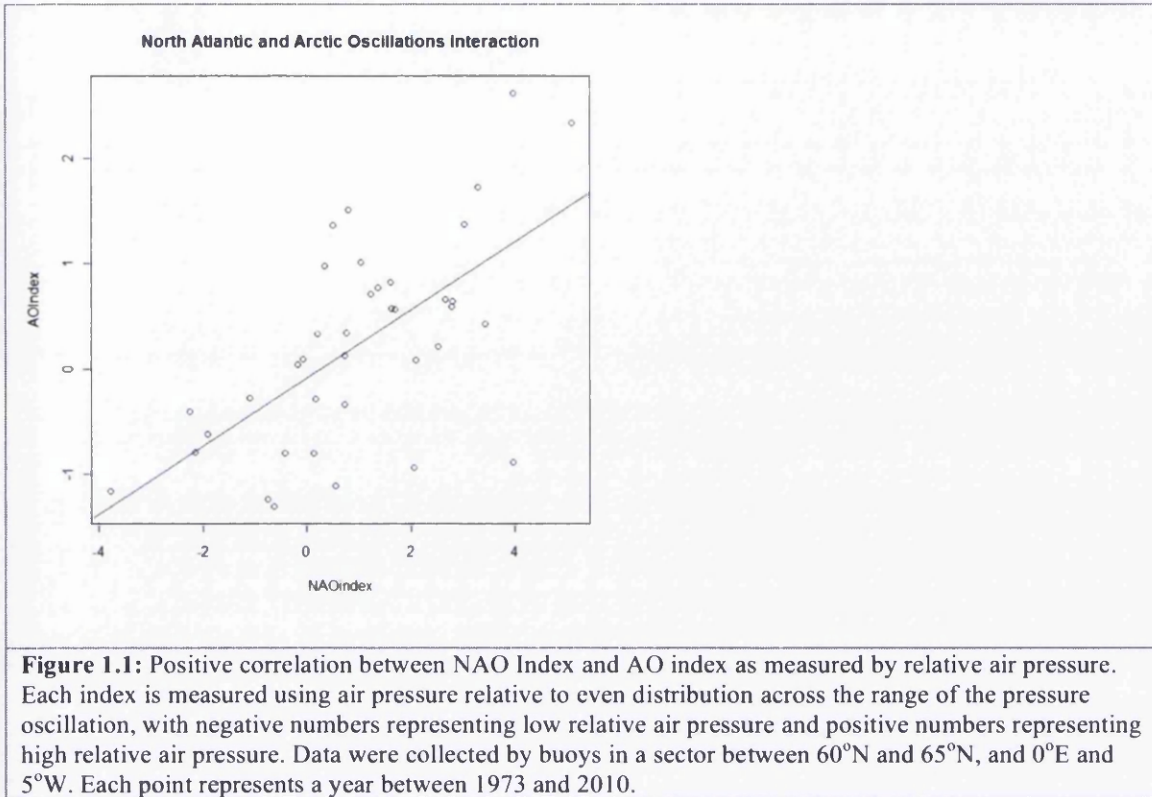
The first round of statistical analysis was simple linear regression models which compared two primary variables using MiniTab 16. Potentially confounding effects were entered as random factors in the analysis. P-values were calculated using a chi-squared goodness of fit test. This technique was used to examine mean winter sea surface temperature variation over time (Figure 1.3), and to quantify the relationship between the AO and NAO (Figure 1.1).

To model the relationship between the two atmospheric oscillations and sea surface temperature, the data were run through a basic lattice analysis in R. R then determined the goodness of fit using a nested regression. To represent this relationship between atmospheric indexes and sea surface temperature visually, I used the topographical mapping formula to plot

each data point on a three-dimensional axis, then extrapolate between points using a connective 'skin' (Figure 1.2).

1.3: Results

The relationship between the North Atlantic Oscillation (NAO), Arctic Oscillation (AO), and winter sea surface temperature in the North Atlantic is nonlinear and highly complex. As seen in Figure 1.1 below, the interaction between the NAO and AO has a strong combined effect on sea surface temperatures. Literature indicates that the Arctic Oscillation is responsible for up to one quarter of variation in North Sea temperatures (Ambaum *et al.* 2001). When the interactions between the North Atlantic Oscillation and Arctic Oscillation are accounted for, the percentage of North Sea temperature variation explained by the Arctic Oscillation approaches forty percent (Wang and Ikeda 2000). Analysis of raw data from Hurrell's work also supports the correlation between the NAO and AO indexes, with variation in the NAO accounting for 37.9% of variation in the AO ($p = 0.00002$).



Matrix analysis confirmed the nonlinear relationship between these two climatic cycles established in the literature is consistent with data used in this analysis (Figure 1.2).

North Atlantic Atmospheric Oscillations and Sea Surface Temperature

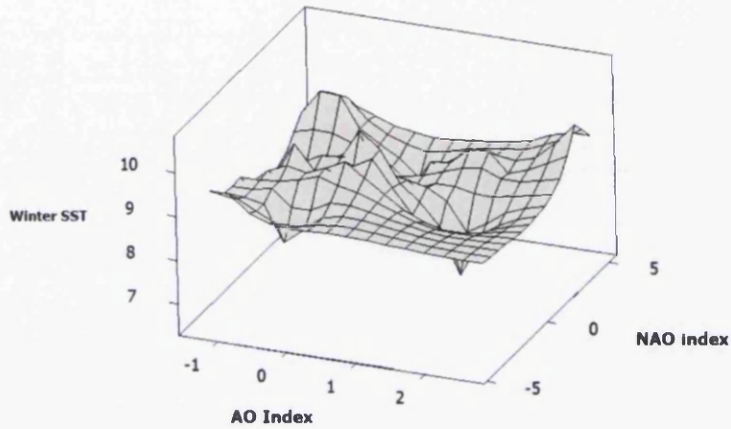


Figure 1.2: Model of interaction between the North Atlantic Oscillation, Arctic Oscillation and average winter sea surface temperature between 1973 and 2010. Each horizontal axis shows the respective oscillation indexes in terms of relative air pressure. Winter sea surface temperature is the average temperature sampled between November 1 and February 28.

However, this model is overly simplistic in that it discounts the effects of anthropogenic climate change, both as a direct influence on average winter sea surface temperature, and as a factor in the strength, direction and oscillation time of the AO and NAO.

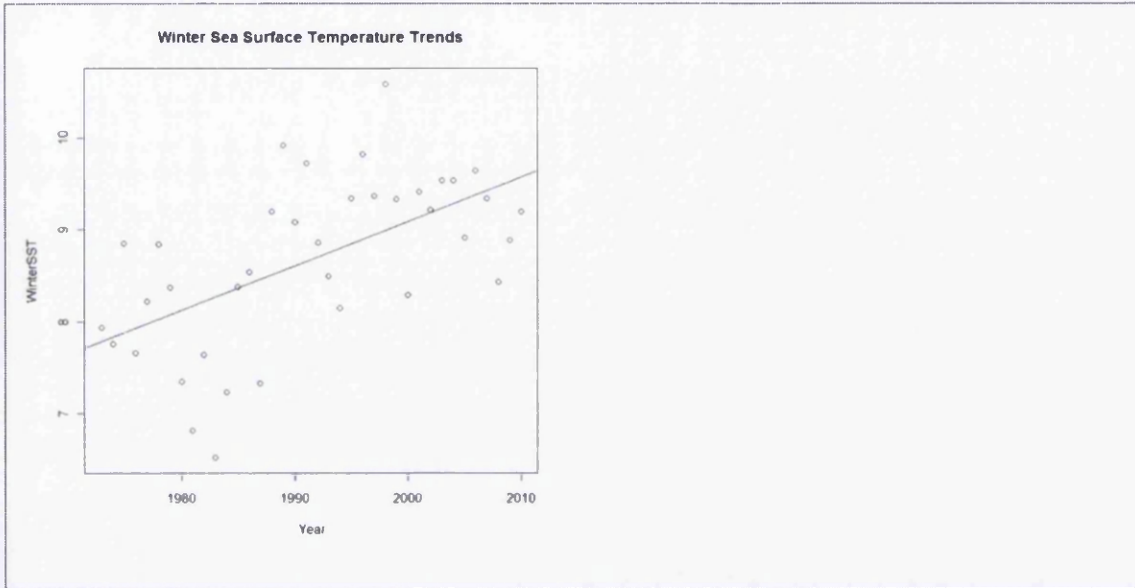


Figure 1.3: Average winter sea surface temperature from 1973 to 2010. The final average sea surface temperature is the average of temperature readings taken between November 1 and February 28 of each year.

Even after incorporating the AO and NAO as random effects, average sea surface temperature between November 1 and February 28 in the North Sea shows a significant upward trend over time ($r\text{-squared} = 32.93$, $p = 0.0001$), indicating that anthropogenic warming is a key factor in determining average winter sea surface temperature in the study area of the North Sea. For purposes of later discussion, we will assume that anthropogenic warming is the major factor in the sea surface temperature trends.

1.4: Discussion

The net effects of anthropogenic global warming are well-documented in climate literature. However, there has been some debate as to the specific effects on North Sea climate, particularly in regards to the reaction of the AO and NAO. The three-dimensional matrix model constructed from the raw data shows a spike in sea surface temperatures correlated with a simultaneous positive AO and NAO Index. There is strong evidence in the literature to support the relationship between positive indexes and higher winter temperatures in the North Sea, although given the strong effect of climate change over time, it is hard to prove the direction of causation from this model, as there is evidence both that global increases in temperature have caused prolonged positive phases in the AO and NAO Indexes, and that positive phase AO and NAO increase local winter temperatures in the North Sea.

Approximately a third of North Sea temperature variation appears to be explained by anthropogenic climate change alone. Assuming that the positive NAO and AO Indexes are both causes and effects of increased net temperature and have an independent effect on about forty percent of variance in North Sea surface temperature, global warming could be speculated to account for over half of temperature variation observed, and may contribute to a positive feedback cycle. However, proving this theory would require more detailed climate models beyond the scope of this investigation.

For the purposes of this paper, the climate observations above contradict—at least in years studied—the predictions by Gillett *et al.* (2002), Vellinga and Wood (2002) and Joos *et al.* (1999) that global warming would lead to a localized decrease in North Sea surface temperatures. Instead, we assume that average North Sea surface temperatures are increasing in our study sector in response to anthropogenic shifts in worldwide climate.

Chapter Two: North Sea Plankton Communities

2.1: Introduction

2.1.1: Phytoplankton in the North Sea

Phytoplankton is the dominant primary producer in the North Sea, comprising most of the algal biomass in Scotland's offshore waters. Most of these species are present throughout the year, residing in a dormant cystic state during the winter and multiplying in the spring (Reid *et al.* 1990).

This phytoplankton cycle, known as the annual bloom, plays a critical role in regulating nutrient flow and ocean biochemistry, particularly carbon and nitrogen cycling (Davies and Payne 1984, Lancelot 1979, Roemmich & McGowan 1995). The spring bloom is high in fatty acids, which provide food for herbivorous zooplankton species and small planktivorous fish (Kattner *et al.* 1983). Once the phytoplankton dies and sinks to the floor, it also becomes a critical food source for benthic organisms (Davies and Payne 1984). Thus drop in phytoplankton population, due to poor climatic conditions, can reduce the carrying capacity for zooplankton in the region (Beaugrand and Ibanez 2004), which in turn reduces the carrying capacity for planktivorous fish species (Greenstreet *et al.* 2006).

Unlike many marine fish, zooplankton and phytoplankton are not commercially harvested. Because of the lack of a fisheries influence, which is usually considered the major factor influencing the abundance of food fish stocks, plankton populations and distribution are more sensitive to other changes in the marine environment, such as sea temperature and chemical content. Furthermore, planktonic organisms have a short life cycle, which means that their response to environmental changes is more immediate than that of longer-lived organisms such as fish or marine mammals (Planque and Taylor 1998).



Figure 2.1: Microscopic view of various North Sea diatom species. Patterning is due to a silicon shell around the diatom cells. Diatoms in this image are drawn to 20x resolution. Picture by S.B. Stolk.

2.1.2: Seasonal Phytoplankton Variation

The North Sea phytoplankton population increases and decreases on a yearly cycle, and is usually described as having population peaks in the spring and autumn. However, a summer bloom is more typical of some regions, and blooms can occur opportunistically when the conditions are favourable (Reid *et al.* 1990). Year to year variation in the North Sea phytoplankton is determined largely by the intensity and direction of local ocean currents and winter sea surface temperature, with nutrient content of the water playing a more important role in the more southern regions (Colebrook 1982). The composition of the plankton community can be determined by samples from the top of the water column, which is home to the bulk of plankton biomass. The species present near the surface also appear to be representative of lower regions of the water column (Gamble 1978).



Figure 2.2: Peak spring diatom bloom off Shetland, as seen from space. The islands have been artificially colored yellow for contrast. Green and turquoise areas show phytoplankton growth, while blue areas show water without significant phytoplankton activity. Photo via NASA.

2.1.3: Effects of Climate Change on Phytoplankton Ecology

North Sea planktonic populations are highly sensitive to changes in sea temperature, with prolonged or abnormally large variations in water temperature leading to large-scale shifts in plankton regime composition, including shifts in the diversity and overall population size (Beaugrand and Ibanez 2004). Stormy weather can also disrupt the composition of the usually stratified vertical thermocline, temporarily altering plankton distribution (Gamble 1978).

Wiltshire *et al.* (2008) note that although many regional plankton communities are resilient, when faced with dramatic year-to-year alterations in climate, a steady trend towards warmer global temperatures has caused noticeable changes in North Sea phytoplankton ecology. First, warmer years are correlated with a delayed phytoplankton bloom. Second, there are a greater proportion of larger diatoms, which are difficult for calanoid copepods to eat. Edwards *et al.* (2002) observed that the winter phytoplankton biomass increased during the late 1980s,

during a period where sea surface temperatures were abnormally high. Those years also showed an exceptionally early date for the spring diatom bloom.

Warmer winter sea surface temperatures have also favoured the establishment of a small number of exotic plankton species in some areas of the North Sea, although the wider ecological effects of these new species are unknown (Nehring 1998). Beaugand *et al.* (2002) report a decrease in arctic and subarctic plankton species in the North Sea, and a northward advance of some more temperate organisms in areas primarily effected by the Arctic and North Atlantic Oscillation weather patterns; however, they observe a significant increase in arctic plankton species in the northwestern Atlantic, where the Gulf Stream exerts a dominant influence on sea surface temperatures. (Edwards *et al.* 2002).

2.1.4: Copepod Diet and Foraging Behaviour

The term “calanoid copepod” refers to a group of planktonic copepods, including over a thousand recognized species, which feed primarily on pelagic or estuarine plankton (Keppel 1993). In the North Sea, calanoid copepods feed primarily on diatoms and microzooplankton (Gasparini *et al.* 2000, Keppel 1993).

Copepods forage non-randomly, using chemosensory cues to locate phytoplankton (Poulet and Marsot 1978). When faced with periodically turbulent environments, the copepods' sensory mechanisms for locating food appear to be disrupted, which can result in inappropriate changes in the rate of foraging behaviour as well as increased escape behaviours. The level of adaptation to a turbulent environment appears to be effected by previous experience (Costello *et al.* 1990). Ignoring turbulence, copepod feeding behaviour appears to be a response to phytoplankton cell density, with copepods filtering more water as food density decreases

(Paffenhofer and Lewis 1990). Different species of copepods forage assortatively, seeking food particles relative to their size, which may be an evolutionary strategy to reduce interspecies competition for food resources (Gamble 1978). In laboratory settings, copepods show the ability to switch between herbivory and carnivory depending on the food availability in their immediate environment, and appear to do so in natural environments as well (Keppel 1993).

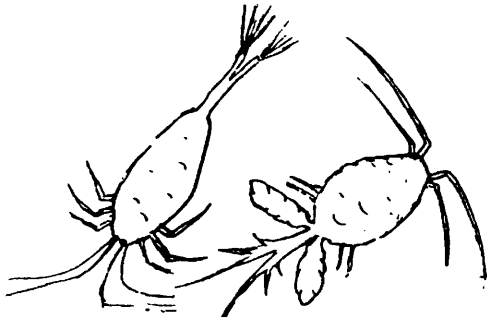


Figure 2.3: Two adult calanoid copepods foraging. Many physiologically and behaviorally similar species of calanoid copepods live in the North Sea. These specimens are drawn to 25x magnification. Adults typically range in size from 0.75 to 0.95mm. Picture by S.B.Stolk

Like many zooplankton species, copepods migrate vertically through the water column, moving to the surface to feed and retreating down the water column at night. They also move down the water column when faced with predators, as copepods are predominantly pursued by visual hunters, such as sandeels (Bollins and Frost 1989, Winslade 1974). Unlike their mode of finding food, which is primarily chemosensory, predator detection appears to rely on visual and mechanical cues (Bollins and Frost 1989).

2.1.5: Copepod Growth and Recruitment

Copepod growth rate appears to be sensitive to food supply in the early stages of development, with a less dramatic feeding effect as the individuals age. In a laboratory environment with stable temperature, individual copepods show a logarithmic increase in body

mass. In the North Sea, however, growth rate appears to be highly sensitive to seasonal temperature variation, with growth slowing by over fifty percent during the winter (Breteler *et al.* 1982). Some North Sea copepod species, such as *Temora longicornis*, produce fertile eggs year-round, while others, such as *Acartia clausi*, do not reproduce during the autumn and winter months (Halsband and Hirche 2001).

The biochemistry of these copepod species appears to be more sensitive to environmental conditions and food species (Miralto *et al.* 1999) than genetics, as variation in feeding conditions will cause significant changes in the number and proportion of fatty acids stored in the copepods' bodies across all species surveyed (Kattner and Krause 1987). However, breeding success, as measured by the number of offspring produced by an individual, appears to be more closely correlated with the size of the individual. Size, in turn, appears to be more strongly influenced by environmental temperature than by food availability (Halsband and Hirche 2001).

Food supply does appear to have an effect, however. Copepods are more successful at producing fertile eggs when consuming a more varied diet, showing an eightfold increase in hatch rate when their diet shifted towards dinoflagellates and protists. Perhaps because of this, the majority of copepod recruitment occurs after the first major diatom bloom has begun to fade (Miralto *et al.* 1999). Miralto *et al.* (1999) propose that this is the result of an evolved chemical defence by the diatoms themselves. Furthermore, the diatoms which the copepods seem to prefer have a relatively low carbon content, significant enough that some copepod populations show signs of food limitation in spite of a large supply of zooplankton and a normal rate of intake (Gasparini *et al.* 2000).

2.1.6: Habitat and Distribution

Like other plankton species, copepods are distributed non-randomly throughout the North Sea. Their distribution appears to be driven mainly by ocean currents, which leads to a greater density of individuals along near-shore upwellings. As currents shift seasonally, these accumulations can also change location (Beaugrand *et al.* 2000).

This chapter will examine two main questions. First, regression analysis will be used to investigate the relationship between sea surface temperature and the bloom timing and population of diatoms. Second, similar methods will be used to determine if a significant relationship exists between diatoms and copepods based on bloom timing, abundance or both. Before either of these relationships is studied, however, there will be some discussion of the inherent limitations of plankton sampling in a field environment and the statistical techniques that can correct some of these problems.

2.2: Methods

2.2.1 Raw Population Data

Data on the population of copepods and zooplankton (including diatoms) were gathered from the records of the Continuous Plankton Recorder survey, which operates under the supervision of the Sir Alister Hardy Foundation for Ocean Science (SAHFOS). This tool samples plankton continuously along an ocean route by capturing plankton on a silk ribbon, which is then spooled and processed in formaldehyde to preserve the collected organisms for study on shore (Reid *et al.* 2003, Warner and Hays 1994).

2.2.2: Centre of Gravity Analysis

To determine the date in Julian days of the peak of the spring phytoplankton bloom, a centre of gravity analysis was used. Initially, data from the entire year were used to determine the centre of gravity. However, analysis of the raw data using a histogram plot showed a bimodal distribution of plankton population consistent with current literature documenting separate spring and autumn blooms. To find the peak of the spring bloom, data were sampled from the months between January and June of the target year, as these dates are consistent with literature describing the duration of the spring phytoplankton bloom.

Each month was assigned a number value corresponding with its calendar order, for example March would be assigned the value 3. The number value of each month was then multiplied by the value of the average plankton population recorded that month.

$$M^{\wedge} = \text{Month number} * \text{average plankton population}$$

The M^{\wedge} values were then added together, and divided by the sum of the average plankton population for each month.

$$(M^{\wedge}_1 + M^{\wedge}_2 + M^{\wedge}_3 + M^{\wedge}_4 + M^{\wedge}_5 + M^{\wedge}_6) / (\text{pop}_1 + \text{pop}_2 + \text{pop}_3 + \text{pop}_4 + \text{pop}_5 + \text{pop}_6) = \text{CoG}$$

This gives the centre of gravity in months. To convert the units of this value to days, it was first changed into a percentage of the year by dividing the centre of gravity value by twelve. This value was then multiplied by 365 to change the units to days and provide the centre of gravity as a Julian date.

2.2.3: Analysis of Plankton Distribution

Because plankton is distributed nonrandomly, the samples were analyzed for potential species bias in distribution using the following equation, as outlined by Parsons *et al.* (1984):

$$(q+p)^k$$

Where k is the maximum number of individuals in the sample, p is the probability of a particular species being sampled, and $q = 1-p$. The mean and variance can then be calculated for this sample by assuming that the mean (μ) is:

$$\mu = kp$$

And that the variation (σ^2) is:

$$\sigma^2 = kpq$$

In a sample of seawater, k is assumed to approach infinity, and q approaches zero, at which point $\mu = \sigma^2$.

To determine distribution, the experimentally determined variance is compared to the mean; alternatively, the theoretical variance can be compared to the theoretical mean. In either of these cases, a value greater than one indicates that the sample is disproportionately dispersed. Kemp and Mitsch (1979) and Weibe and Holland (1968) both predict a high degree of patchiness for North Sea plankton populations, due to non-random foraging behaviour by zooplankton, seasonal wind and wave turbulence, and competition for space between plankton species.

Individual analysis of each sample allowed the calculation of a corrected population estimate for each data point. These corrected data were used in the remaining analysis.

2.2.4: Regression Analysis

Data sets were tested for autocorrelation and non-normal distribution. Correcting for spatial bias, as described in section 2.2.3, restored normal distribution patterns in the plankton samples, although further transformation of the data was performed to aid resolution, as the high plankton counts made graphical observation of trends difficult. The data were transformed using a square root function. No statistically significant temporal autocorrelation was observed in the plankton datasets.

Initial regression analysis was performed in MiniTab 16 using the linear regression function. For non-linear relationships, the data were transferred to R 2.13.0, where they were graphically analysed using a smoothing spline regression.

2.2.5 Model Selection

Statistical models were chosen with the goal of describing the relationships between variables in an efficient and simple way, maintaining both enough detail to keep the model effective, but simple enough to distil the underlying relationships. Because of the high degree of error inherent in the sampling process, particularly in the plankton collection in the field, precise models could not be created. Furthermore, this limited the types of models that could be used to analyse the data. Because of these constraints, smoothed regression plots were selected to allow both flexibility for the highly variable data and non-linear relationships present, but capable of being

simplified to give streamlined models which maintained statistical significance as measured by a value of $p \geq 0.05$ and a high value of r relative to superficially similar models.

2.2.6: Data Limitations

Due to the nature of data collection and the subsequent use of mathematical techniques to compensate for nonrandom spatial distribution described above, a high degree of uncertainty is inherent in the dataset. This means that the resulting models will have a greater degree of uncertainty than experiments conducted in a controlled environment.

2.3: Results

2.3.1: Plankton Patchiness

Analysis of the raw plankton data using the technique outlined by Parsons *et al.* (1984) reveals that the samples taken by the Continuous Plankton Recorder in the target sector under-represent the average plankton population, thus skewing the total population estimates downwards by approximately thirty percent (Figure 2.4).

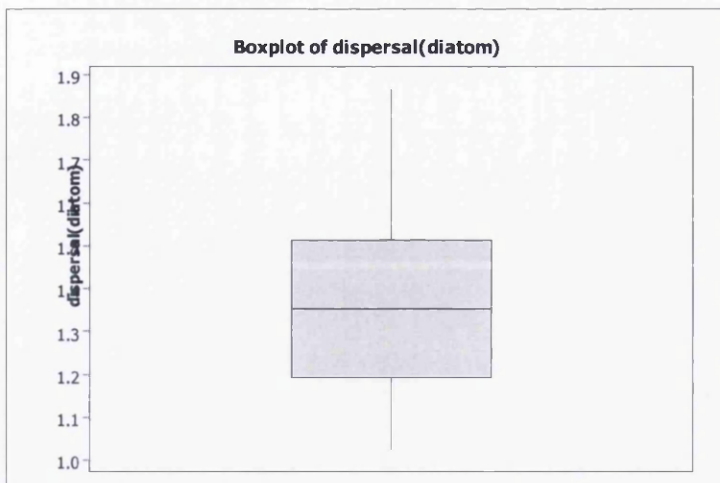


Figure 2.4: Plankton patchiness calculated from samples taken in the North Sea near Shetland between 1976 and 2010 using the equation described in section 2.2.2. The average sample shows underestimates of plankton population between 20% and 50%, with a mean underestimate of 35%.

2.3.2: Climate

Interactions between plankton and climate were examined for both the diatom and copepod populations in the study area. Regression analysis of the relationship between diatom population reveals no significant linear relationship between diatom population and winter sea surface temperature ($r\text{-squared} = 0.9$, $p = 0.859$), even when the analysis was adjusted to account for sampling error (Figure 2.5).

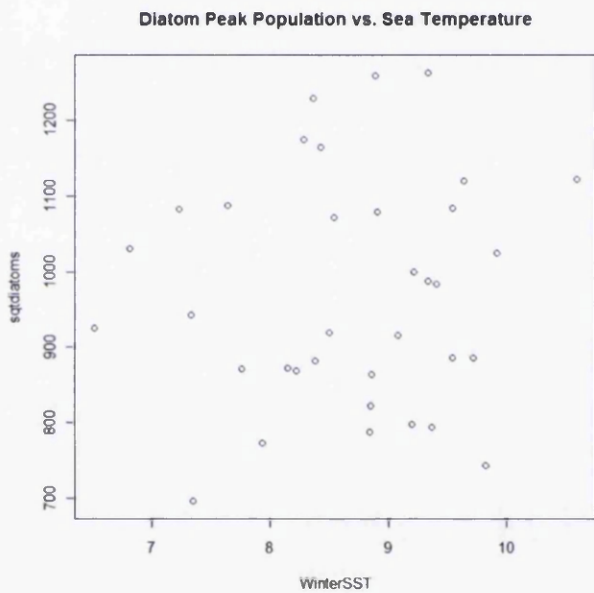


Figure 2.5: The peak diatom population, calculated by using average samples from the peak bloom date, plotted against average winter sea surface temperature for that year. No statistically significant correlation was found.

However, a significant relationship exists on the timing of the peak of the spring diatom bloom (Figure 2.6). Higher sea surface temperatures correlate with significant delay in the date at which the diatom population peaks ($r\text{-squared} = 15.00$, $p = 0.030$).

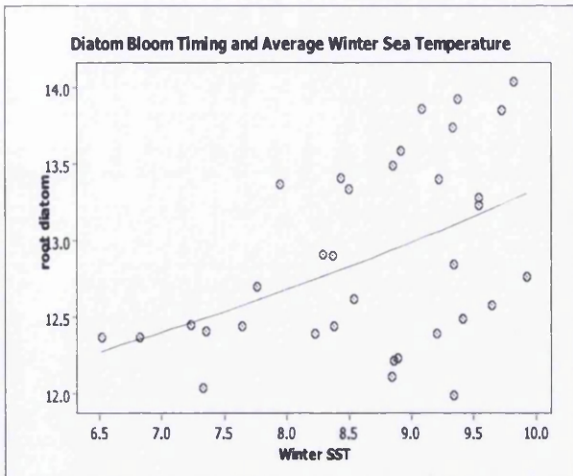


Figure 2.6. The Julian date of the peak diatom bloom compared to average winter sea surface temperature of that year. The date data are transformed with a square root function to aid resolution. Higher Julian dates indicate a later plankton bloom.

The total copepod population also does not have a significant relationship to average winter sea surface temperature (Figure 2.7). However, the timing of peak copepod recruitment shows a significant correlation with both sea surface temperature (Figure 2.8) and diatom population and bloom timing (Figure 2.9-2.11).

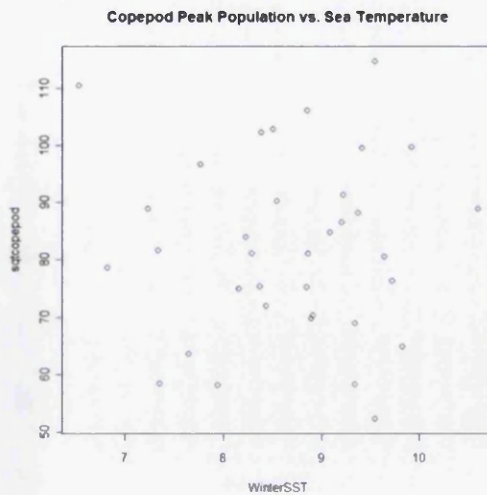


Figure 2.7: Copepod peak population, determined by an average of samples taken at the date of the peak copepod bloom, plotted against average winter sea surface temperature for that year. The effect of diatom population has been accounted for in this model. No statistically significant relationship was found.

Higher average winter sea surface temperatures are shown in Figure 2.8 to correlate with an earlier peak in copepod population (r -squared = 8.31, p = 0.046).

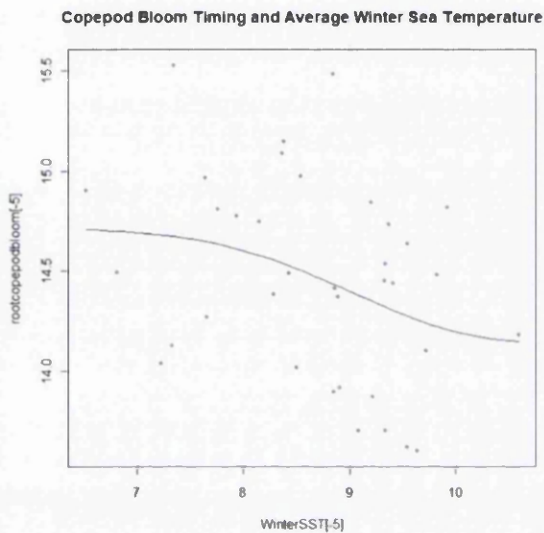


Figure 2.8: The Julian date of peak copepod bloom, transformed using a square root function to aid resolution, plotted against average winter sea surface temperature for that year.

2.3.3: Interaction between copepods and diatoms

There is a significant nonlinear relationship between the total populations of copepods and diatoms, consistent with current literature (r -squared = 23.9, p = 0.005). Copepod population and population variability peaks when the diatom population reaches approximately 10,000,000 estimated individuals in the sample sector. This relationship remains statistically significant, though slightly weakened, when sampling error is factored into measurements of diatom population (r -squared = 19.4, p = 0.012).

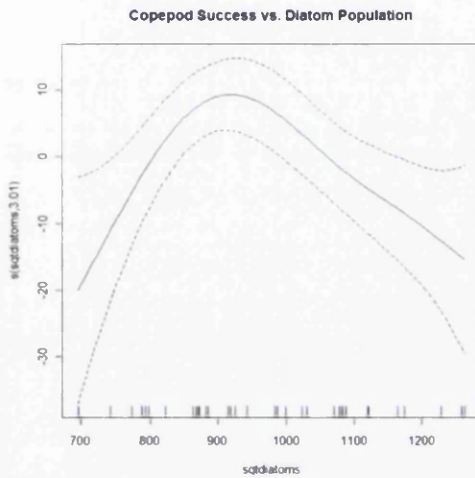


Figure 2.9: Average copepod population plotted against average diatom population for each month. Both sets of data are transformed using a square-root function to aid resolution. Dotted lines represent the 95% confidence interval for this smoothed regression plot.

Diatom bloom timing also has a significant effect on the timing of peak copepod abundance (r -squared = 10.28, $p = 0.032$), with a later diatom bloom correlating with an earlier peak in copepod population. Possible reasons for this pattern will be discussed in the next section.

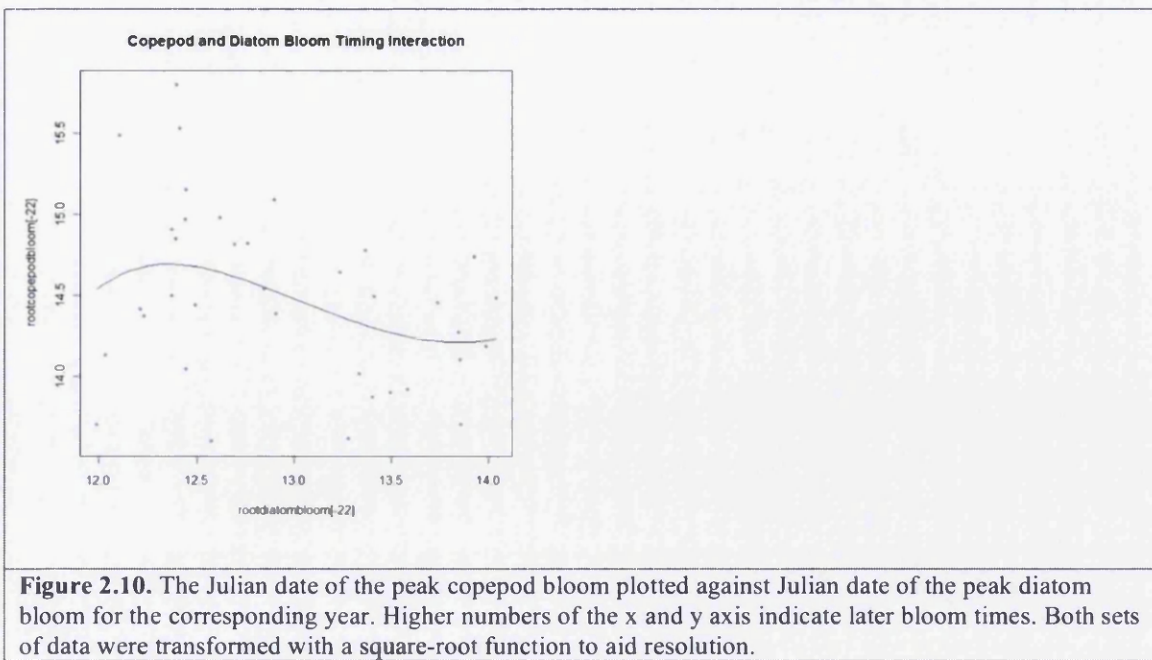
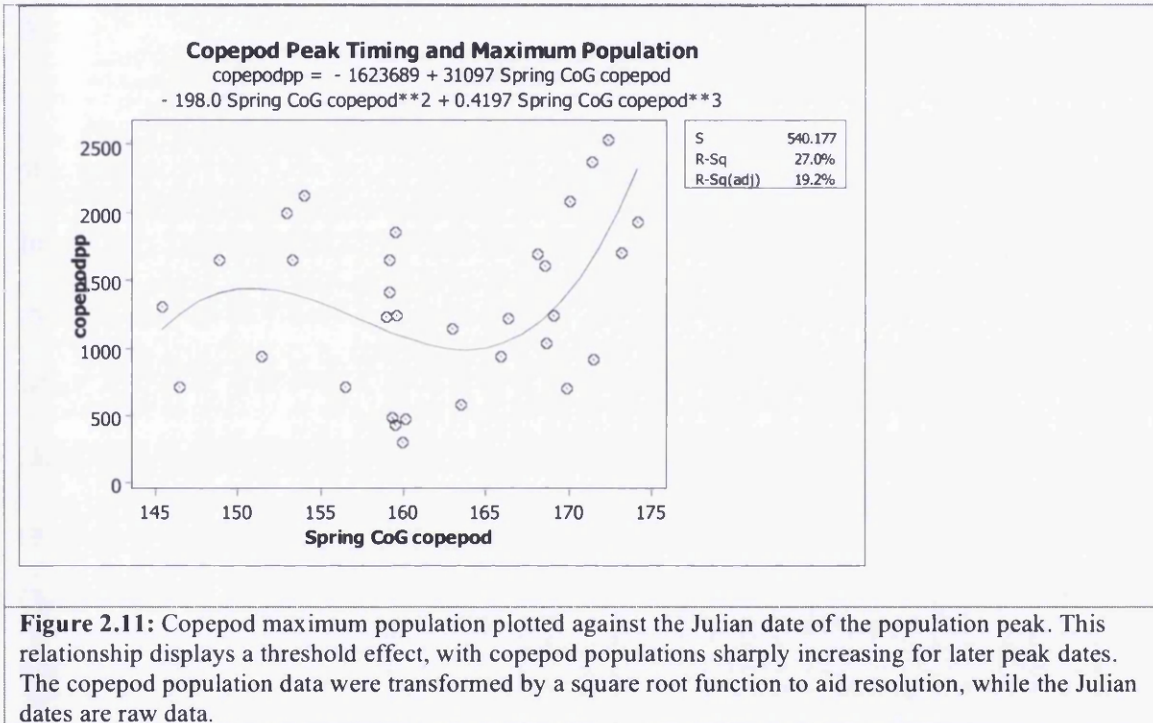


Figure 2.10. The Julian date of the peak copepod bloom plotted against Julian date of the peak diatom bloom for the corresponding year. Higher numbers of the x and y axis indicate later bloom times. Both sets of data were transformed with a square-root function to aid resolution.

Bloom timing has a significant effect on the maximum copepod population, with later peak dates correlating with higher maximum copepod populations (r -squared = 19.2, $p = 0.03$). This relationship is quadratic rather than linear, and displays a threshold effect, with a sharp increase in copepod population when their population peaks after 170 Julian days.



2.4: Discussion

The relationship between the relative diatom population and copepod recruitment is critical to understanding why the timing of the diatom bloom has such an effect on the copepod population.

While copepods rely on the diatom bloom for nutrition, too great a proportion of diatoms in their diet deprives them of critical nutrients needed for reproduction (reference). This means the copepod population will peak when diatoms reach an optimal proportion of the plankton population. The lack of a correlation between copepod population and average winter sea surface temperature, separate from diatom variation, indicates that copepod population is directly affected by the diatoms, with negligible direct influence from temperature.

In years with normal bloom timing, this means that the peak of copepod recruitment occurs later in the season, after the peak diatom bloom has begun to fade (Miralto *et al.* 1999). However, when the diatom bloom is delayed by higher sea surface temperatures, the optimal level of diatom density for the copepod diet is achieved before the peak bloom, allowing the copepods to peak in recruitment earlier in the season, which results in a lower overall copepod population.

One possibility is that if the copepods begin to peak as the diatom population is still rising, the high proportion of diatoms in the plankton population may stifle copepod reproduction. Proving this explanation would require observational data on the duration of the copepod peak, as well as foraging behaviour. However, the alteration of diatom bloom timing is clearly a factor in the alteration of copepod population and recruitment timing in the North Sea.

Chapter Three: Sandeels

3.1: Introduction

3.1.1: Sandeel Habitat and Distribution

Sandeels, or Sand Lance, excluding the relative rare predatory Greater Sandeel of the genus *Hyperoplus*, are a cluster of planktivorous species in the genus *Ammodytes* which occur in the northern regions of both the Atlantic and Pacific Oceans. In the North Sea, the two species present are *A. tobianus* and *A. marinus* with the latter being far more numerous and widely distributed (Robards and Piatt 1999).

Ammodytes species are found primarily near shore, preferring depths between six and fifty meters, although some populations will live as far as one hundred meters below the surface (Robards and Piatt 1999). Because of their burrowing behaviour, sandeels show a strong preference towards loose, coarse-grained sand substrate with good porosity and a low level of mud and silt; substrates contaminated by oil are specifically avoided (Dick and Warner 1982, Pinto *et al.* 1984). Because of their specialized habitat preferences, and lack of large migration patterns, regional populations within the greater North Atlantic are genetically and ecologically distinct groups (Pedersen *et al.* 1999). Traditionally, all North Sea resident sandeels were treated as either part of a single large North Sea shoal or part of a local Shetland population. However, in 2010, it was decided to recognize that the North Sea stock is in fact composed of several distinct, geographically separate shoals with different stock dynamics (ICES 2010).

In contrast to their specific needs for clean, sandy substrate, sandeels can tolerate a wide range of water temperatures. Individual species have approximately a 13C window of temperatures in which they can live (Inoue *et al.* 1967). Unlike some other fish species, however, the growth and survival rates of larval sandeels appears to be unaffected by water temperature (Buckly *et al.* 1984). However, all species appear to favour colder waters (Inoue *et al.* 1967); a high North Atlantic Oscillation Index, which results in warmer sea surface temperatures in the northeastern Atlantic, is negatively correlated with sandeel breeding success and recruitment in

the North Sea (Arnott and Ruxton 2002). Arnott and Ruxton (2002) also found a negative correlation between water temperature throughout the water column and sandeel recruitment, independent of the NAO.

3.1.2: Behavioural Adaptations

Unlike many pelagic fish, sandeels spend a large portion of their lives buried in substrate (Robards and Piatt 1999). On a daily basis, the burrowing behaviour appears to be triggered by low light levels (Inoue *et al.* 1967) or avoidance of predators. Sandeels also exhibit an annual cycle of dormancy, in which they burrow into the substrate for an extended period during the winter. To survive this period of dormancy, adult sandeels must accumulate a reserve of body fat during the summer and early autumn (Winslade 1974, Greenstreet *et al.* 2006). During dormancy, their metabolism drops drastically, slowing digestion and oxygen consumption (Robards and Piatt 1999).

Extended periods of swimming further up the water column occur during the winter mating season, and again in the summer, near the peak of the North Sea plankton bloom. During this time, the sandeels are particularly vulnerable to predation by fish and diving birds (Reay 1970).

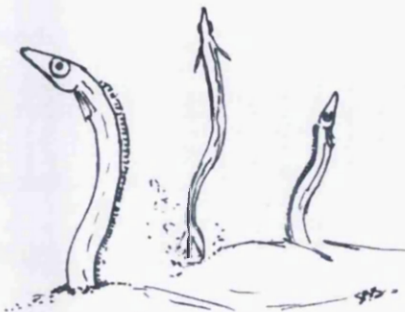


Figure 3.1: Lesser Sandeels (*Ammodytes tobianus*) emerging *en masse* to forage. Picture by S.B. Stolk

3.1.3: Diet and Foraging

Work on *A. americanus* indicates that sandeels are sensitive to changes in the food supply. In the Buckley *et al.* (1984) study, larval mortality decreased dramatically in response to increased feeding. Calanoid copepods make up sixty-three percent of the *A. tobianus* diet, with ninety-two percent of those being planktonic species. Another thirteen percent of the sandeel diet is composed of mysid shrimp, with the remainder made up of mixed plankton, including juvenile crustaceans, insect debris, and fish eggs (O'Connell and Fives 1995). Copepods are critical enough to the sandeel diet that calanoid copepod population can be used as a proxy for predicting sandeel recruitment (Arnott and Ruxton 2002).

Sandeels are diurnal, and emerge from the substrate when both light and food are present. Olfactory stimulus appears to prompt foraging behaviour in individuals which have just emerged from their burrows; when olfactory stimulus is absent, the fish return to their hiding places in the sediment. Observations of *A. marinus* in a laboratory setting suggest that sandeels are primarily visual predators (Winslade 1974). This pattern of emerging from the substrate in response to stimulus which indicate an optimal hunting environment is also seen in field observations of *A. tobianus* (Kuhlman and Karst 1966). While light seems to be an important cue for foraging behaviour, as evidenced by attraction to underwater lamps in the laboratory (Inoue 1967), wild and laboratory sandeels have been observed to partially emerge from their burrows at a predictable time regardless of light stimulus, indicating a daily endogenous cycle which is then reinforced by external information (Davis and Bardach 1965, Winslade 1974). Winslade (1974) suggests that this allows sandeels to remain fully buried, which reduces predation risk, until a suitable foraging opportunity arises.

3.1.4 Fisheries and Management Strategies

The main commercial sandeel fishery (predominantly of *Ammodytes marinus*) in the North Sea, provided a fishery yield of approximately 900,000 tonnes per year in the 1990s, but collapsed in 2006 (ICES 2010). At its peak, North Sea fisheries removed up to forty percent of the biomass of targeted species, excluding mortality from bycatch. Fishing activity such as trawling also caused structural disruptions to the benthic environment (Gislason 1994). However, as of 2002, there was no conclusive evidence of any detrimental effects to the ecosystem from the commercial sandeel fishery, although stocks of piscivorous fish had been reduced in the same region (Furness 2002, Furness and Tasker 2000). There is concern, however, that fisheries quotas have failed to account for the needs of marine predators, particularly seabird species which have limited flexibility in diet and foraging time (Furness and Tasker 2000).

The Shetland stock was also the target of industrial fishing, beginning in the early 1970s and closing in 1990 due to extremely low sandeel numbers. Following strong recruitment in 1991, the fishery was reopened and partially recovered during the 1990s, but the sandeel population crashed again in 2000 (Furness 2000).

Whilst the fishery was active, a number of techniques were tried for monitoring sandeel stocks. In a number of assessments, sandeels in the North Sea have been treated as a single, contiguous population, with the related assumptions that fishing pressure did not vary between countries (Pedersen *et al.* 1999). Pedersen *et al.* (1999), however, point out that not only do sandeel populations differ ecologically between locations, but regional differences in fisheries management also effect local stock dynamics.

Greenstreet *et al.* (2006) compared the efficacy of acoustic surveys, nocturnal sediment grabs, and demersal trawl samples as methods for assessing sandeel population, but did not find one method to be conclusively most effective.

The focus of this chapter is statistical analysis of the relationship between sandeel biomass and copepod population and population peak timing. This will include analysis designed to account for a potential direct relationship between sandeel biomass and sea surface temperature.

3.2: Methods

3.2.1: Sandeel Population Data

Sandeel population data for the Shetland stock were gathered by Marine Scotland, in association with ICES. Total population was estimated from a combination of commercial catch data (used in Virtual Population Analysis), along with selective sampling research trawls to extend the time

series after the closure of the commercial fishery when the stock was depleted (the fishery closed in 1990).

3.2.2: Basic Statistics

A simple ANOVA regression was used to find significant relationships between variables.

Before raw data were used in these analyses, a normality test was used to determine whether or not the data sets showed a normal distribution. Regression analysis for linear, cubic and quadratic regressions was conducted using MiniTab 16 software.

Where data sets showed a skewed or non-normal distribution, an attempt was made to normalize the data sets by taking the natural log (ln) or the square root of the values. This technique was also used to adjust data measured on scales which varied widely on orders of magnitude.

3.2.3: Multivariate Analysis

Where general linear models showed multiple significant relationships, the lattice analysis function of R 2.12.2 was used to calculate the relative effect of each explanatory variable. Linear regression with multiple explanatory variables was used in MiniTab 16 when the effect of the explanatory variables appeared to be at least partially additive.

3.3: Results

3.3.1: Sandeels and Sea Surface Temperature

Shetland sandeel stock biomass shows a strong negative correlation with winter sea surface temperatures, as shown in figure 3.2 (r -squared = 34.63, p = 0.0001). When the correlation of lowered copepod population and sea surface temperatures are accounted for, the relationship of

sandeel population to temperature is stronger, and still highly significant (r -squared = 35.5, p = 0.002).

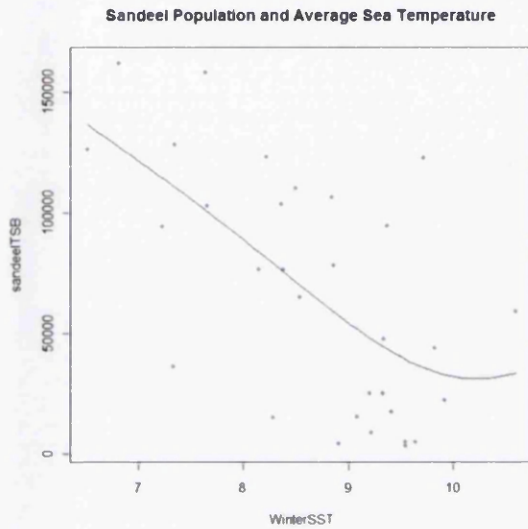


Figure 3.2. Raw data of average Shetland sandeel stock biomass plotted against winter sea surface temperature for each year between 1973 and 2009. Higher sandeelTSB numbers indicate a higher population.

Lattice analysis of sandeel stock biomass (Figure 3.3) shows that the correlation between sandeel population and average winter sea surface temperature is partially a correlation between sandeel biomass and the date of peak copepod population.

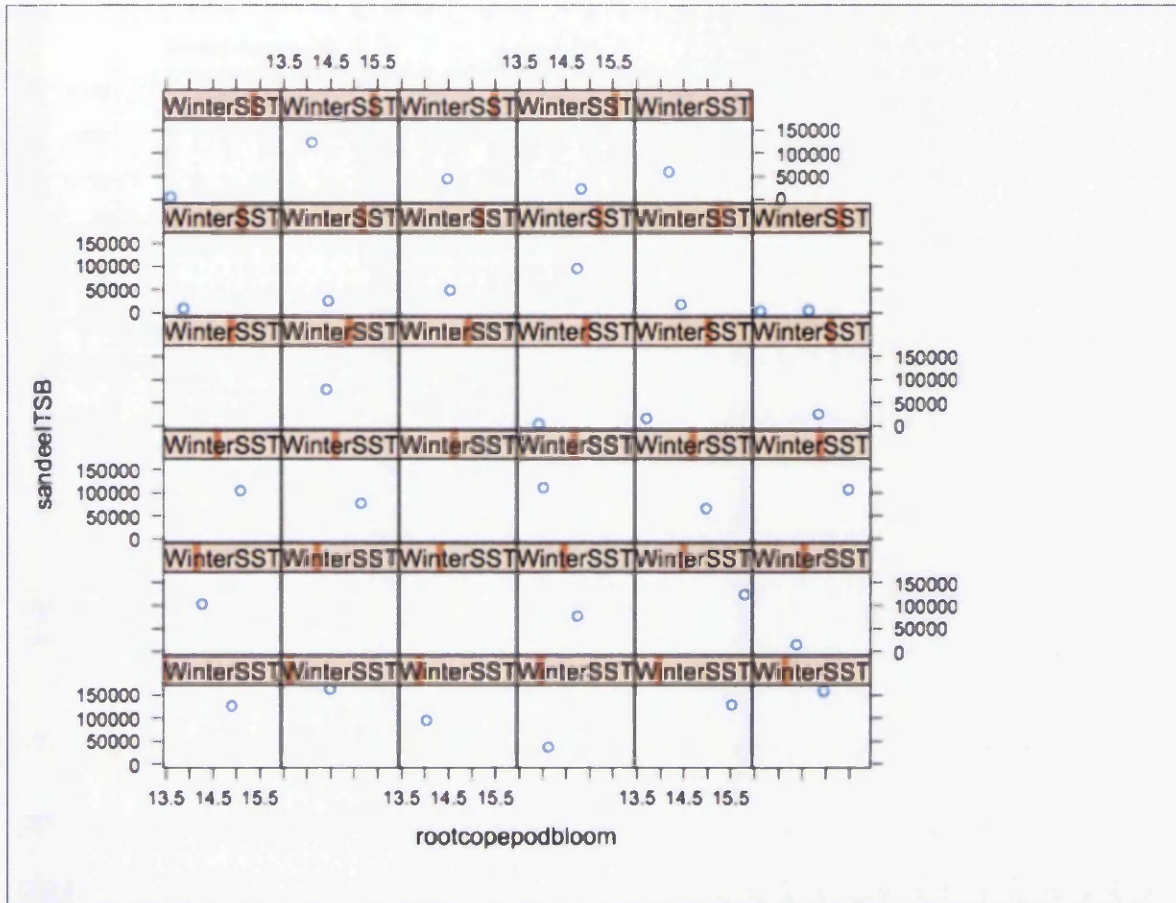


Figure 3.3: Simultaneous comparison of the effects of average winter sea surface temperature and copepod peak timing on sandeel stock in Shetland. Sandeel population data is average yearly counts, winter sea surface temperature is seasonal averages, and the copepod peak date data is the Julian peak bloom date transformed with a square root function. Each circle represents a year between 1973 and 2009.

3.3.2: Sandeels and copepods

Shetland sandeel biomass shows a significant relationship with peak copepod population for the season, as seen in Figure 3.4 below (r -squared = 20.3, p = 0.012), which is consistent with the literature (Arnott and Ruxton 2002).

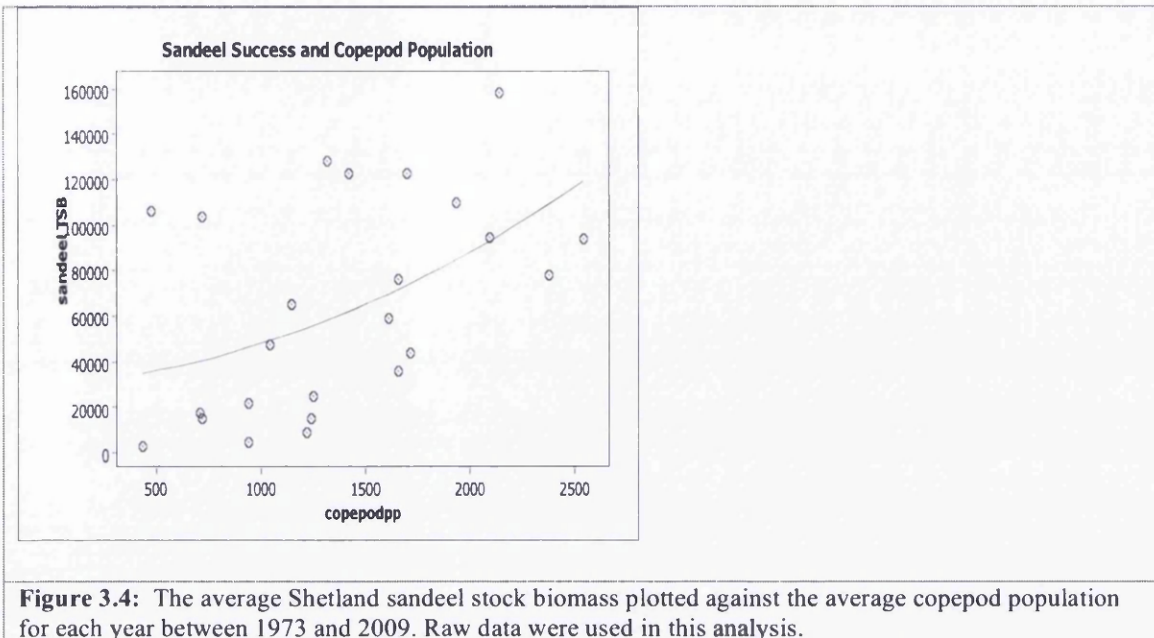


Figure 3.4: The average Shetland sandeel stock biomass plotted against the average copepod population for each year between 1973 and 2009. Raw data were used in this analysis.

There is also a significant positive relationship between the timing of the peak in copepod population and the recorded sandeel population as shown in Figure 3.5 (r -squared = 18.9, p = 0.038).

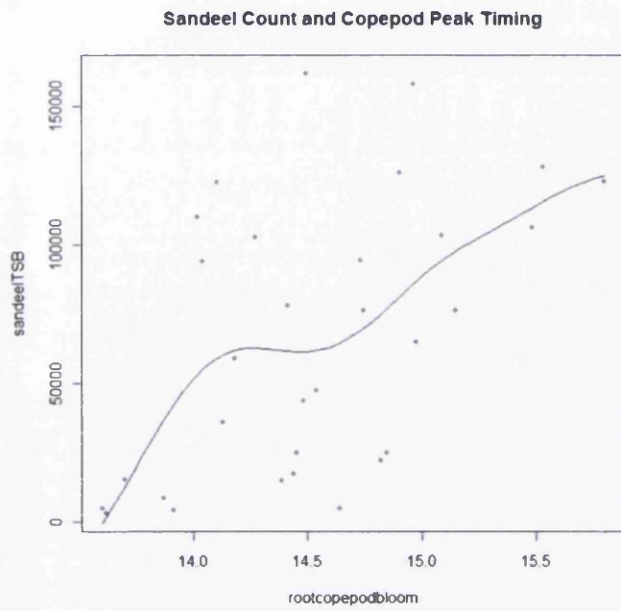


Figure 3.5: Average yearly sandeel population plotted against the Julian date of peak sandeel population for that year. The Julian date of sandeel population has been transformed by a square root function to aid resolution.

3.4: Discussion

The relationship between sandeel population and the timing of peak copepod recruitment is probably the result of the interaction between sandeel hibernation and foraging patterns and the alteration in copepod peak population timing discussed in the previous chapter, as well as the more obvious linear relationship between sandeel and copepod populations.

The correlation between sandeel success and average winter sea surface temperature persists even when the correlation between copepod peak recruitment timing and temperature has been controlled for, which indicates a direct effect of temperature on sandeel behaviour or physiology. One possibility is that hibernation patterns are affected by temperature, although there is not conclusive evidence that this is the case. However, it is reasonable to assume that metabolic rate, and consequently food requirement, will increase for the sandeels as sea temperatures rise.

The strong relationship between the timing of copepod recruitment and sandeel success is probably a product of the relationship between copepod peak population date and maximum copepod population discussed in the previous chapter. If sandeel emergence from hibernation is not mediated by winter sea temperatures, but rather by an endogenous cycle or another external cue which is unaltered by climate variation—as the experiments on light exposure and sandeel behaviour conducted by Davis and Bardach (1965) and Winslade (1974) suggest, the altered timing of the copepod population peak may result in mis-timing if the sandeels emerge when the copepod population is already in decline.

One final possibility is that the effective sandeel population biomass is effected by sandeels demonstrating prolonged hibernation due to limited food availability. Kuhlman and Karst (1966) demonstrate that external stimuli—in this case the presence of prey—may play a

part in the timing of sandeel emergence. In this scenario, the population estimates from samples may not represent the true sandeel stock strength. However, since sandeels are only available to predators and fisheries after they have migrated into the water column, a population count which excludes individuals still buried in the substrate may be a better measure of the sandeel stock as an element of the wider ecosystem. The relationship seems to have two linear phases depending on copepod peak bloom timing, which may imply a combination of these scenarios is in effect.

Chapter Four: Skuas

4.1: Introduction

4.1.1: Migration and Phenology

Arctic and Great Skuas are migratory species, travelling between southern hemisphere or low-latitude feeding grounds in the autumn and winter and high latitude breeding territories in the spring and summer. The timing of this return to the breeding grounds is correlated with weather conditions in the North Sea, particularly the yearly temperature fluctuations mediated by the North Atlantic Oscillation (NAO). In warmer years, individuals return significantly later in the year (Rainio *et al.* 2006). Barbraud and Weimerskirch (2006) have observed similar patterns in related skua species in the Antarctic.

The timing of breeding is also influenced by the sex and condition of the parents. In Arctic Skuas, breeding pairs lay eggs earlier when the males are in better condition. Female condition appears to have no significant effect (Phillips and Furness 1998). This effect is less clear in Great Skuas (Catry *et al.* 1999). Furthermore, while individual Arctic Skuas show high repeatability in clutch volume over time, Great Skuas show more long-term variation, implying that laying date is more strongly mediated by environmental conditions in this species (Phillips and Furness 1998, Catry *et al.* 1999).



Figure 4.1: An Arctic Skua (*Stercorarius parasiticus*) skims the water. Photo by Mark Darlaston



Figure 4.2: A Great Skua (*Stercorarius skua*) landing on the water in the Outer Hebrides. Photo by C. Booth

4.1.2: Nutrition and Foraging Behaviour

Both Great Skuas and Arctic Skuas are predatory and parasitic seabirds that primarily feed on pelagic fish captured at sea or stolen from pelagic diving birds. In the presence of human trawl fishing activity, about sixty percent of the Great Skua's breeding season diet is white fish, such as gadiforms, with the remainder of their intake made up of sandeels, herring, mackerel, marine invertebrates, small mammals and seabird nestlings and adults (Votier *et al.* 2004). Great skuas can feed on sandeels when these come to the sea surface, either to feed on zooplankton or to escape from predatory fish attacking from below. Because skuas, like other larids, cannot dive, they are unable to prey directly on fish from deep in the water column; fish of this type must be stolen from diving seabirds or gleaned from human fishing activities (Bearhop *et al.* 2001, Garthe *et al.* 1996, Hamer *et al.* 1991, Hudson and Furness 1988, Phillips *et al.* 1997). Pelagic oil-rich fish have significantly more calories than gadiform fish that otherwise make up a larger proportion of the skua diet (Frederiksen *et al.* 2002, Hislop *et al.* 1991). Marine invertebrates, such as gooseneck barnacles, appear to be the least preferred food even though they are readily obtained, perhaps because of their relatively low nutritional value compared to fish or young seabirds (Phillips *et al.* 1997).

Some evidence indicates that commercial fishing activity can boost seabird nesting success, perhaps as a result of readily available discarded bycatch (Furness 2002, Furness 2003, Garthe *et al.* 1996, Hamer *et al.* 1991, Hudson and Furness 1988). A small number of Great Skua pairs specialize in preying on smaller seabirds, which appears to reduce foraging costs during the breeding season, as these specialists forage over a smaller range than their piscivorous counterparts, and thus spend more time guarding their offspring. Seabirds also yield a higher number of calories, reducing the amount of work expended by the adult skuas to obtain the same level of nourishment. While Great Skuas range widely in search of food, particularly those individuals feeding primarily on fish, each breeding adult defends a discrete foraging territory (Votier *et al.* 2004). Arctic Skuas adapt their foraging strategy to food distribution and abundance in their region, defending a distinct territory when food is ample and evenly distributed, and behaving less territorially when presented with unpredictable resources (Andersson and Götmark 1980, Furness and Birkhead 1984). In Shetland during their breeding season, Arctic Skuas feed almost exclusively on fish stolen from other seabirds, especially terns, kittiwakes and auks (Caldow and Furness 2000).



Figure 4.3: A Great Skua attacks a Greater Black-backed Gull (*Larus marinus*) off the coast of Lewis. The goal of such an attack is normally to cause the pursued bird to drop or regurgitate fish, although Great Skuas will occasionally kill birds attacked in this way. Photo by Rosanna Milligan

4.1.3: Breeding and Nesting

Like most seabirds, Great Skuas nest colonially (Andersson and Götmark 1980, Hamer and Furness 1991). In Arctic Skuas, the pattern of nest distribution is linked to the foraging patterns discussed above. Thus, territorial birds will build solitary nests (as on the Arctic tundra), while birds foraging from a patchy resource will nest colonially (Andersson and Götmark 1980). In Shetland, Arctic Skuas tend to nest in colonies in the vicinity of the colonies of their preferred hosts (Davis *et al.* 2005).

During their first five years, young Great Skuas are continuously at sea, and do not breed. Arctic Skuas start breeding at a slightly younger age. In years where fish are scarce, older pairs of both species are likely to breed, while younger pairs are more likely to forgo nesting altogether. This pattern may optimize lifetime reproductive success, as younger, less experienced birds are more likely to jeopardize their own survival in a lean year, thus decreasing their long-term ability to pass on their genes, while older birds have relatively less to lose by attempting to breed (Catry *et al.* 1998, Davis *et al.* 2005). However, there is some evidence from studies of other larid species that non-breeders are simply individuals with low fitness, as lack of breeding success tends to be correlated with lower adult survival (Cam *et al.* 1998).

Arctic Skuas arrive at their breeding sites with reserves of body fat, which are retained over the course of the breeding season, with females showing a slight drop in weight just after the eggs hatch. Because there is normally no steady decline in body mass over the breeding season, the fat reserves may function as insurance against stressors or food shortage, as opposed to being an energy supply for the breeding process (Phillips and Furness 1997). While some theoretical models have predicted a reduction in seabird breeding effort in years with low food availability in order to protect adult survival, field studies indicate a smaller reduction in

breeding success than might be predicted, with adults working harder to mitigate scarcity of food, and a noticeable reduction in adult survival in response to food scarcity (Davis *et al.* 2005, Furness 2007).

Like many long-lived seabirds, skuas produce a small number of offspring each year and invest a relatively high amount of energy in those offspring's survival. Mortality primarily occurs in first-year birds, which are more likely to be killed by humans or fishing nets, as well as being more likely to die of exhaustion or starvation due to rough weather or inexperience in foraging (Furness 1978). The year-to-year adult survival rate increases with age, from seventy-three percent in five-year-old birds to between eighty and ninety-six percent in birds between the ages of seven and twenty-two years (Ratcliffe *et al.* 2002). Like breeding success, adult survival rate in Arctic Skuas appears to be significantly sensitive to food availability (Davis *et al.* 2005).

Skuas also increase the level of parental investment with age, expending more energy bringing food to the nest and fighting off potential nest predators (Caldow and Furness 2000). Older birds are also more successful at fledging young (Ratcliffe *et al.* 1998). Ratcliffe *et al.* (2002) propose that the deaths and nest failures in young birds may remove unhealthy individuals from the population, as well as reflecting the foraging skill of these birds. However, clutch volume, which is linked to breeding success, increases with female age, peaking around age fourteen, which indicates parental condition and age may play a direct physiological role in the health of the chicks (Caldow and Furness 2000).

4.1.4: Chick Rearing and Parental Care

During the incubation period, the males of both skua species forage for the female, who incubates a pair of eggs (Ratcliffe and Furness 1999). Once the skua chicks have hatched, both

parents provide food and guard the chick from predators. However, in years with an abundant food supply, the male forages significantly more than the female, with the larger female taking the primary guard duties (Hamer and Furness 1991). During abnormally warm years, nest attendance by both parents decreases, at least partially due to heat stress, which forces parents not only to sacrifice nest attendance time to bathe more frequently, but appears to be correlated with increased foraging time (Oswald *et al* 2008).



Figure 4.4: Great Skua bathing on a beach on Orkney. Photo by Alex Snyder

When less food is available, the female increases time spent foraging away from the territory, which results in higher chick mortality from predation. Time spent protecting the nest from predators, as well as the level of aggression against potential threats, appears to be positively correlated with the age of the breeding female (Caldow and Furness 2000, Hamer and Furness 1991). Protective behaviour is also strongly linked with offspring survival, implying that older birds may be more successful due to learned behavioural adaptations in nest guarding, rather than foraging ability (Ratcliffe *et al.* 1998), particularly as the correlation between nest guarding and age is only present once the eggs have hatched (Caldow and Furness 2000). The stress of the increased foraging demands may also affect parental behaviour, as chronic stressors, such as food shortage, have been shown to decrease levels of prolactin in birds; as prolactin

stimulates parental behavior in birds, this hormonal change prompts some species of birds to reduce parental behaviour when food is scarce (Angelier *et al.* 2007, Angelier and Chastel 2009, Angelier *et al.* 2009). This may also partially explain the increased breeding success of older skuas, as Angelier *et al.*'s (2007) study of snow petrels (*Pagodroma nivea*) found that older birds showed less of a decrease in prolactin in response to stress than their younger counterparts.



Figure 4.5: Great Skua chicks at the nest. Each breeding pair typically hatches two eggs. Picture by S. B. Stolk

As decreased nest attendance increases the odds of chick mortality by predation, there is a direct incentive for the parents to reduce time spent foraging. In Arctic Skuas, it appears the birds may adapt by increasing their kleptoparasitic behaviour in times of food scarcity, which reduces their time away from the nest (Caldow and Furness 2000). Arnason and Grant (1978) observed that these birds maximize their returns further by targeting birds carrying large fish, as the effort expended stealing food is constant regardless of what the target bird is carrying. In essence, this means reducing the area over which foraging takes place, and minimizing time away from the nest while maximizing calories collected (Phillips *et al.* 1997). Phillips *et al.* (1997) note that even with the relative degree of food specialization between individual birds, breeding skuas were more likely to prey on seabirds than their non-breeding counterparts, as this

strategy not only decreases foraging time and distance, but provides a high level of nutrition for the chicks.

Sandeels, an oily fish which provides a high level of nutrition and calories (Hislop *et al.* 1991) have been a major part of the skua diet, and the increased availability of these high-calorie fish in the 1970s which is thought to have resulted from declines in predatory fish stocks, appears to have allowed a population increase among Great Skuas in the Shetland Islands (Furness and Hislop 1981), followed by a dramatic decline in both nestling and adult survival when sandeel abundance declined in the 1980s (Phillips 1997). Phillips *et al.* (1996) confirm that this decline follows a threshold pattern, as predicted by Cairns (1987).

Other seabirds which depend on sandeels to feed their offspring show similar patterns. Widespread breeding failures in North Sea seabird populations appears to be linked to a drop in the sandeel population, which forced parent birds to feed their young with the less nutritious alternatives. This resulted in more parental absences from the nest, as the parents tried to compensate for the lower quality of the food by collecting more; nestlings also showed reduced rate of weight gain when there was lower calorie content of fish (Wanless *et al.* 2005).

This chapter studies the relationship between sandeel biomass and several measures of skua breeding success. The first section covers the creation of growth curves used to establish the age of skua chicks, and subsequently the timing of breeding. The subsequent sections explore the relationships between skua breeding success—as measured by the number of chicks raised by each pair—and sandeel biomass, as well as the timing of breeding and sandeel biomass.

4.2: Methods

4.2.1: Hatch Date Data

A specific chick growth curve was created for the study population of skuas. This was done by plotting known chick ages against the known wing lengths of the study individuals at that age. Once these points were recorded in MiniTab 16, a linear regression was plotted to describe wing growth over the period of ages for which wing growth followed a linear progression. This curve was then used to predict chick age for birds where a wing length was recorded in the absence of a hatch date.

4.1.2: Bird Arrival and Population Data

The date of the first Arctic Skuas or Great Skuas to arrive at colony sites was gathered from archived observations. Arrival dates for the Fair Isle population come from the Fair Isle Bird Observatory Annual Report, while dates for the Shetland population were extracted from the Shetland Bird Club Annual Bird Report. These reports were also the source of the last recorded skua sighting each year, although these data are less reliable, as the birds observed may be

incidental migrants instead of nesting pairs. All dates were recorded as Julian day for ease of statistical analysis. These reports, along with work by the Furness lab, provided counts of chicks and breeding pairs.

4.2.3: Breeding Success Data

As young skuas are precocial and highly motile, it is difficult to assess the breeding success of individual pairs without intensive marking of newly hatched chicks (Furness 1983). As such data are not readily available for our target colonies in all years, we use average chicks reared per pair in a study plot to assess the overall breeding success of the colony. This is the number of observed chicks in a given area of colony divided by the number of breeding pairs. Data on average chicks per pair were collected at the Great and Arctic Skua colonies on Foula each year following standardized methodology (Walsh *et al.* 1995).

4.2.4 Statistical Analysis

Initial investigation of the data using the autocorrelation (ac) in R showed strong temporal autocorrelation in the skua breeding population counts and breeding success data, possibly due to the slow recruitment process discussed in the literature review. Using a generalized least squares (gls) method to correct this, however, proved problematic because of the significant linear trend in average winter sea surface temperature over time. Because sea surface temperature, in turn, had a strong effect on other variables, as discussed in the previous chapters, a simple gls model to correct for the temporal autocorrelation was insufficiently precise, and removed significant correlation between skua breeding success and population data and other environmental factors studied.

Although significant temporal autocorrelation was found in the data, a nested ANOVA analysis revealed that most of this was a correlation with climate and ecological events which showed linear trends over time, as discussed in the previous chapters. The contribution of autocorrelation due to similarities in year-to-year nesting behaviour was statistically negligible.

Linear regressions plotted in R and MiniTab16 were used for the bulk of the analysis of data, as most of the comparisons only examined one response and one explanatory variable. To model threshold effects, a cubic regression was originally used in MiniTab16. For simplicity, this was refined to a fitted curve using a flexible smoothing regression in R.

4.3: Results

4.3.1: Wing Growth Functions

For Arctic Skuas, the curve (shown in Figure 4.6) is:

$$A_{AS} = 0.2493 + 0.1062W_{AS}$$

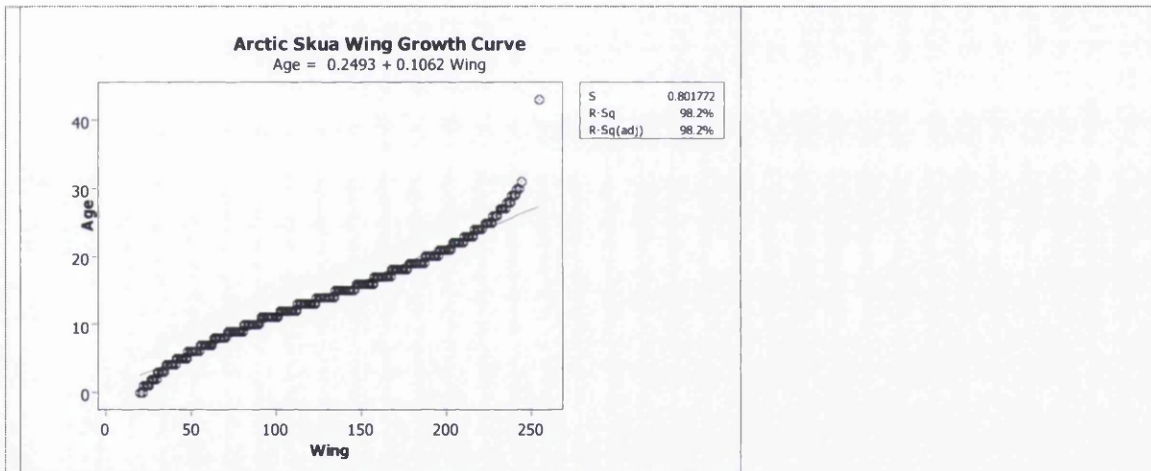


Figure 4.6: Arctic Skua chick wing length in millimeters plotted against the age of the chick in days. A fitted line is superimposed on the raw data plot. This line is calculated to give the best fit for our data.

Where A is age in days and W is wing length in millimeters. For Great Skuas, the curve (shown in Figure 4.7) is:

$$A_{GS} = 2.953 + 0.1269W_{GS}$$

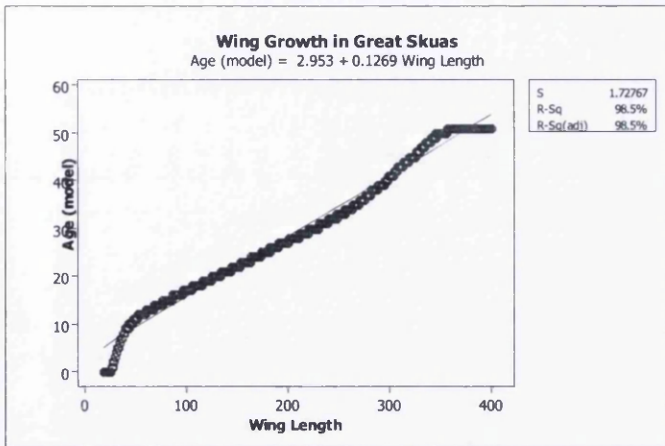


Figure 4.7: Wing length in millimeters plotted against the age of the Great Skua chick in days. A fitted line is superimposed on the raw data plot. This line is calculated to give the best fit for the data.

4.3.2: Breeding population

Both Arctic Skuas (Figure 4.8) and Great Skuas (Figure 4.9) show a similar pattern of decreased numbers of breeding pairs in years with low sandeel population (r -squared = 63.3, $p = 0.0001$; r -squared = 29.6, $p = 0.009$) This correlation is stronger in both magnitude and explanation of variability in Arctic Skuas than in Great Skuas.

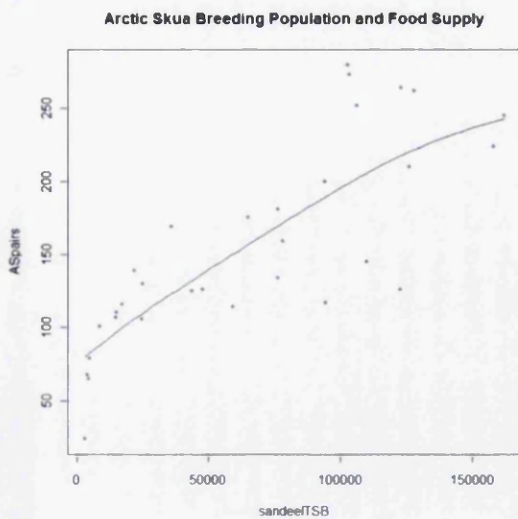


Figure 4.8: The number of Arctic Skua nesting pairs on Foula plotted against the average sandeel count of each year from 1973 to 2009.

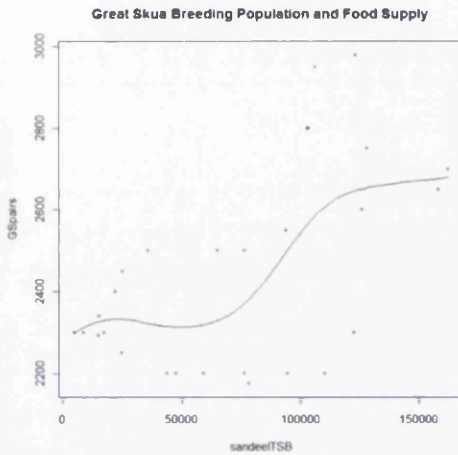


Figure 4.9: The number of Great Skua breeding pairs on Foula plotted against the average sandeel population for each year between 1973 and 2009.

4.3.3: Fecundity

Both skua species show a positive relationship between sandeel population and breeding success.

Higher sandeel populations were strongly correlated with a higher average number of chicks per breeding pair ($r\text{-squared} = 74.7$, $p = 0.0001$; $r\text{-squared} = 27.49$, $p = 0.001$). Once again, the correlation is stronger in Arctic Skuas (Figure 4.10) than in Great Skuas (Figure 4.11).

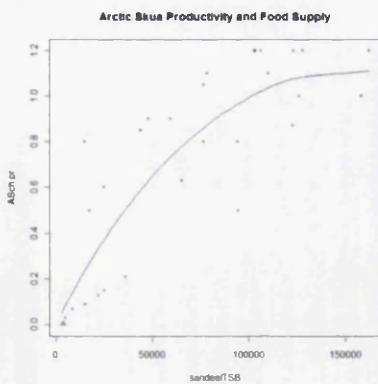


Figure 4.10: The average number of Arctic Skua chicks reared per pair in the Foula colony. This was calculated by dividing the number of chicks by the number of nesting pairs. This was plotted against the average sandeel population for each year from 1973 to 2009.

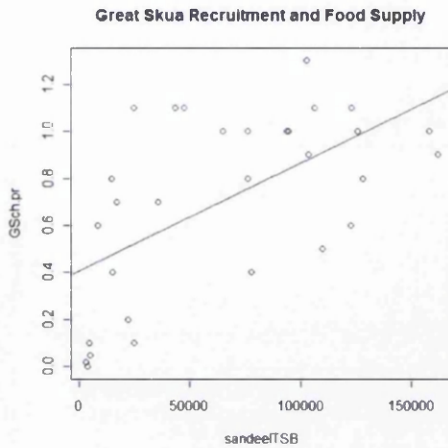


Figure 4.11: The average number of Great Skua chicks reared per pair in the Foula colony plotted against the average sandeel population for each year from 1973 to 2009. The number of chicks per pair was calculated by dividing the number of surviving nestlings by the number of breeding pairs.

4.3.4: Timing of breeding

In Arctic Skuas, the timing of breeding displays a significant threshold effect in response to changes in Shetland sandeel stock biomass, as seen in Figure 4.12 (r -squared = 70.5, p = 0.001). Nesting date remains relatively stable when the sandeel biomass is greater than 40,000 tonnes in the study area. When the sandeel biomass in this region drops below 40,000 tonnes, the nesting date is significantly delayed.

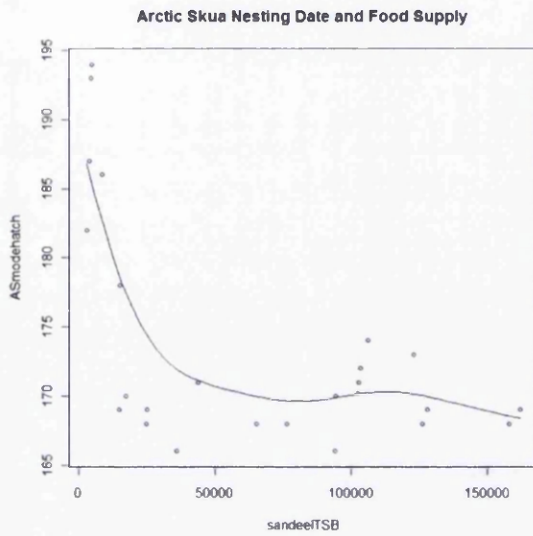


Figure 4.12: The mode Julian hatch of the Arctic Skua colony on Foula, plotted against the average sandeel stock biomass for each year between 1973 and 2009. This date indicates when most pairs in the colony began the nesting and breeding process.

As seen in Figure 4.13 below, Great Skuas show a more subtle, though significant, relationship between breeding date and sandeel population (r -squared = 29.0, p = 0.024)

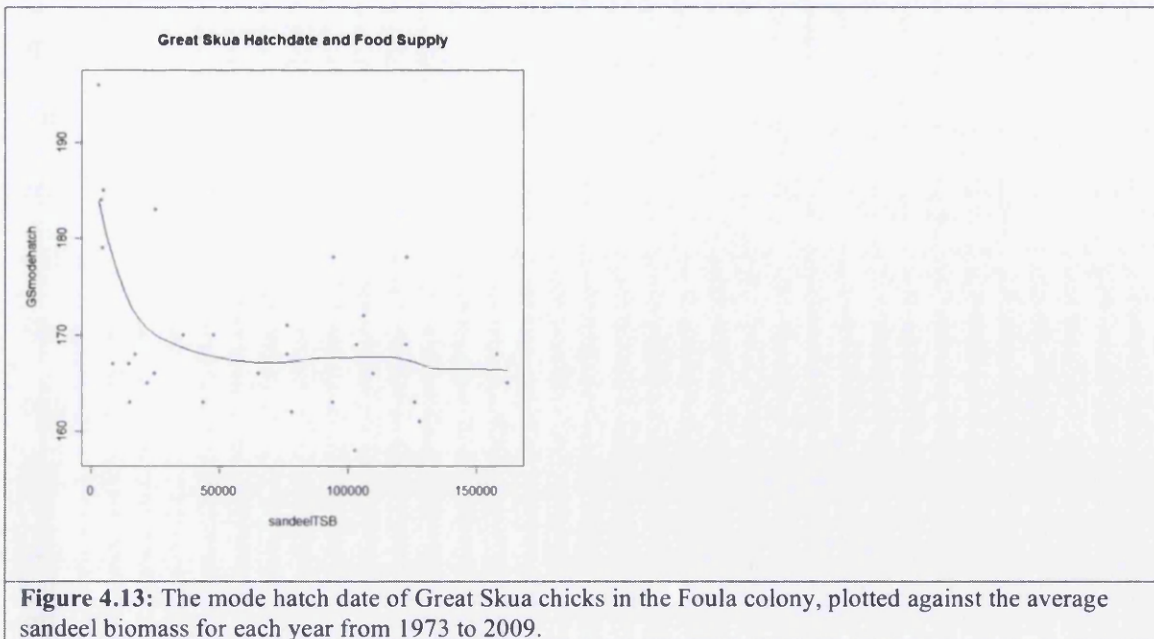


Figure 4.13: The mode hatch date of Great Skua chicks in the Foula colony, plotted against the average sandeel biomass for each year from 1973 to 2009.

4.4: Discussion

The reproductive success of both Great Skuas and Arctic Skuas, as measured in the number of offspring in relation to the number of breeding pairs, appears highly sensitive to food supply, as predicted in the literature. Some of this sensitivity may be due to a lack of suitable high-calorie food for the skua chicks (Wanless *et al.* 2005), or fewer feedings as the parents forage further afield. There is also a cost to lowered nest attendance—possibly prompted by a hormonal response to the stress of decreased calories-- that accompanies increased foraging behaviour, as parental absence leaves the skua chicks more vulnerable to predation (Ratcliffe *et al.* 1998). The linear relationship between sandeel supply and skua breeding success indicates that the increased kleptoparasitic behaviour observed by Phillips *et al.* (1997) does not adequately compensate for lower food densities. Although sandeels appear to be a key food source during the nesting season, as they provide critical high-calorie meals for growing skua chicks (Wanless *et al.* 2005), further studies would have to be conducted to determine if similar effects exist for other food species, such as whitefish discards.

The delayed breeding in both Great and Arctic Skuas is probably a learned behavioural adaptation in response to low fish population, as skuas appear to arrive at their breeding grounds with the requisite fat needed to fuel egg production. The effect is more prominent in Arctic Skuas, where there is a significant threshold effect, implying that the birds attempt to breed at an optimal date. Great Skuas also show a threshold effect, although somewhat less pronounced, indicating that either the Great Skuas rely more on endogenous cues to time their breeding, or can take advantage of a greater variety of food resources, thus partially mitigating the effect of sandeel population declines.

Since increased temperatures are correlated with lower sandeel populations, as discussed in the previous chapter, heat stress itself may compound the effects of low food availability, as the need for the adult skuas to bathe and drink decreases the time spent at the nest (Oswald *et al.* 2008). However, as lower-quality birds are less likely to breed during warmer years due to limited food supply, the birds which remain represent a selected sample of unusually successful and experienced pairs, which makes proving the effect of heat stress on the breeding success of the overall skua population complex.

Conclusion

Overview and Analysis

Climate change on the North Sea and Shetland ecosystem affects every level of the food web. These diverse impacts, however, all stem from one small event. Diatoms, the major primary producers of the North Sea, experience a delayed bloom event. This phytoplankton bloom, so large that it is visible from space, not only regulates chemical and nutrient cycling in the ocean, but provides major food source for copepods, one of the most abundant zooplankton species in this system.

The predator-prey relationship between diatoms and copepods is more complex than a simple linear relationship. Although diatoms are the favoured food of most calanoid copepod species, they are low in nutrients compared to other food sources, such as microzooplankton (Gasparini *et al.* 2000). Additionally, diatoms may carry a chemical defence that reduces copepod fecundity. Because of this tradeoff, copepods show optimum reproduction when diatoms are at non-peak population. Under normal climate conditions, the copepod population begins to increase after the diatom population has already peaked, forcing the adult copepods to diversify their diet, which leads to greater overall reproductive success and a higher peak copepod population (Miralto *et al.* 1999). If the copepod population begins its ascent to peak population whilst the diatom population is still rising, the high proportion of diatoms in the plankton population will eventually limit copepod reproduction. This leads to a shortened window for copepod recruitment and a lower peak population. In years with warmer temperatures, it appears that the second scenario occurs, due to mis-timing between the copepods and the diatom bloom.

For organisms which rely on the copepods for food, the effect is significant. Data is not available for a wide range of organisms, but is available for sandeels, which are a key fish species in the North Sea ecosystem (Arnott and Ruxton 2002). This oil-rich fish, in turn, provides food for a variety of piscivorous marine species, including herring, cod and seabirds (Reay 1970). Although North Sea sandeels had been the target of a commercial fishery before 2006, evidence that the commercial fishing activity itself was the cause of the eventual sandeel population crash is not conclusive for all populations (Furness 2002, Furness and Tasker 2000). The collapse of the Shetland sandeel fishery in 2000 appears to have been driven by excessive fishing, but has failed to recover as it did in the 1990s (ICES 2010), which points to other causes of sandeel population decline. That, combined with the strong link between sandeel population and copepod peak population and timing, suggests that the decline in sandeel counts in the North Sea is linked to climate change and the resulting mis-timing of plankton recruitment. This disruption of the sandeel food supply may have caused increased vulnerability to overfishing, and in inability to recover from exploitation.

One possibility, which has not been eliminated due to the sampling method and the behavior of the sandeels is that the fish are prolonging their hibernation due to lack of available food. However, as both the fishery and the marine predators require sandeels to emerge into the water column before capture, this scenario has the same overall effect on the ecosystem as a decline in overall sandeel biomass.

The final piece of this chain of events is of course the effect on marine predators. Because of their relative accessibility, Great and Arctic Skuas provide much of our marine predator data sets for this ecosystem. Some caution should be used when applying these results to predators such as marine mammals and piscivorous fish, as seabirds are known to be

particularly sensitive to changes in food supply, especially their year-to-year breeding success season (Frederiksen *et al.* 2004, Furness 2007, LeCorre and Jaquemet 2000, Mallory 2006, Phillips *et al.* 1997). The percentage of variability in skua breeding success in response to sandeel population is far greater than that of the sandeels or copepods in response to variation in their food supply, which supports the idea that seabirds and other predators show a far greater sensitivity to environmental changes than organisms in lower trophic levels. Because of this sensitivity, skuas appear to be an excellent biomonitor for the North Sea.

Directions for Further Research

As discussed in the chapter on skua breeding and chick-rearing behavior, parental nest attendance is highly correlated with nestling survival, which is one of the measures of skua population success used in this paper. Because low food supply is correlated with more time spent foraging by both parents, and as a result, decreased nest attendance. To determine how much of the decreased number of chicks reared per pair during years with low sandeel biomass is an effect of limited food or lowered nest attendance, further study would have to be conducted. One possibility is tracking adult breeding birds via radio transmitter to determine their foraging range during the breeding season and comparing this to nestling survival for the tracked pairs.

Second, more study of the behavior of sandeels in response to decreased or mis-timed food availability will elucidate whether the decreased sandeel stock numbers sampled reflect prolonged hibernation or lowered population. A possible avenue is laboratory experiments to monitor sandeel behavior in detail. This could guide plans for stock recovery in Shetland.

Finally, although there is a clear relationship between sandeel biomass and skua breeding success, further investigation to determine if a similar relationship exists between skuas and

other fish species. Being able to determine the presence or absence of such a relationship would broaden the usefulness of seabirds as marine biomonitors in Shetland and the North Sea.

Implications for Fisheries Management

The data discussed above indicates that fisheries management strategies for the Shetland sandeel stock have discounted the effect of climate change on the sandeel population. Much of the discussion of sandeel management has centered on the impact of commercial fishing and the interaction between commercial fishing activity and marine predators. However, more insight into the connection between climate change and fisheries health could broaden the scope of management efforts for Shetland sandeel population, as stock vulnerability due to climate change could be considered when modeling the impact of predation and commercial fishing on the ecosystem.

The significant relationship between anthropogenic climate change, and the resulting rise in sea surface temperatures, and the decline in North Sea sandeel biomass indicates that the traditional focus on fishing quotas and the restriction of fish extraction as the primary method of protecting fish stocks is inadequate to prevent further sandeel stock declines. Management of this species in the Southern North Sea must be seen as integrated with efforts to mitigate the effects of anthropogenic climate change. Furthermore, given the reduction of population resilience due to the effects of climate change on the ecosystem, a permanent closure of commercial fishing of the Shetland sandeel stock may be the most effective way to reduce the negative effects of sandeel population decline on marine predators.

Appendix 1: Residuals for Linear Models

Chapter 1

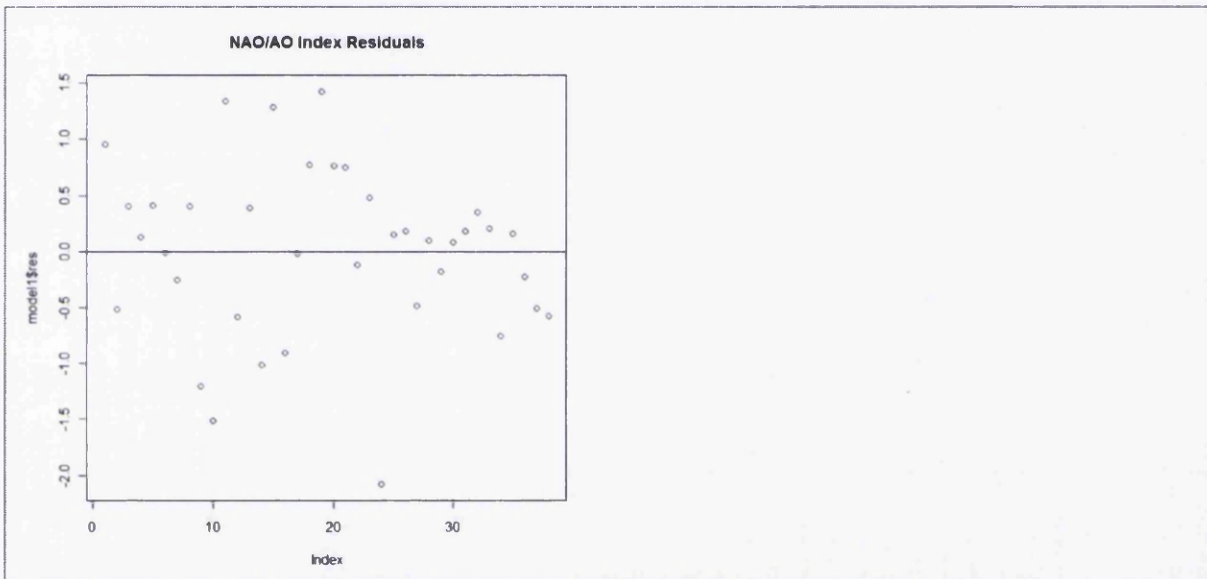


Figure 1.1 distribution of residuals. . Although a high level of variation occurs, this is expected with data sets gathered in the field, and with the inability of the model to incorporate all potential random effects. Otherwise, residuals are evenly distributed and support the significance of the model.

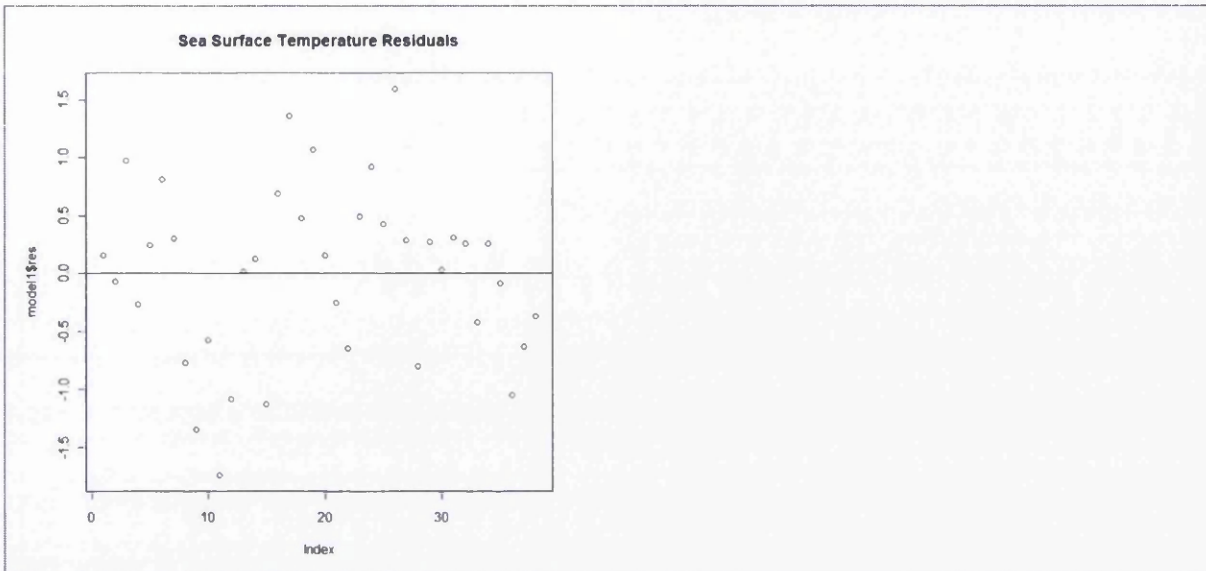


Figure 1.3 distribution of residuals. . Although a high level of variation occurs, this is expected with data sets gathered in the field, and with the inability of the model to incorporate all potential random effects. Otherwise, residuals are evenly distributed and support the significance of the model.

Chapter 2

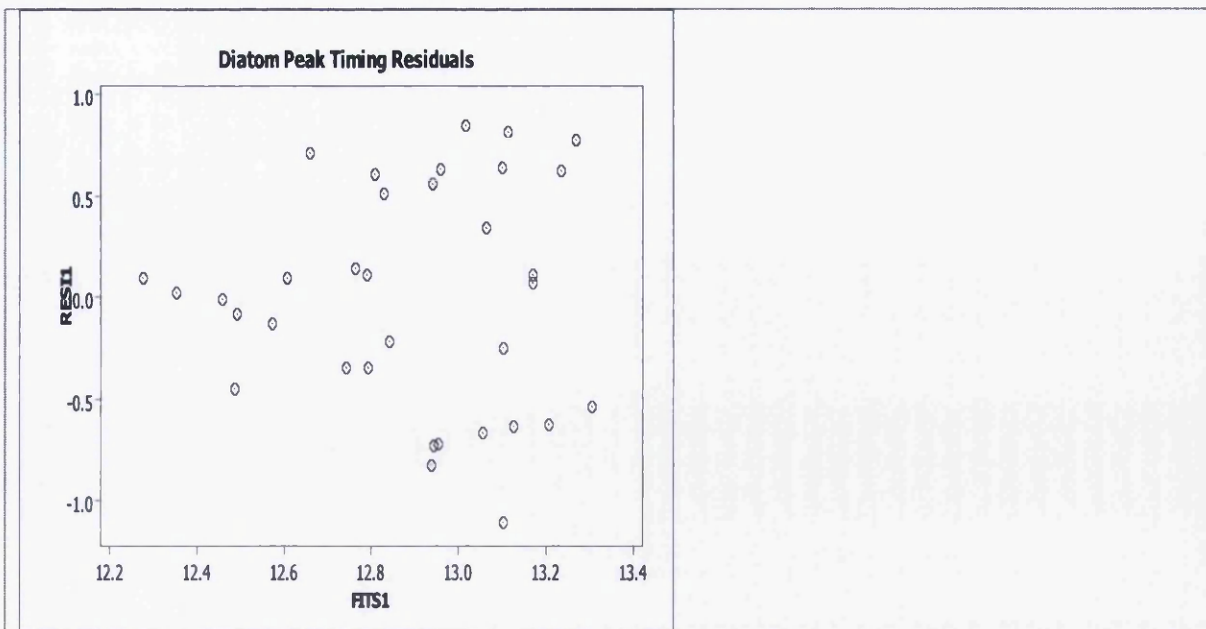


Figure 2.6 distribution of residuals. . Although a high level of variation occurs, this is expected with data sets gathered in the field, and with the inability of the model to incorporate all potential random effects. Otherwise,

residuals are evenly distributed and support the significance of the model.

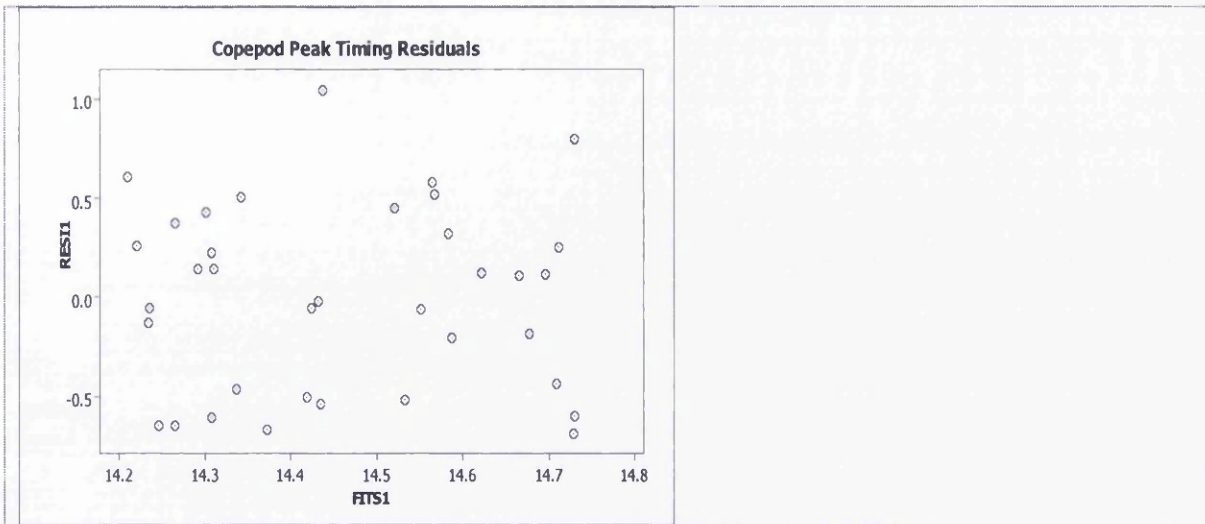


Figure 2.8 distribution of residuals. . Although a high level of variation occurs, this is expected with data sets gathered in the field, and with the inability of the model to incorporate all potential random effects. Otherwise, residuals are evenly distributed and support the significance of the model.

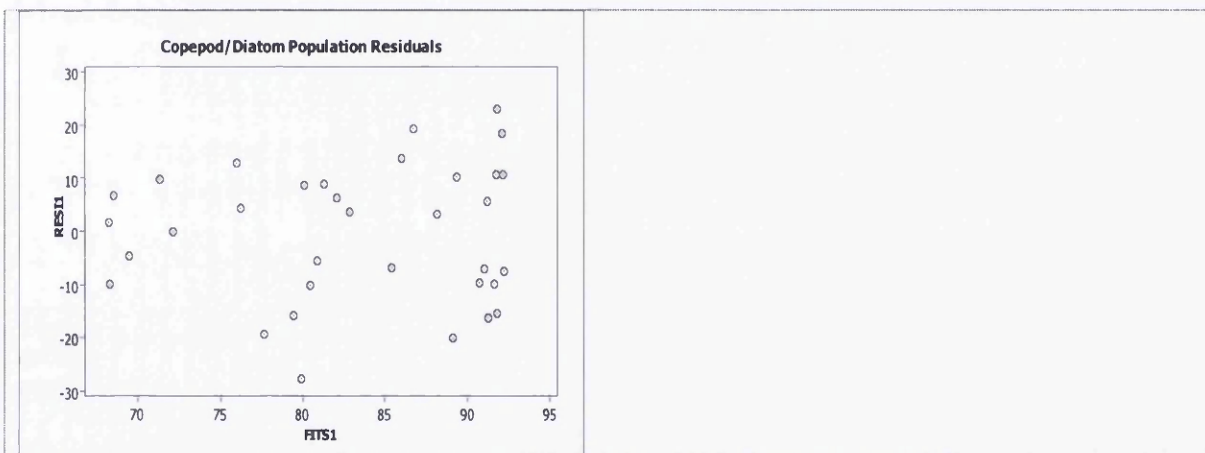


Figure 2.9 distribution of residuals. . Although a high level of variation occurs, this is expected with data sets gathered in the field, and with the inability of the model to incorporate all potential random effects. Otherwise, residuals are evenly distributed and support the significance of the model.

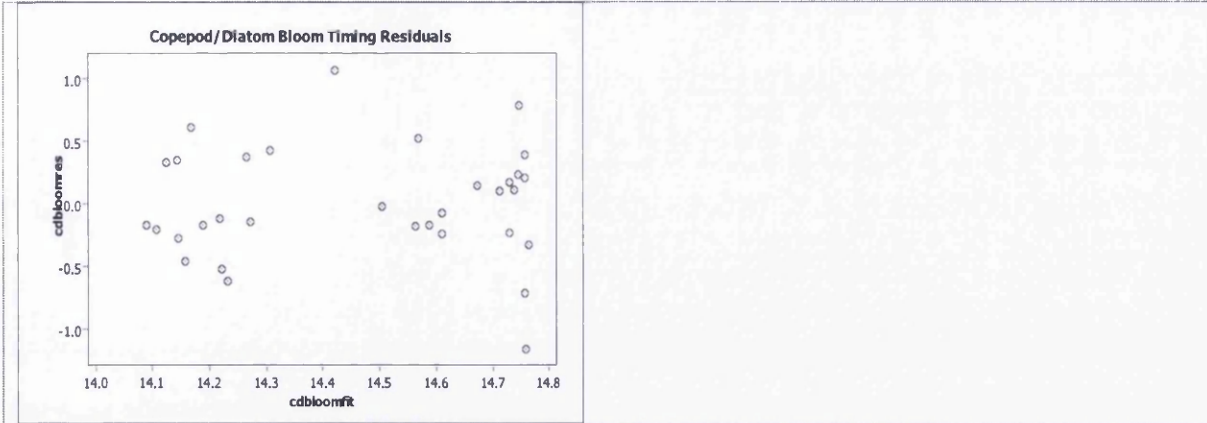


Figure 2.10 distribution of residuals. . Although a high level of variation occurs, this is expected with data sets gathered in the field, and with the inability of the model to incorporate all potential random effects. Otherwise, residuals are evenly distributed and support the significance of the model.

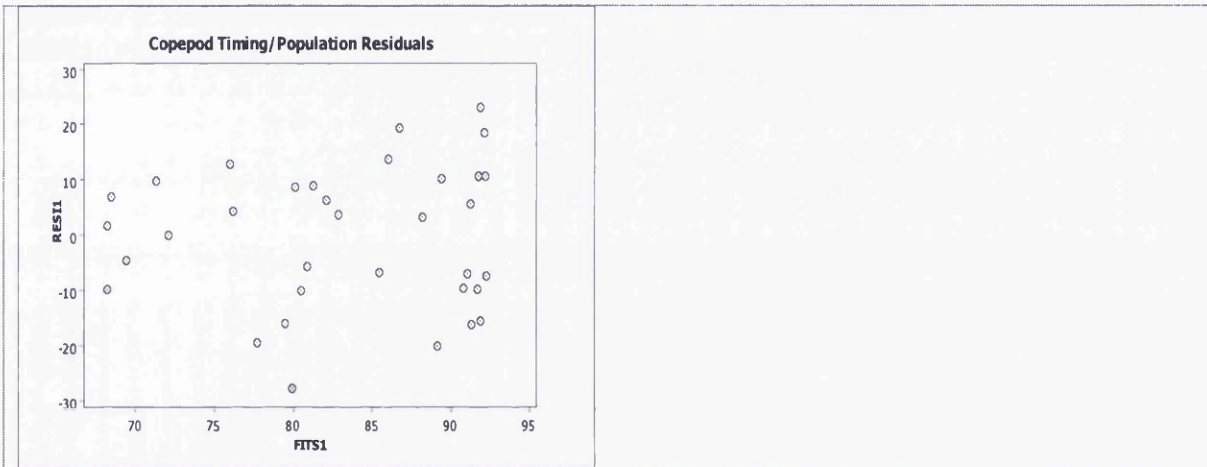


Figure 2.11 distribution of residuals. . Although a high level of variation occurs, this is expected with data sets gathered in the field, and with the inability of the model to incorporate all potential random effects. Otherwise, residuals are evenly distributed and support the significance of the model.

Chapter 3

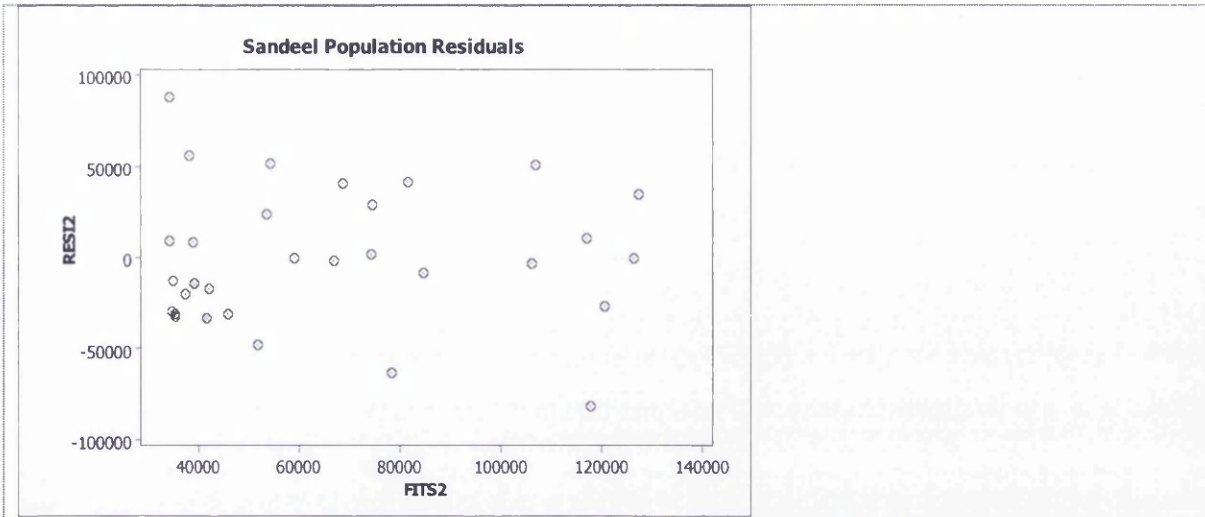


Figure 3.2 distribution of residuals. . Although a high level of variation occurs, this is expected with data sets gathered in the field, and with the inability of the model to incorporate all potential random effects. Otherwise, residuals are evenly distributed and support the significance of the model.

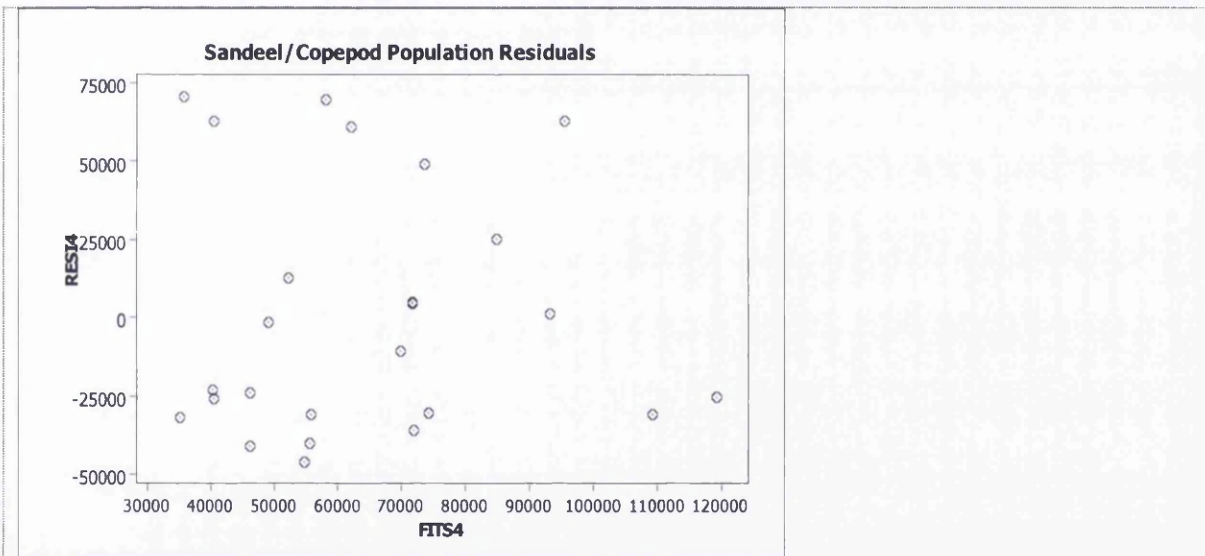


Figure 3.4 distribution of residuals. . Although a high level of variation occurs, this is expected with data sets gathered in the field, and with the inability of the model to incorporate all potential random effects. Otherwise, residuals are evenly distributed and support the significance of the model.

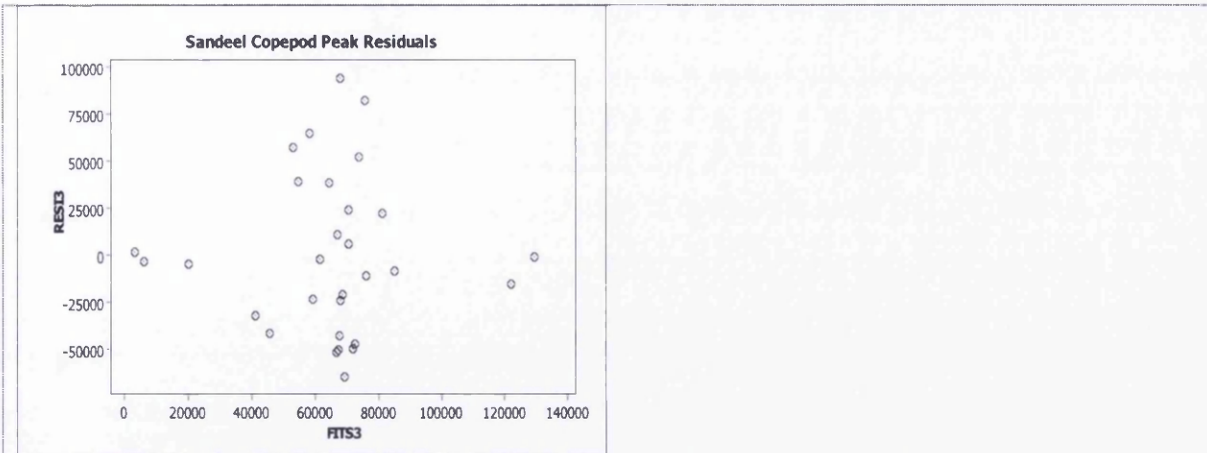


Figure 3.5 distribution of residuals. Variation is concentrated in the centre of the model, with little variation towards the ends. This is quite probably a reflection of variation in sandeel biomass caused by the periodic reopening of the commercial sandeel fishery in Shetland.

Chapter 4

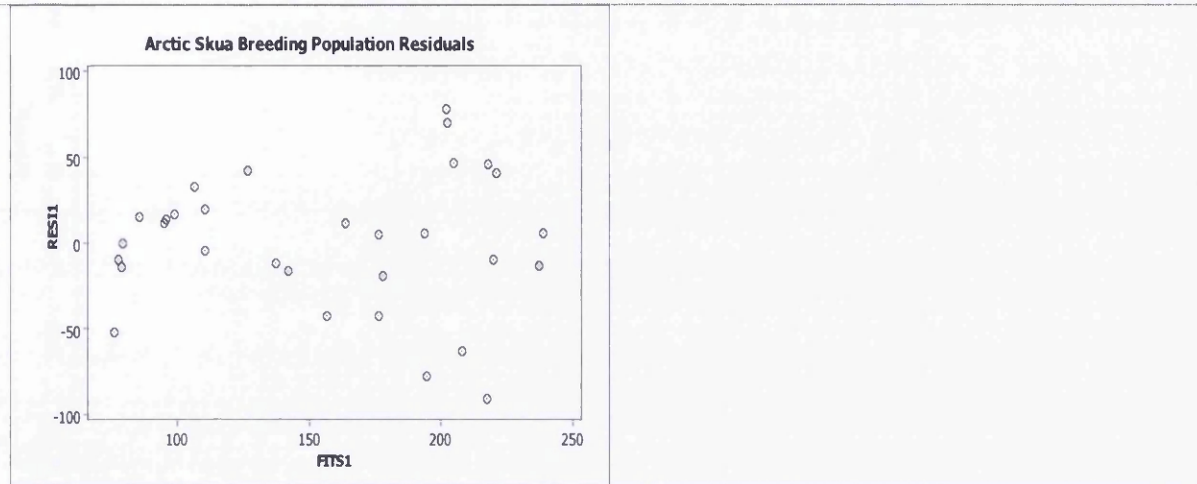


Figure 4.8 distribution of residuals. Although a high level of variation occurs, this is expected with data sets gathered in the field, and with the inability of the model to incorporate all potential random effects. Otherwise, residuals are evenly distributed and support the significance of the model.

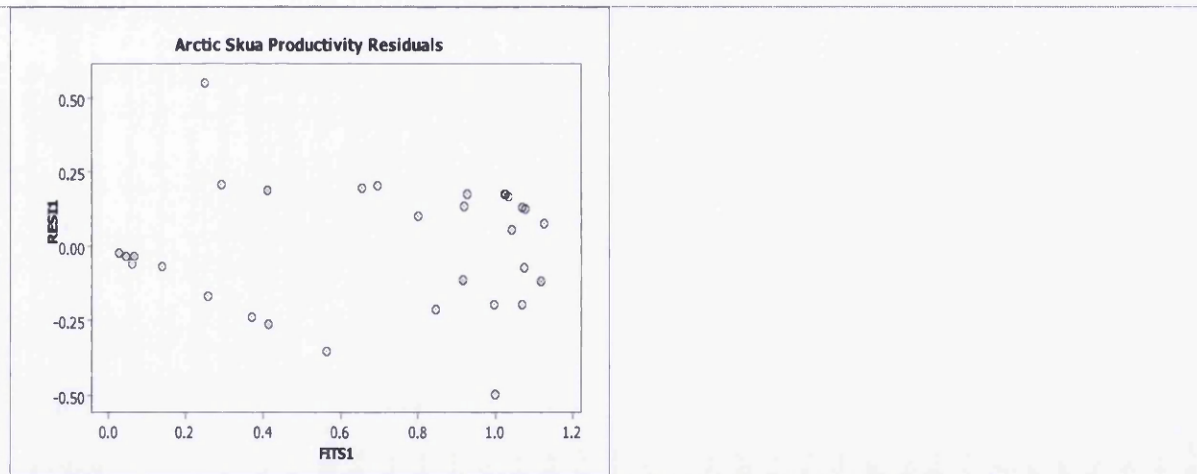


Figure 4.10, distribution of residuals. Although a high level of variation occurs, this is expected with data sets gathered in the field, and with the inability of the model to incorporate all potential random effects.

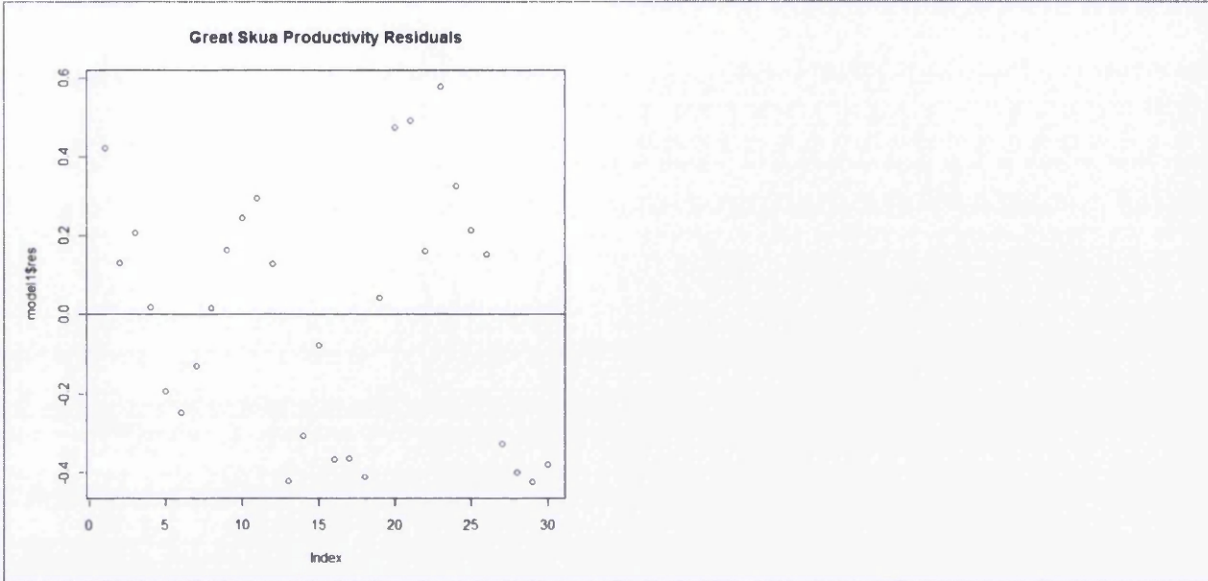


Figure 4.11 distribution of residuals. Although a high level of variation occurs, this is expected with data sets gathered in the field, and with the inability of the model to incorporate all potential random effects.

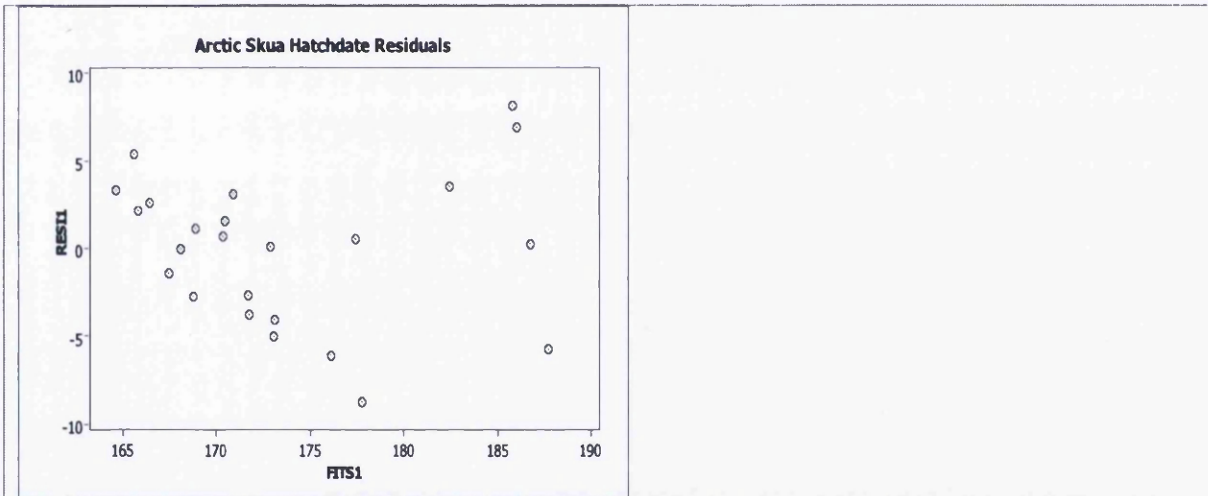


Figure 4.12, distribution of residuals. The wider pattern of scattering shows a higher degree of variability in years with a high sandeel population; this probably reflects that when food availability is low, which may reflect the influence of additional stressors in addition to food shortage.

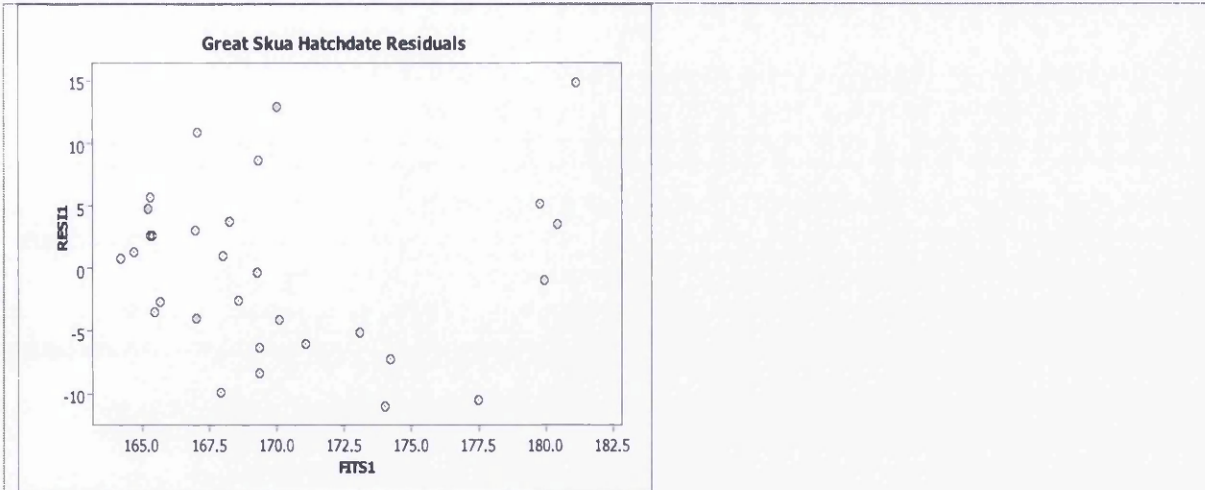


Figure 4.13, distribution of residuals. The wider pattern of scattering shows a higher degree of variability in years with a high sandeel population; this probably reflects that when food availability is high, other factors affecting breeding success become more prominent sources of variation.

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