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A view from above: changing seas, seabirds and food sources

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EXECUTIVE SUMMARY

In this review we summarize what is known about mechanisms by which climate change may be affecting the populations of seabirds around the UK. Breeding success and adult survival are the key factors affecting changes in seabird populations, and food intake is implicated as a major determinant of both. The diet of most UK seabird species is almost exclusively sandeels, small clupeoid fish or zooplankton and it is clear that the marine pelagic food web is the key ecological system determining food supply. Hence, we develop the review by first considering how climate changes may affect primary production, and then examine how this propagates through the food web to zooplankton and fish culminating in fluctuations in seabird numbers.

A trend of increasing numbers of many seabird species since 1970, particularly puffins, guillemots and razorbills, appears to have been reversed since 2000. The proximate cause of the recent declines seems to be a succession of 5 years of low breeding success for a range of species due to a shortage of food, especially sandeels. However, the connection with climate change remains uncertain, though there are indications that declines in the productivity of sandeel populations may be linked in some complex way to warming sea temperatures. The main conclusion is that no part of the marine food web, including fisheries, can be considered in isolation when trying to understand and predict the consequences of climate change for seabirds. Impacts can be expected in all parts of the system, and all parts of the system are interconnected.

1.   INTRODUCTION

Adult seabirds survival rate is high and most species are long-lived and do not commence breeding until several years old. Hence, short-term changes (<5 years) in breeding population size are most affected by factors that influence the adult survival, rather than year-to-year variability in breeding success and post-fledgling survival (Boyd *et al.*, 2006). However, long-term changes in breeding success should dictate underlying trends in population size. Factors leading to reduced adult survival and reduced breeding success include disease, reduced food availability, predation,

hunting/culling and stochastic events such as oil spills and severe storms (Furness and Tasker, 2000; Rindorf *et al.*, 2000; Davis *et al.*, 2005; Frederiksen *et al.*, 2005; Mitchell *et al.,* 2004). Several recent studies show a trade-off between adult survival rate and reproductive performance (e.g. Davis *et al.*, 2005). But variation in breeding success is much greater, and easier to measure than adult survival, and so is likely to provide a much clearer signal of food shortage, though only over a limited spatial area and time period each year (Furness, 2002; Mitchell *et al.*; 2004, Mavor *et al.* 2006).

Both breeding success and adult survival of some seabirds in the North Atlantic have been linked to climate indices such as the North Atlantic Oscillation index (NAO), with food availability being implicated as the causative link (Frederiksen *et al.*, 2004a; Sandvik *et al.*, 2005). Some of the predicted physical consequences of climate change in UK waters, such as sea-level rise, increased incidence of extreme weather events and rises in sea/air temperatures could all hypothetically affect seabird populations. For example, sea-level rise could reduce the breeding habitat available for shoreline nesting species such as terns, whilst extreme weather events can cause mass mortalities or 'wrecks' of seabirds and flooding or destruction of nests in breeding colonies (Frederiksen *et al.*, 2008b). The remit for our review is the ecological, or food-web linkages between climate change and seabirds, so we do not consider physical impacts of climate on seabird survival, and focus instead on the factors which affect the availability of food.

The diet of the 26 major seabird species monitored during the Seabird 2000 survey (1998-2002) (Table 1) is almost exclusively sandeels (mainly *Ammodytes marinus*), small clupeoid fish or zooplankton, whether self-caught (e.g. guillemots, razorbills) or stolen from other birds (e.g. skuas) . Exceptions are the scavenging species (e.g. fulmar and gulls) which feed more opportunistically and rely partly on discarded fish and offal from vessels, and some of the diving species whose diet may include a proportion of seabed (benthic) organisms. Nevertheless, it is clear that the marine pelagic food web (phytoplankton – zooplankton – pelagic fish – seabirds) is the key ecological system determining food supply to UK seabirds, and examination of changes in primary production is a logical starting point for any consideration of the impact of climate change on production of food for seabirds (Figure 1; Dulvy *et al.*, 2009). Hence, we develop the review by first considering how climate changes may affect primary production, and then examine how this propagates through the food web to zooplankton and fish culminating in fluctuations in seabird numbers. We refer, where possible, to knowledge based on studies in European waters, but also draw on the results of studies worldwide as appropriate.

Scientific name	Common name
Gavia stellata *	Red-throated diver *
Fulmarus glacialis	Northern fulmar
Puffinus puffinus	Manx shearwater
Hydrobates pelagicus	European storm-petrel
Oceanodroma leucorhoa	Leach's storm-petrel
Morus bassanus	Northern gannet
Phalacrocorax carbo	Great cormorant
Phalacrocorax aristotelis	European shag
Stercorarius parasiticus	Arctic skua
Catharacta skua	Great skua
Larus melanocephalus	Mediterranean gull
Larus ridibundus	Black-headed gull
Larus canus	Mew gull
Larus fuscus	Lesser black-backed gull
Larus argentatus	Herring gull
Larus marinus	Great black-backed gull
Rissa tridactyla	Black-legged kittiwake
Sterna sandvicensis	Sandwich tern
Sterna dougallii	Roseate tern
Sterna hirundo	Common tern
Sterna paradisaea	Arctic tern
Sterna albifrons	Little tern
Uria aalge	Common guillemot
Alca torda	Razorbill
Cepphus grylle	Black guillemot
Fratercula arctica	Atlantic puffin

Table 1. Species of seabirds regularly breeding in the British Isles, which are included in the JNCC's Seabird Monitoring Programme, and the Seabird Colony Register.

*All except the Red-throated diver were included in the Seabird 2000 census or Seabird Colony Register. Source: JNCC
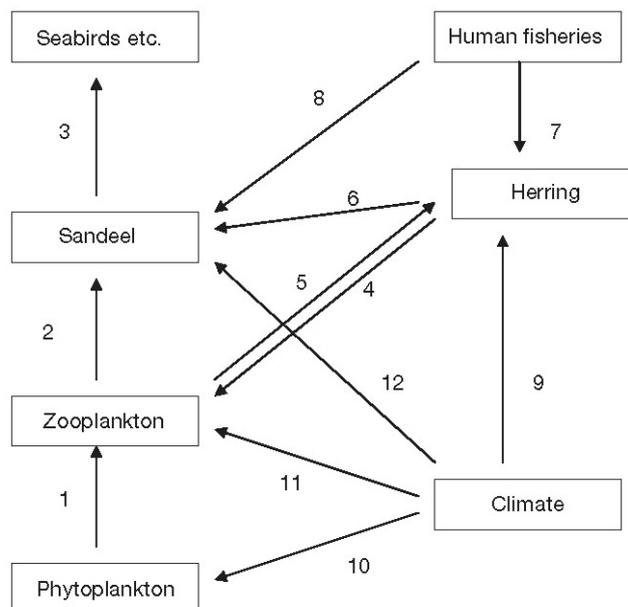
Figure 1. Simplified diagram of some documented and probable trophic and climatic controls in the North Sea pelagic ecosystem. 1: bottom-up control of zooplankton by phytoplankton (Richardson & Schoeman, 2004); 2: bottom-up control of sandeel larvae by zooplankton (Frederiksen et al,. 2006); 3: bottom-up control of seabird breeding success by sandeels (Hamer et al., 1993; Frederiksen et al., 2006); 4: top-down control of zooplankton by herring predation (Arrhenius, 1997); 5: bottom-up control of herring by zooplankton (Corten, 2001; Beaugrand, 2004); 6: top-down control of sandeels by herring predation (Friederikson et al., 2007); 7: top-down control of herring by human fisheries (Jennings et al., 2001); 8: local top-down control of sandeels by human fisheries (Rindorf et al., 2000); 9: climatic control of herring recruitment (Sætre et al., 2002); 10 and 11: climatic control of phyto- and zooplankton (Edwards & Richardson, 2004, Hays et al., 2005); 12: climatic control of sandeel recruitment (not known if direct) (Arnott & Ruxton, 2002). Reproduced from Friederikson et al, (2007).

2.   PRIMARY PRODUCTION

2.1.   Introduction

The production of zooplankton, fish and higher trophic levels in the marine ecosystem must ultimately be related to primary production, and the efficiency of transfer between trophic levels (Aebischer *et al.*, 1990; Schwartzlose *et al.*, 1999; Chavez *et al.,* 2003). Transfer efficiencies being equal, impoverished regions which are starved of nutrient inputs and the necessary trace elements required for phytoplankton growth would be expected to support smaller populations of top predators per unit area than regions where oceanographic process (e.g. upwelling) or major river inputs deliver large quantities of nutrient to the surface waters. Hence, comparing across ecosystems in, for example, the north-western Atlantic, there is a positive correlation between long-term average chlorophyll concentration and fishery yield (Frank *et al.*, 2005). However, within individual ecosystems the relationships over time between primary and fisheries yield is more variable depending on a range of factors affecting the transfer of energy up the food web and the intensity of exploitation of the fish stocks.

Analyses of satellite remote sensing data on ocean colour suggest that global phytoplankton abundance has increased and then declined over the 10 years from mid-1990s due to ENSO cycles (Gregg & Conkright, 2002; NASA, 2002; Behrenfeld *et al.*, 2006). Although this time-series is only short it does show a strong negative relationship between sea surface algal abundance and sea surface temperature, and

is evidence of a closely coupled relationship between ocean productivity and climate variability at a global scale. In the North Atlantic and over multi-decadal periods, both changes in phytoplankton and zooplankton species and communities have been associated with northern hemisphere temperature trends and variations in the NAO index. These have included changes in species distributions and abundance, the occurrence of sub-tropical species in temperate waters, changes in overall phytoplankton biomass and seasonal length, changes in the ecosystem functioning and productivity of the North Atlantic. An increase in overall phytoplankton biomass in the North Sea has been associated with an increase in smaller flagellates which are promoted by warmer and more stratified conditions. Over the whole NE Atlantic there has been an increase in phytoplankton biomass with increasing temperatures in cooler regions but a decrease in phytoplankton biomass in warmer regions. (Barton *et al.*, 2003)

2.2.   Coastal waters

2.2.1.   Changes which have occurred already
Temperature, light, and the supply of macro-nutrients (nitrate, ammonia and phosphate) are generally considered to be the key drivers of primary production in shelf seas. In coastal waters of salinities less than about 34, the main source of nitrate and ammonia is from rivers. In general ammonia inputs derive mainly from human activities, and less from natural geochemical processes in the terrestrial river catchments. Nitrate inputs also derive from human activities, particularly agriculture, but also from land erosion processes which are a function of rainfall patterns (Nixon *et al.*, 1996). Current world patterns suggest that nutrient inputs to the sea are increasing (Jones *et al.,* 1998; Dumont *et al.,* 2005), while inputs to European seas may be decreasing as a result of legislation to control discharges (OSPAR, 2003). Radach and Patsch (2007) determined the monthly and annual riverine freshwater, nitrogen (N) and phosphorus (P) loading into the North Sea from Belgium, The Netherlands, and Germany for over the period 1977–2000. They found that for continental European rivers with inputs to the southern North Sea the annual N loads had decreased by about 17 kt N /yr between 1977 and 2000. The total phosphorus and phosphate loads had decreased from about 80 and 50 kt P /yr in the 1980s to 25 and 12 kt P /yr, respectively, in the 1990s.

2.2.2.   Changes that may occur in the future
Predictions of future climate patterns over the UK under high and low carbon dioxide emission scenarios suggest that winter precipitation will increase over south-eastern UK while summers are expected to become much dryer (UKCIPO2; Arnell, 2007). However, there is already evidence that dry summers may also be associated with an increase in peak rainfall events. The resultant increased runoff will lead to pulses of nutrients with uncertain consequences in terms of coastal productivity. Overall, annual precipitation is expected to reduce over south-eastern UK. Based on these predicted trends in precipitation, and the historical patterns of discharge and flow weighted concentration (Heath, 2007b) it is predicted that, assuming land-use and anthropogenic sources of nitrate within the catchments remain approximately constant, then annual fluxes of nitrate and nitrate to coastal waters of southern and south-eastern UK (North Sea south, Channel and Celtic Sea) should decrease in line with precipitation patterns under both high and low emission scenarios. Other factors being constant, this should result in declining annual primary production in these coastal waters.

Annual fluxes of nitrate and nitrate to coastal waters of the northern and north-western UK are harder to predict, being more dependent on concentrations in river waters and hence on land-use and anthropogenic sources. In general, there is a

need for catchment-scale modelling of hydrology and nutrient sources to understand the dependency of future patterns of nutrient discharges on climate change (e.g. Wilby *et al.*, 2006).

2.3.   Open-shelf waters

2.3.1. Changes which have occurred already
In the Celtic Sea, and northern North Sea at salinities greater than about 34, concentration of nitrate in the water may be more determined by the concentration in ocean source waters than in river inputs (Hydes *et al.*, 1999; Gowen *et al.*, 2002; Heath & Beare 2008). The similarities in variation between sites found by Laane *et al.* (1996) suggest that long range processes may be important such as the variation in transport of ocean water on to the shelf.

At the end of winter, concentration of nitrate in surface waters of the Atlantic Ocean adjacent to the shelf are higher than those found over much of the shelf (Hydes *et al.*, 2004). Limited information is available on how these concentrations vary from year to year and on the variability of the exchange of these waters across the shelf break. Some time series data show that changes from year to year of 50% are possible (Kelly-Gerreyn *et al.*, 2007) as a result of changes in the depths of winter mixing (Valencia *et al.*, 2004). These variations can be translated directly into variations in annual primary production (Heath & Beare, 2008).

In the northern North Sea there has been a correlation between the annual vertical flux of nitrate from below the seasonal thermocline into the sunlit surface waters, and the North Atlantic Oscillation Index (Heath & Beare 2008). This correlation probably reflects the effects of wind mixing on the intensity of stratification in open shelf waters.

2.3.2. Changes that may occur in the future
Climate change scenarios predict increased wind mixing of the upper layers of the ocean, and this may increase the depth of mixing in winter and bring higher concentrations of nutrients to the ocean surface. Other factors being equal, this will enhance annual primary production in the ocean waters, and in open shelf waters by increasing the flux of nutrient across the shelf edge. However our understanding of the transfer process, especially the horizontal exchange across the shelf edge, is poor. Hydrographic models do not work well in this region and observations are sparse (Huthnance, 1995, 1997).

Based on past changes, increased wind mixing should also enhance open shelf annual primary production by increasing the vertical flux of nutrients during the summer productive season, though the timing of the onset of the spring bloom should be delayed. However, if this is combined with warmer sea temperatures which tend to increase the intensity of stratification, then the outcome of a climate change for primary production is harder to predict.

Climate change is predicted to affect rainfall patterns across Europe, with expected increases in the incidence of extreme flooding events. Such runoff events carry high sediment loads to coastal waters, as well as large fluxes of nutrient. The nutrient flux would be expected to increase primary production if occurring during summer months, but sediment flux increases turbidity and restricts the penetration of sunlight into the water column thereby reducing primary production. Thus, the consequences of climate change for primary production are complex and difficult to predict with any degree of confidence for a wide variety of reasons.

2.4.   Biogeochemical processes

Denitrification is a process of bacterial respiration in anoxic environments which utilises nitrate as a source of oxygen, and releases nitrogen gas. Conversely, nitrification utilises the hydrogen in ammonia and generates nitrate. The balance between nitrification and denitrification is an important factor in the nutrient budget of shelf seas (Brion *et al.,* 2004). Microbiological studies suggest that increased temperatures may decrease denitrification rates, with unknown consequences for primary production (Kelly-Gerreyn *et al.*, 2001).

2.5.   Role of acidification

In addition to the effects of temperature change, many biogeochemical processes are sensitive to the pH of the environment. Hence, ocean acidification can be expected to have some impact on nutrient cycling and primary production, but we are not yet in a position to quantify these at the system level. However, there are some categories of process that will clearly be sensitive to acidification with predictable consequences for specific groups of organisms. In particular, microbes which are characterised by calcareous structures are likely to be strongly affected. These include the foraminifera (microbes involved in the breakdown on detritus and hence nutrient recycling), and coccolithophiids (phytoplankton which produce calcium carbonate plates around their outer membrane). At certain times and locations these groups of species can be dominant players in the microbial food web, and their productivity is likely to be significantly impaired by acidification (Orr *et al.*, 2005).

3.   ZOOPLANKTON PRODUCTION

Some seabirds have been noted to feed directly on crustacean zooplankton, which occasionally form swarms near the surface (e.g. Leach's Storm Petrel; Steele & Montevecchi, 1994). However, the principal role of zooplankton in the food web which supports seabirds is as a vector for transferring primary production to fish. Hence, we review here the changes which have occurred in the zooplankton community and production, rather than considering zooplankton as a direct food source for seabirds.

3.1.   Changes which have occurred already

Strong biogeographical shifts in all calanoid copepod species assemblages have been identified in European waters since the 1960s, with a poleward extension of more than 10° in latitude of distribution limits of warm-water species such as *Centropages typicus*, *Candacia armata*, *Calanus helgolandicus*, and an associated retreat in colder-water species such as *Calanus finmarchicus* (Beaugrand *et al.*, 2002; Drinkwater *et al.*, 2003; Reid *et al.*, 1998, 2001). In addition, changes since 1960 in the phenology (seasonal timing of occurrences) of a large range of plankton species, including the timing of the spring phytoplankton bloom, have been documented and are correlated with indices of climate change (Edwards & Richardson, 2004). Some of these changes may affect the efficiency of trophic transfer of energy up the food web due to changes in the temporal coincidence of planktonic predators and their preferred prey. In the North Sea the population of the previously dominant and ecologically important zooplankton species, (the cold water species *Calanus finmarchicus*) has declined in biomass by 70% since the 1960s. Species with warmer-water affinities are moving northward to replace this species but these species are not as numerically abundant or nutritionally beneficial (lower lipid contents) to higher trophic levels. This has had inevitably important ramifications for the overall carrying capacity of the North Sea ecosystem. Temperature has also had an effect of the size-range of zooplankton with a move towards smaller species as the temperature has increased.

Hydroclimatic changes have also been related to jellyfish increases recorded in European waters (Lynam *et al.*, 2004; Attrill *et al.*, 2007). Temperature appears to be one of the main triggering mechanisms for exceptional outbreaks of these gelatinous carnivores (CIESM, 2001; Purcell, 2005). Warm temperatures may be related to a prolonged period of occurrence and increased abundance of the ctenophore *Mnemiopsis leidyi* (Purcell, 2005). This gelatinous predator was introduced into the Black Sea, and contributed to the reduction in the fisheries there (see references in Purcell, 2005).

Despite the documentation of changes in species distribution that have occurred, there is no clear evidence of changes in zooplankton production. This is largely because zooplankton community production is exceptionally difficult to estimate, even by direct experimental measurements, and certainly from only data on species abundances. Food supply, temperature, mortality, and a range of other factors will materially affect the production of each component species in the community in different ways.

3.2.   Changes that may occur in the future

There is a clear expectation that poleward shifts and expansions of latitudinal distributions of plankton species will continue with increasing sea temperatures. These changes can be modelled empirically, based on the historical multivariate environmental envelope of given species established from analysis of the historical distributions of taxa in relation to sea surface temperatures (Beaugrand & Helaouët, 2008**)**. We can have reasonable confidence in such predictions for different climate change scenarios, subject to the assumption that the underlying processes governing the environmental envelope will remain constant in the future (Davis *et al.*, 1998; Pearson & Dawson, 2003). In addition we can be quite confident that the zooplankton diversity in UK waters will increase with continued warming, with a progressive shift towards smaller-sized plankton. However, it is not possible to say with any confidence what the consequences of climate change may be for zooplankton production at the community level. We can speculate, for example, that a shift towards smaller plankton may lead to reductions in trophic transfer efficiency due to increased food chain length, and there is recent experimental evidence that ocean acidification may be detrimental to egg hatching success for some copepod species (Mayor *et al.*, 2007). But, it is unclear how these effects might translate into production by populations or the plankton community as a whole.

4.   FISH

Seabirds prefer, or are able to catch, only a few of the fish species present in UK waters (principally sandeels, sprat (*Sprattus sprattus)* and young herring and gadoids). Nevertheless, the other fish species are also potentially important in determining the food availability for birds since many of them (e.g. cod, haddock, whiting, saithe) are also predators on sandeels and clupeoids, and hence act as competitors to the seabird populations. Others may represent potential alternative, though less nutritious prey when sandeels and clupeiods are scarce. Hence, we begin our review of climate effects on fish by considering changes which have occurred in the community as a whole, and then focus on sandeels as the key species for seabirds.

4.1. CHANGES WHICH HAVE OCCURRED ALREADY

4.1.1. Fish communities

Shelf sea fish assemblages in the north-eastern Atlantic have shifted their distribution into deeper water since the 1970s in parallel with warming sea temperatures so as to maintain themselves in a preferred temperature range (Hedger *et al.*, 2004; Perry *et al.*, 2005; Poulard & Blanchard, 2005, Desaunay *et al.*, 2006; Heath, 2007a; Dulvy *et al.*, 2008). In some areas, this is manifest as a poleward shift in distribution, but not necessarily so if local topography and hydrography provides a thermal refuge through movement in some other direction.

Despite the community level changes in fish which correlate with climate fluctuations, there are few cases where individual species productivity can be unambiguously attributed to climate change. This is mainly because fishing has an overriding effect on the abundances of all of the major commercial species, and disentangling effects due to climate is extremely difficult. The exception is the case of cod in the North Sea, where it is clear that recruitment is negatively affected by warm sea temperatures (Clarke *et al.*, 2003; O'Brien *et al.*, 2000). Maximum sustainable yields of North Sea cod decline with increasing temperature and fishing mortalities which were sustainable in a cold climate phase such as the 1960s are no longer sustainable in a warm climate phase such as since 2000 (Cook & Heath, 2005). However, it remains unclear whether the negative effect of temperature on North Sea cod recruitment is a direct physical impact, or acts through a food web or predation effect (Beaugrand *et al.*, 2003).

Some fish species have extended their distribution ranges to such an extent as to inhabit areas where they were absent prior to the 1980s. Examples include; anchovy and sardine (Beare *et al.*, 2004a); red mullet, (Beare *et al.*, 2004b); blue-mouth, (Mamie *et al.*, 2007); Genner *et al.*, (2004); Stebbing *et al.*, 2002). Similarly, there has been a much-reported influx of snake pipefish (*Entelurus aequoreus*) into European waters since 2003 (Lindley *et al.*, 2006; van Damme & Couperus, 2006; Harris *et al.*, 2007; Kloppmann & Ulleweit, 2007). It is unclear why snake pipefish numbers have apparently increased, though the increased abundance of larval and juvenile *E. aequoreus* in Continuous Plankton Recorder plankton samples as far west as the Mid-Atlantic Ridge may coincide with a rise in winter, spring and summer sea temperatures (January–September), when the eggs, which are brooded by the male, are developing and the larvae are growing in the plankton (Kirby *et al.*, 2006). Alternatively, the sudden appearance of this species may be a result of changes in zooplankton availability which in turn has been caused by changes in the hydroclimatic environment (van Damme & Couperus, 2006).

It has been suggested that the snake pipefish influx might pose a threat to certain marine predators, notably seabirds (Harris *et al.*, 2007), and they have also been reported as occurring in the stomach contents of important commercial fish species (Stafford *et al.*, 2006), possibly associated with a lack of 'usual' prey types such as sandeels. These fish may represent a food of "last resort" since they are a poor quality resource; low in lipid, bony and difficult to digest (Harris *et al.*, 2008). The fact that seabirds did not feed snake pipefish to chicks in large numbers prior to 2002 may reflect the fact that abundances of preferred fish prey, such as sandeels, were much higher than they have been in the last few years or that snake pipefish have increased in availability.

4.1.2. Changes in sandeel populations

Sandeel recruitment in the southern North Sea has been negatively correlated with high winter sea temperature (Arnott & Ruxton, 2002) though the exact mechanism through which temperature might affect affect sandeel recruitment remains unclear. Apart from a direct effect of temperature on some aspect of the sandeel life history, regulation through changes in the abundance of zooplankton is also a plausible explanation. Sandeels feed mainly on zooplankton, and there has been a marked decline on the growth rate of sandeels in the north-western North Sea, with consequential delayed maturation (Boulcot *et al.*, 2007; Boulcot and Wright, 2008; Wanless *et al.*, 2004). Other possibilities include predation control by fish that consume sandeel larvae (Frederiksen *et al.*, 2007). For example, herring *Clupea harengus* feed on larval sandeels, and stocks in the North Sea have increased from less than 100,000 tonnes in the late 1970s to 2 million tonnes in 2004 (ICES, 2004), approximately inverse relationship with sandeel abundance. However, though adult herring biomass has been high since 2000, survival of larvae has declined, which might suggest a common environmental factor affecting the recruitment of both sandeels and herring. Still further possible mechanisms involve changes in the dispersal patterns of larvae from spawning sites to settlement sites for juveniles which have a direct effect on survival and recruitment (Proctor *et al.*, 1998), and changes in seasonal behavioural patterns of sandeels, in particular the time they spend buried in sediments, in relation to temperature and the timing of the spring plankton bloom (Greenstreet *et al.*, 2006a; Scott *et al.*, 2006).

The recent decline in sandeel abundance in the North Sea shows a strong regional pattern, with the greatest decrease in the north, off Shetland and southern Norway, and lesser decreases in the southern North Sea and around Dogger Bank. Different factors may affect sandeel populations in different parts of the North Sea (Frederiksen *et al.*, 2007). The total stock biomass of sandeels around Shetland has varied on approximately inverse relationship with the spawning stock biomass of herring in the North Sea. Such a mirror-image pattern may indicate a top-down effect of herring predation on sandeel in the northern North Sea, and it has long been known that sandeel larvae form an important part of herring diet in spring (Hardy, 1924; Last, 1989). Elsewhere, herring predation has previously been shown to affect the recruitment to stocks of another small pelagic species, such as Barents Sea capelin (Gjøsæter and Bogstad, 1998).

Recruitment to all of the sandeel areas around the UK has been continually low since 2002, with a consequent decline on overall abundance. The industrial fishery for sandeels in the North Sea was closed completely by the European Commission from 15 July 2005 (Anon, 2005), after annual landings during the 1990s of 600,000–1,100,000 tonnes, declined to around 300,000 tonnes in 2003 and 2004 (ICES, 2004).

4.1.3. Demersal fish predators on sandeels and pelagic fish

A range of demersal fish species in UK waters consume sandeels and small clupeoids as a significant component of their diet, and hence could compete with seabirds. Amongst these, whiting, is one of the most piscivorous predatory fish species in the North Sea, and studies relating diet composition to body condition suggest that whiting have poorer body condition in years when sandeels and young clupeoids are scarce (Stafford *et al.*, 2006). In such years, whiting were found to have an increased proportion of crustaceans and nutritionally poor fish such as pipefish in their diet. Cod have a more flexible diet and may be less affected by fluctuations in the abundance of sandeels and clupeoids. However, whiting and cod are only a component of the piscivorous fish assemblage in the North Sea, and

estimating the total competition for food between fish and seabirds requires a comprehensive analysis of feeding fluxes in the food web.

Estimating the consumption of fish by seabirds in the North Sea depends on assumptions about the feeding habits of various key bird species, for example whether fulmars feed mainly on fishery discards and offal or on live fish, and on the estimates of bird species abundance. Given the range of possible assumptions, consumption of pelagic fish and sandeels by seabirds during the period 1983-1986 in the North Sea has been estimated as 109,000-173,000 tonnes and 125,000-199,000 tonnes per year respectively (Bryant and Doyle, 1992). This compared with approximately 18,000 and 40,000 tonnes per year respectively by mammals (seals and cetaceans). In contrast, the combined fisheries for pelagic species (herring, sprat, Norway pout) and sandeels in the same periods removed 1.5 million tonnes per year. But these figures are small compared to the consumption of pelagic fish and sandeels by fish predators in the North Sea, which was estimated to be 7.4 million tonnes per year during 1983-1986 (Heath, 2005) (Figure 2). Thus, seabirds apparently accounted for only 2-4% of the removals of combined pelagic fish and sandeels. Locally, and in certain seasons (e.g. breeding months) seabirds may account for a substantially larger proportion of removals, for example at Shetland and off the east coast of Scotland (Furness, 1990; Monaghan, 1992; Wanless *et al.*, 1998; Duant *et al.*, 2008), but at the regional scale it is clear that the piscivorous fish assemblage has a far greater impact on food for seabirds than do seabirds themselves. Hence, climate and fishing impacts on the fish community as a whole have the potential to influence the food availability for seabirds through highly indirect food-web links which are not easily predictable.
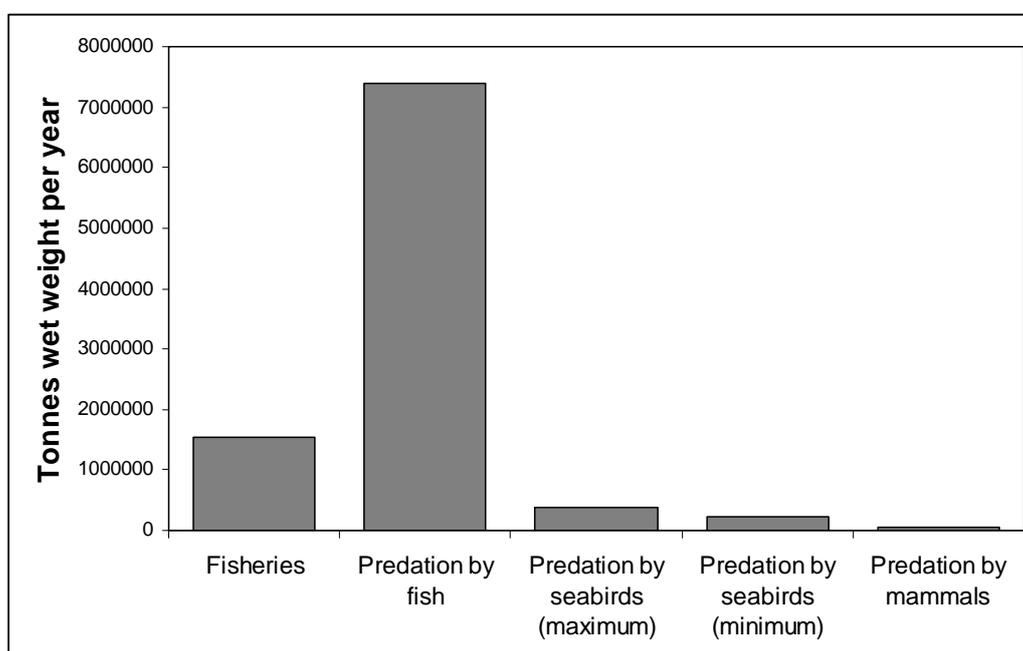

Figure 2. Annual removals of pelagic fish and sandeels from the North Sea by fisheries, predation by other fish, and predation by seabirds and marine mammals. Maximum and minimum estimates of seabird predation are given, reflecting assumptions about the numbers and diet of fulmars. Data compiled from Bryant & Doyle, 1992; Heath, 2005)

4.2.   Changes that may occur in the future

Predicting the likely changes in fish populations of UK waters due to projected climate change is extremely difficult because of the very large influence of fishing.

What will happen in the future will depend mainly on how European fisheries management policy develops in response to the requirement to conserve and restore fish communities and habitats as well as the stocks of commercially exploitable species. However, it is clear that the environment in which fisheries operate is changing due to climate and the paradigm of North Sea cod is generally applicable – fishing mortality targets intended to confer sustainability are not constant, and targets developed from analysis of past data will need updating at intervals in response climate change. For some species e.g. those at the northern edge of their latitudinal range, this may mean that higher fishing mortality rates become sustainable. For others, such as cod, the evidence is that fishing mortality targets need to be reduced as sea temperatures increase.

Regarding the key sandeel species, it is clear that UK waters are at the southern edge of the latitudinal range of *A. marinus.* In addition, unlike many other fish species, sandeels are not free to move into deeper waters in response to warming sea temperatures because they are tightly associated with sandy sediments of rather narrow range of grain size composition. Hence, the sequence of poor sandeel recruitments since 2002, associated with warm conditions, may well represent a direct climate impact and the early stages of a poleward retreat for this species. The pattern of recruitment to sandeels populations suggests that, like cod, productivity and hence the capacity to sustain exploitation is likely to decline with a warming climate.

## 5.	SEABIRDS AND CLIMATE CHANGE IN UK WATERS

### 5.1.	Changes which have occurred already
Three censuses of seabird numbers around the UK have been conducted since 1970, and show sustained increases in abundance of, for example skuas, guillemots, gannets, rarzorbills and Atlantic puffins, whilst black-legged kittiwakes and many gull species have declined in numbers (Figure 3). However, since the 2000 census, numbers of some of the species which had been increasing have started to decline at many breeding sites (e.g. Atlantic puffin www.nerc.ac.uk/press/releases/2008/30-puffins.asp). The causes are not completely clear since there is little or no information on adult survival rates. Most species in the North Sea have suffered a higher than usual proportion of years of breeding failure since 2003, but the consequences of this should only become apparent in the coming few years as these year-classes of birds mature and join the breeding population (Frederiksen *et al.*, 2004b; Mavor *et al.,* 2005, 2006, 2007; Reed *et al.*, 2006). Within any one year, some species have bred successfully, others not. Within the same species, some regions have shown a successful breeding and others not. However, the most severe problems, including total failures of some species, occurred in Shetland and Orkney in the northernmost part of the North Sea. In 2004 exceptionally low breeding success was also observed in colonies along the east coast of Britain (Harris *et al.,* 2004; Mavor *et al.,* 2005). Although bad weather during the chick-rearing period was partly to blame at some colonies, other possible causes at, for example the Isle of May colony in the Firth of Forth, include a lack of high-quality food (Davis *et al.*, 2005; Wanless *et al.,* 2005).
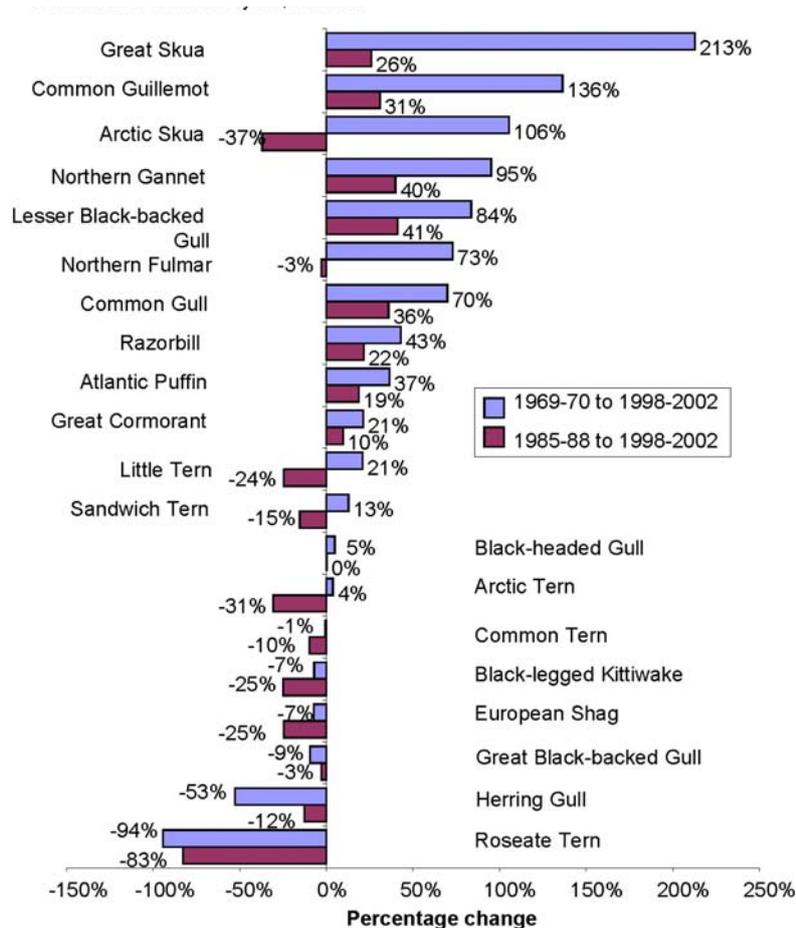
Figure 3. Changes in the numbers of breeding seabirds in the United Kingdom 1969-2002. Percentage changes refer to coastal-nesting seabirds only - inland colonies were not surveyed during the Operation Seafarer (1969-70) and the SCR Census (1985-88). Manx shearwater, Leach's storm-petrel and European storm-petrel are omitted as they were not surveyed during the Operation Seafarer (1969-70) and the SCR Census (1985-88). Survey methods for black guillemots during Operation Seafarer (1969-70) were not comparable with Seabird 2000 (1998-2002). Reproduced from Mitchell et al. (2004).

5.2.   Role of sandeels in the breeding success of seabirds

Most seabirds in the North Sea feed mainly on sandeels during the breeding season (Wanless *et al*., 1998; Furness & Tasker, 2000; Furness, 2002). The ecological characteristics of seabird species in the North Sea have been ranked according to their sensitivity to fluctuation in the abundance of sandeels, from highly sensitive (e.g. terns, black-legged kittiwake, Arctic skua) to insensitive (e.g. northern gannet) (Furness & Tasker, 2000). The most sensitive seabirds are those with high foraging costs, little ability to dive below the sea surface, little 'spare' time in their daily activity budget, short foraging range from the breeding site, and little ability to switch diet.

In recent decades, sandeels have been the only common high-lipid schooling fish around Shetland, and unsurprisingly the breeding success of most species of seabirds is closely related to sandeel abundance in that region (Hamer *et al*., 1993; Davis *et al*., 2005). This dependence is clearly illustrated by data on breeding success of Arctic skuas and black-legged kittiwakes on the island of Foula, which show a close correlation with each other across the years, and strong correlation with the Shetland sandeel total stock biomass. Arctic skuas in Shetland feed almost exclusively on sandeels, although they obtain these by stealing them from terns, black-legged kittiwakes and auks, and so the link between their breeding success and sandeel stock size is indirect (Furness, 1987; Pennington *et al*., 2004; Davis *et*

al., 2005). The amount of sandeels consumed by Arctic skuas can be estimated from data on their numbers and energy requirements. The annual consumption of sandeels by Arctic skuas at Shetland in the period 1980–2000 is estimated to have been around 65 tonnes per year. This contrasts strongly with the observation that Arctic skua breeding success at Shetland fell to less than half of the level seen in years of high sandeel abundance when the sandeel stock biomass was below about 30,000 tonnes. The data indicate that Arctic skuas require a sandeel stock biomass about 460 times greater than the amount that they consume, in order to be able to gain energy at a rate sufficient to sustain a good level of breeding success.

Further south in the North Sea, off SE Scotland and NE England, sandeels are also the main prey of most seabird species (Wanless *et al.*, 1998). In contrast to Shetland, other fish prey are also available, and in particular young clupeids (mainly sprat) are taken in some years by seabirds (Bull *et al.*, 2004; Harris *et al.*, 2004; Wilson *et al.*, 2004), and since 2003 there have been increasing observations of attempted feeding on snake pipefish (Harris *et al.*, 2007). Snake pipefish probably represent a food of "last resort" since they are a poor quality resource; low in lipid, bony and difficult to digest (Harris *et al.*, 2008). There are no long-term data on sandeel abundance in this area, but during the 1990s local sandeel biomass was reduced by an industrial fishery, and this was associated with low breeding success of black-legged kittiwakes on the Isle of May in the Firth of Forth (Rindorf *et al.*, 2000; Frederiksen *et al.*, 2008a). Frederiksen *et al.* (2005) used Continuous Plankton Recorder data to develop an index of sandeel larval abundance, and this index was positively correlated with breeding success of four seabird species in the following year. The sandeel larval index was also strongly positively related to the abundance of phyto- and zooplankton, suggesting strong bottom-up control (Frederiksen *et al.*, 2005). In 2004, breeding success was exceptionally low for most seabird species on the Isle of May, despite sandeel larvae being abundant in the spring of 2003. Detailed studies showed that the energy content of both sandeels and sprat fed to seabird chicks in 2004 was extremely low, indicating poor food availability for the fish (Wanless *et al.*, 2005). Data from chick-feeding Atlantic puffins and Continuous Plankton Recorder samples also indicate that the size-at-date of both larval, 0 group and older sandeels has declined substantially since 1973, although it is unclear the exact cause of this decline might be (Wanless *et al.*, 2004).There is thus evidence that both abundance and quality of seabird prey is under bottom-up control in this region, and this is likely to have affected seabird breeding success (Kitaysky *et al.*, 2006).

In the case of seabirds that feed extensively by scavenging at fishing vessels (especially great skuas, fulmars *Fulmarus glacialis*, great black-backed gulls *Larus marinus*) part of the impact on their breeding success may be due to reduced amounts of fishery discards and offal in recent years (Votier *et al.*, 2004, 2007; Käkelä *et al.*, 2005, 2007; Furness *et al.*, 2006, 2007). Although these seabirds appear to feed by preference on sandeels when available, they turn to fishery offal and discards as an alternative food, and in the last few years there have been large reductions in amounts of discards and offal provided to seabirds in the north-west North Sea at a time when sandeels have also been depleted. Great skuas have attempted to mitigate this situation by increasingly killing other seabirds, but have also suffered breeding failures due to food shortage, part of which results from the fact that great skuas will kill chicks of neighbouring skua pairs. The depredations on other seabirds will also reduce their breeding success, as the chances of chicks surviving if a parent has been killed during the breeding season will be much reduced. Although northern gannets mainly feed on pelagic fish in summer, discards at fishing vessels makes up a significant component of the diet in winter. A trend for gannets to be moving further south in winter than they did previously may be related to reductions in discarding (Furness, unpublished data).

5.3. Link between climate change and seabird numbers

It is tempting to attribute the sustained reduction in breeding success of many seabird species since 2003 to climate change (e.g. Kitaysky & Golubova, 2000; Royal Commission on Environmental Pollution, 2004; RSPB, 2004; BBC, 2005). The causative links between climate and seabirds could be i) warming sea temperature and changes in primary production patterns, leading to ii) changes in zooplankton communities and production, leading to iii) suppression of sandeel growth rate and recruitment, iv) changes in sandeel behaviour, v) declining sandeel abundance, and hence vi) reduced food availability for seabirds and vii) reduced seabird breeding success, frequency of breeding, adult survival and/or increased age of first breeding. However, much depends on the nature of each of the stages in such a complex chain of effects and the degree of dependence on sandeels. For example, it is clear that declines in Atlantic puffin and guillemots numbers have occurred only since 2003, coincident with exceptionally warm sea temperatures. Prior to this, numbers of these species had been increasing on average since 1970, throughout a period of warming. For the proposed connection between climate change and seabirds to be viable, one or more of the links in the connection must exhibit a dome-shaped or threshold-type response whereby rates increase below some threshold temperature, and decrease once the threshold is exceeded. Additionally, there is considerable scope for regional differences in response (Harris *et al.*, 2005; Votier *et al.*, 2005). In some areas (northern UK waters) sandeels are the only significant prey so populations of birds are tightly bound to that of sandeels. Elsewhere (southern UK waters) there are various alternative prey such as sprat and juvenile herring, so the linkage to sandeel availability is less tight.

A test of the climate-seabird system such as outlined above would be whether sandeel abundance and seabird breeding success responded positively to a succession of cool years within the expected overall warming trend. In addition, research is needed to mathematically formulate the response relationships in the system, including switching to alternative prey, so that a dynamic model can be assembled to investigate the overall responses of seabird populations to fluctuating temperatures.

Adult survival is also an important component of seabird population dynamics. We do not know how adult survival may have changed over time, or the relative contributions of breeding success and adult survival to recent changes in seabird numbers. Climate change could have a significant effect on adult survival through increases in the incidence extreme weather events leading to mortalities through starvation or exhaustion (Frederiksen *et al.*, 2008b).

5.4. Changes that may occur in the future

In the short term (less than 5 years), we can predict with reasonable confidence that the recent succession of poor breeding years will propagate through the population to a decline in the adult breeding numbers. Beyond this, changes will depend on the balance between breeding success, maturation rate and adult survival, which are difficult to predict.

If it turns out that recent declines in sandeel recruitment and abundance are a response to climate change so that sandeel stocks do not recover over time with continued warming, then the future patterns of seabird breeding maturation and survival will depend critically on the scope for feeding on alternative prey. Currently, the only abundant alternatives to sandeels are sprat and juvenile herring, which are distributed mainly in southern UK waters. However, it cannot be ruled out that climate change could result in the growth of sprat populations in northern UK waters or the

establishment of some other currently scarce species as an alternative food resource. The explosion of snake pipefish numbers since 2002 may be an example of the latter, though as it turns out they represent a nutritionally poor alternative to sandeels.

6. CONCLUSIONS

The main message from this review is that no part of the marine food web, including fisheries, can be considered in isolation when trying to understand and predict the consequences of climate change for seabirds. Impacts can be expected in all parts of the system, and all parts of the system are interconnected.

Some features of the system are more readily predictable than others. For example, the shift in distributions of fish communities into deeper water, apparently tracking isotherms as sea temperatures rise, and the poleward movement of the zoogeographic boundaries between plankton communites, are clear and expected responses to climate change. However, the origins and causes of changes in regional abundance of fish species, including sandeels, are compounded by the effects of fishing, and the basis for changes in primary production are complex and uncertain.

Seabirds are amongst the top predators in the marine system, so unless there is tight linkage between climate, the abundance of food, and the dynamics of seabird populations, the relationship between climate and birds is very hard to predict. Such strong linkages are well documented for plankton, fish and bird populations in, for example, the Galapagos Islands where primary production is tightly linked to ocean upwelling and El Nino events cause large fluctuations in production (Anderson, 1989). However, in UK waters the climate fluctuations are less extreme, and changes in the food web are more subtle. So, whilst the decline in breeding success of many UK seabird species since 2003 is most likely to be linked to the availability of sandeels, there is only a tentatitive basis for a connection with climate change.

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