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Climate, copepods and seabirds in the boreal Northeast Atlantic – current state and future outlook

Running title: Climate, copepods and seabirds

MORTEN FREDERIKSEN[1,2], TYCHO ANKER-NILSSEN[3], GRÉGORY BEAUGRAND[4]
and SARAH WANLESS[2]

[1]*Department of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde,*

Denmark

[2]*Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB, UK*

[3]*Norwegian Institute for Nature Research, PO Box 5685 Sluppen, 7485 Trondheim, Norway*

[4]*Laboratoire d'Océanologie et de Géosciences, Centre National de la Recherche*

Scientifique, UMR LOG CNRS 8187, Station Marine, Université des Sciences et Technologies

de Lille – Lille 1 BP 80, 62930 Wimereux, France

Correspondence: Morten Frederiksen, tel. +45 8715 8673, fax +45 8715 5010, e-mail:

mfr@dmu.dk

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Abstract

The boreal Northeast Atlantic is strongly affected by current climate change, and large shifts in abundance and distribution of many organisms have been observed, including the dominant copepod *Calanus finmarchicus*, which supports the grazing food web and thus many fish populations. At the same time, large-scale declines have been observed in many piscivorous seabirds, which depend on abundant small pelagic fish. Here, we combine predictions from a niche model of *C. finmarchicus* with long-term data on seabird breeding success to link trophic levels. The niche model shows that environmental suitability for *C. finmarchicus* has declined in southern areas with large breeding seabird populations (e.g. the North Sea), and predicts that this decline is likely to spread northwards during the 21st century to affect populations in Iceland and the Faroes. In a North Sea colony, breeding success of three common piscivorous seabird species (black-legged kittiwake (*Rissa tridactyla*), common guillemot (*Uria aalge*) and Atlantic puffin (*Fratercula arctica*)) was strongly positively correlated with local environmental suitability for *C. finmarchicus*, whereas this was not the case at a more northerly colony in west Norway. Large seabird populations seem only to occur where *C. finmarchicus* is abundant, and northward distributional shifts of common boreal seabirds are therefore expected over the coming decades. Whether population size can be maintained depends on the dispersal ability and inclination of these colonial breeders, and on the carrying capacity of more northerly areas in a warmer climate.

Introduction

One of the most important issues currently facing ecologists is understanding, predicting and

anticipating the population-level response of organisms to climate change (Walther *et al.*,

2002; Beaugrand, 2012). Important questions include whether populations will increase or

decline, perhaps to the point of local extinction, and whether ranges will shift, expand or

contract (Parmesan, 2005). Answering these questions requires an understanding of the

thermal tolerance, trophic relationships and dispersal capacity of the focal organism, as well

as the extent of phenotypic plasticity and rate of microevolutionary change in these traits

(Visser, 2008). This task is particularly challenging for endothermic organisms at high

trophic levels, because trophic effects may be more important than direct physiological

effects of rising temperatures (Kirby & Beaugrand, 2009; Luczak *et al.*, 2011). Robust

predictions thus necessarily involve detailed knowledge of the likely climatic response of key

organisms at lower trophic levels.

Observed changes in ocean climate have been both fast and complex (Burrows *et al.*,

2011), and some of the most pronounced large-scale biological responses to climatic

variability and global climate change have been observed in marine ecosystems (Harley *et*

al., 2006). Because of the high heat capacity of the oceans, short-term temperature variability

is low, and many marine ectotherms are therefore adapted to a specific thermal environment,

particularly during reproduction (Hirche *et al.*, 1997; Pörtner & Peck, 2010). Oceanic

currents are also linked to climate and thus likely to change with increasing temperatures,

leading to shifts e.g. in the location of upwelling zones and in dispersal patterns of marine

organisms (Brander *et al.*, 2003). Large distributional shifts linked to changing temperatures

or currents are consequently common, particularly among marine plankton (Hays *et al.*,

2005) and fish (Perry *et al.*, 2005), with potentially far-reaching consequences for dependent

endothermic predators including seabirds.

Seabirds are land-based during reproduction, and therefore their population dynamics and demography are relatively well known. Many studies have shown strong correlations between seabird demographic parameters (fecundity and survival) and various aspects of ocean climate, including indices of large-scale atmospheric circulation patterns (e.g. Jones *et al.*, 2002; Jenouvrier *et al.*, 2005) as well as local sea surface temperature (e.g. Frederiksen *et al.*, 2004; Harris *et al.*, 2005a). Nevertheless, the underlying mechanisms linking demography and climate remain poorly understood, although most published studies have implicitly or explicitly assumed that trophic links were important (e.g. Durant *et al.*, 2003). In the boreal Northeast Atlantic (ca. 55-70° N), many seabird populations have shown repeated breeding failures and pronounced declines in recent decades (JNCC, 2009; Frederiksen, 2010; Barrett *et al.*, 2012). Although the reasons for these declines are only partially understood, circumstantial evidence points towards an important role of climate change (Heath *et al.*, 2009). It is therefore timely to improve our understanding of the mechanisms through which climate affects seabirds in this region, including the role of important organisms at lower trophic levels.

The copepod *Calanus finmarchicus* is a key species for the trophodynamics of boreal ecosystems of the North Atlantic Ocean (Planque & Batten 2000). This species generally constitutes > 50% of the total copepod biomass, and can even reach > 90% in some regions (Planque & Batten, 2000). The species is a very important prey for small pelagic fish favoured by seabirds, as well as for larval or juvenile stages of commercially important larger fish (Beaugrand *et al.*, 2003; Beaugrand & Reid, 2003). Recent studies suggest that the species is likely to experience a rapid northward shift in distribution over the coming decades (Reygondeau & Beaugrand, 2011). Large declines in abundance of *C. finmarchicus* have occurred along the southern range limit, e.g. in the North Sea (Reid *et al.*, 2003; Heath *et al.*,

2009), and low reproductive success of several forage-fish dependent seabird species has been linked to these declines (Frederiksen *et al.*, 2006).

Here, we combine estimates of historical and future environmental suitability for *C. finmarchicus* from an ecological niche model with time series of seabird reproductive success from two long-term studies in the Northeast Atlantic, with the aim of predicting potential consequences for breeding seabird populations of climate-driven changes in the abundance and distribution of this key-structural species.

Materials and methods

Data

Climate data. Annual sea surface temperature (SST) data from 1953 to 2010 originated from the ERSST_V3 dataset, which come from a reanalysis on a 2° x 2° spatial grid that is based on the most recently available International Comprehensive Ocean-Atmosphere Data Set (ICOADS) SST data. Improved statistical methods were applied to produce a stable monthly reconstruction based on sparse data (Smith *et al.*, 2008).

We chose the climatic scenario A1B described in the Special Report on Emissions Scenarios (SRES) (Solomon *et al.*, 2007) to calculate projections of environmental suitability of *C. finmarchicus*, and used the first run (Scenario A1B) of the Hadley Centre Coupled Model, version 3 (HadCM3; Gordon *et al.*, 2000). HadCM3 is a coupled climate model that has been applied extensively for climate prediction, detection and attribution, and climate sensitivity. The oceanic component of this model has a horizontal resolution of 1.25 x 1.25 degrees to represent important details in oceanic current structures (Stott *et al.*, 2000).

Two large-scale hydro-climatic indices were used to examine the relationship between long-term changes in annual SSTs and hydro-climatic variability. The North Atlantic Oscillation (NAO) describes the basin-scale gradient of atmospheric pressure over the North

Atlantic, between the high pressure centred on the subtropical Atlantic and low pressure around Iceland. This phenomenon, detected in all months of the year, is particularly strong in winter and explains about 37% of the variability in monthly Sea Level Pressure (SLP) from December to February (Marshall *et al.*, 2001). Several slightly different NAO definitions exist (Hurrell & Deser, 2009). The winter NAO index used in this study is based on a Principal Component Analysis of sea level pressure over the North Atlantic sector for months from December to March (Hurrell *et al.*, 2001). The Northern Hemisphere Temperature (NHT) anomaly (relative to 1961-1990) provided by the Hadley Centre for Climate Prediction and Research (Brohan *et al.*, 2006) was used as a proxy for the effect of global warming in the Northern Hemisphere, although it also integrates hydro-climatic variability (Beaugrand & Reid, 2003).

Biological data. Two of the most comprehensive long-term studies of seabird ecology in the Northeast Atlantic take place at the Isle of May in east Scotland (56° 11' N, 2° 33' W), and at Røst in the Lofoten archipelago in northwest Norway (67° 30' N, 12° E). We included three common boreal seabird species: black-legged kittiwake (*Rissa tridactyla*, hereafter kittiwake), common guillemot (*Uria aalge*, hereafter guillemot, Isle of May only), and Atlantic puffin (*Fratercula arctica*, hereafter puffin). All three species feed their chicks on small pelagic fish, mainly lesser sandeel (*Ammodytes marinus*) and European sprat (*Sprattus sprattus*) on the Isle of May (Daunt *et al.*, 2008), and juvenile Atlantic herring (*Clupea harengus*) for kittiwakes and puffins at Røst (Anker-Nilssen *et al.*, 1997; Durant *et al.*, 2003). Guillemots and puffins obtain prey by diving, while kittiwakes feed at or near the surface (Gaston & Jones, 1998; Hatch *et al.*, 2009). Details on distribution and population size of the three species are provided in Appendix S1.

At the Isle of May, data on breeding success were available for kittiwakes, guillemots and puffins for respectively 1985-2010, 1982-2010 and 1977-2010. Methods were consistent

within each species across the study period, but varied among the species (Harris *et al.*, 2005b). For kittiwakes, nests in 15 plots (mean $n = 801$) distributed throughout the colony were checked when most pairs had finished laying. Nests where an incubating bird was present were marked on photographs of the area. Plots were checked again the day after the first fledged chick was seen in the colony, and the number of young present at each nest and their stage of development noted. Subsequent checks of nests where small or medium-sized chicks were present on this initial check were made over the subsequent month, and annual success was estimated as the number of large chicks, i.e. those assumed to fledge, out of the total number of well-built nests recorded. For guillemots, daily checks of breeding sites in five study plots (mean $n = 803$), where breeding density ranged from low to high, were made from before the first pair laid to after the last chick fledged. Annual breeding success was estimated as the proportion of sites where an egg was laid that a chick fledged. For puffin, up to 50 burrows containing eggs were marked in each of four different parts of the colony (mean $n = 126$) soon after laying was judged to be complete. Burrows were revisited ca. 8 weeks later, and success estimated as the proportion of burrows where a chick was present.

Details of field procedures at Røst are documented by Anker-Nilssen & Aarvak (2006). The breeding success of kittiwakes in the main colony (Vedøy) was measured annually 1980-2010 (except 1986-87) in 5-6 fixed study plots (mean $n = 449$), and expressed as the number of large chicks immediately prior to fledging per apparently occupied nest (AON) counted within the same plots in the incubation period. The addition of one plot in 1996 increased the total plot coverage from 2.4% to 3.7% of colony size, which dropped gradually from about 25,000 AON in 1979 to 7,500 AON in 2010. Mean breeding success in the new plot ($0.437 \pm$ SE 0.080) did not deviate significantly from ($t_{14} = 2.049$, $P = 0.060$) and correlated strongly ($r = 0.789$, $P < 0.001$) with that in the traditional five plots ($0.322 \pm$ SE 0.090) (T. Anker-Nilssen, unpubl. data). The breeding success of puffins was measured annually 1976-2010 as

the mean number of chicks fledged per egg hatched in an annual selection (mean 64) of study

burrows, inspected at 3-4 (1-6) d intervals from late incubation throughout the chick period.

The many years with low or no fledging success included a few years when virtually no eggs

hatched, in which fledging success was set to zero.

We consider the potential temporal bias from measuring breeding success of puffins

over a shorter part of the breeding season at Røst (per chick hatched) than on the Isle of May

(per egg laid) to be of minor importance in the context of our study, as we do not control for

any within-year differences in timing of events or between-year variation in the proportion of

non-breeding. Although hatching success was extremely variable at Røst, where most birds

abandoned their egg in the poorest seasons, the fledging success of the few that did hatch in

such years was always very poor (T. Anker-Nilssen, unpubl. data).

Statistical methods

Long-term changes in the spatial patterns of Pearson correlations between annual SSTs

and both the winter NAO index and NHT anomaly were investigated by splitting the time

series into two periods (1953-1979 and 1980-2006), with the number of years in each

period (27) kept constant to compare the strength of the correlations. Probabilities were

adjusted for temporal autocorrelation (Beaugrand, 2009).

The ecological niche of *C. finmarchicus* was calculated using the Non-Parametric

Probabilistic Ecological Niche (NPPEN) model (Beaugrand *et al.*, 2011). The NPPEN model

is a technique that estimates the ecological niche of a species. Once the niche is calculated,

the technique projects the probability of occurrence of the species in space and/or time. The

technique is based on the Generalised Mahalanobis distance and a simplified version of the

non-parametric test Multiple Response Permutation Procedure (MRPP). Applied at a year-to-

year scale, the method gives the probability of occurrence of *C. finmarchicus* for a given

year. A high probability of occurrence corresponds to an environment highly suitable for the

species and vice versa. The probabilities are constrained between 0 and 1. The model NPPEN was applied on three physical variables: bathymetry, annual sea surface salinity (SSS; as a proxy for the ecological effects of salinity-induced stratification and impacts on osmotic tolerance) (Levitus, 1982), and annual SST. The lower and upper limits for bathymetry (8000-0 m), annual SSS (30-36 psu) and annual SST (0-12°C) were selected based on expert knowledge of *C. finmarchicus* (Helaouët & Beaugrand, 2007; Reygondeau & Beaugrand, 2011).

Based on observed annual variation in SST and constant values of bathymetry and sea surface salinity, we calculated the annual environmental suitability for *C. finmarchicus* (1960-2010) in four areas of relatively similar size that are important for breeding seabirds: (1) East Scotland (56-58°N, 2-0°W); (2) Faroes (61-63°N, 8-6°W); (3) South Iceland (62-64°N, 22-19°W); (4) Lofoten (67-69°N, 10-14°E). Using a moderate climatic scenario (Scenario A1B), we forecasted the environmental suitability of *C. finmarchicus* in the four areas for each decade of the 21st century. We did not include annual variation in SSS for two reasons: firstly, spatial variance in salinity is much more pronounced than temporal variance, and secondly, temporal variance is currently poorly assessed in atmosphere-ocean general circulation models (M. Visbeck, pers. comm.).

The relationship between environmental suitability for *C. finmarchicus* and seabird breeding success was assessed using correlation analysis, with probability levels adjusted to account for temporal autocorrelation (Beaugrand, 2009). The relationships were tested with and without a one-year lag, because previous studies at the Isle of May have shown such a lag between SST and breeding success, probably reflecting dependence on 1-year-old fish (Frederiksen *et al.*, 2006). For kittiwakes at the Isle of May, the presence of a sandeel fishery during 1990-99 was included as an additional binary predictor, as previous studies have shown that breeding success was depressed during this period (Frederiksen *et al.*, 2004;

Frederiksen *et al.*, 2008). Impacts of potential changes in seabird breeding success on population growth rate were assessed with simple age-structured matrix population models (Caswell, 2001) constructed in ULM (Legendre & Clobert, 1995), using realistic values for other demographic parameters (Appendix S2).

Results

Figure 1 shows the results of the correlation analyses performed between annual SST and both NHT anomalies and the NAO index for the two periods 1953-1979 and 1980-2006. The statistics of the correlation analyses are summarized by Figure 1. The colour scale indicates the sign and the magnitude of the correlations, and the symbol + shows that these correlations are significant at the threshold level of 0.1. Temperatures in the Northern Hemisphere and specifically in the North Atlantic have increased substantially since the end of the 1970s (Beaugrand *et al.*, 2002). Interestingly, since 1980 the formerly significant positive correlation between mean annual SST in the North Sea area and the winter NAO index has disappeared, and mean annual SST is now significantly positively correlated with NHT anomalies throughout the Northeast Atlantic (Fig. 1). In the Irminger Sea and the North-central Atlantic, there is at the same time a significant negative correlation between annual SST and the winter NAO index.

The probability of occurrence of *C. finmarchicus* was calculated from the model NPPEN. As explained above, a high probability of occurrence of the species shows that the values of the environmental parameters are highly suitable for the species. Within the boreal Northeast Atlantic, mean environmental suitability for *C. finmarchicus* as predicted by the NPPEN model increases from south to north (Fig. 2). The observed changes in temperature have resulted in a declining environmental suitability for *C. finmarchicus* off east Scotland and in some recent years off south Iceland, while environmental suitability has remained

more constant around the Faroes and Lofoten (Fig. 2). Over the 21st century, mean suitability is projected to gradually decrease in east Scotland, the Faroes and south Iceland, while it is expected to remain relatively high at Lofoten until late in the century if climate-induced changes in temperatures follow Scenario A1B (Fig. 3). It is important to note that these projections are decadal means and therefore mask potentially substantial shorter-term variations, which may have large ecological consequences.

Observed breeding success of kittiwakes (when controlling for the presence of a sandeel fishery in 1990-1999), guillemots and puffins was positively correlated (significantly for kittiwakes and puffins) with predicted environmental suitability for *C. finmarchicus* in the previous year at the Isle of May, but not at Røst (Table 1, Fig. 4). The observed patterns (Fig. 4) suggest a threshold-like relationship, where 'optimal' breeding success (> 1 and > 0.8 fledged chick/pair for kittiwakes and guillemots/puffins, respectively) is possible (i.e. highest values observed fall in this range) as long as suitability for *C. finmarchicus* remains above 0.4, and likely (i.e. predicted by the linear regression) when environmental suitability is above 0.6. The niche model indicates that mean suitability is expected to fall below 0.4 off east Scotland in the 2020s, and off the Faroes in the 2060s, whereas it is expected to remain above this threshold for the remainder of the 21st century at south Iceland and Lofoten (Fig. 3). Other factors may act to reduce seabird breeding success from this optimal level (see Discussion), as indicated by the many poor seasons for puffins and kittiwakes at Røst despite high decadal suitability for *C. finmarchicus* (Fig. 4).

A simple age-structured population model indicated that declines in mean breeding success from 1 to 0.3 fledged chick/pair for kittiwakes, and from 0.8 to 0.5 fledged chick/pair for guillemots and puffins (corresponding to observed differences between 'good' and 'bad' years, cf. Fig. 4) would cause formerly stable populations to decline by respectively 6% and 3% annually, all else being equal. This estimate is likely to be conservative, as other

demographic parameters also are likely to be affected by food shortages (Frederiksen *et al.*, 2004; Harris & Wanless, 2011).

Discussion

Our statistical projections indicate that over the 21st century, it will become increasingly difficult for several boreal seabird species to maintain adequate breeding success and thus stable populations towards their southern range limit, and that these problems are likely to spread north in the later part of the century. These projections rely on the assumption that adequate abundance of *C. finmarchicus* is critically important for successful seabird reproduction. Previous studies show that breeding success of kittiwakes on the Isle of May and neighbouring colonies was negatively correlated with SST in the previous year (Frederiksen *et al.*, 2004; Frederiksen *et al.*, 2007b), and here we extend these results to two other species and suggest a partial mechanism: the negative association of *C. finmarchicus* with mean annual SST over this range. However, the seabirds in question do not feed their chicks on copepods, and the underlying assumption is that successful recruitment of the forage fish seabirds depend on to feed their chicks requires *C. finmarchicus* abundance to be high. There is some evidence to support this. Recruitment of lesser sandeel in the North Sea (the main prey of most chick-feeding seabirds in this region, Daunt *et al.*, 2008) is strongly positively correlated with *C. finmarchicus* abundance (van Deurs *et al.*, 2009). Similarly, *C. finmarchicus* is the most important prey of the Norwegian Sea – Barents Sea stock of herring throughout its life cycle (Prokopchuk, 2009). Thus, it is biologically plausible that sufficient abundance of *C. finmarchicus* is a necessary condition for successful breeding of kittiwakes, guillemots and puffins, at least as long as herring and sandeel remain their most important prey during breeding. Alternatively, *C. finmarchicus* could be considered as an indicator of the integrated influence of SST on the food web (Kirby & Beaugrand, 2009). The species is a

key indicator of subarctic ecosystems (Helaouët *et al.*, 2011), and its decline might reflect the adverse effect of increasing temperatures on the subarctic provinces of the Atlantic Arctic biomes (*sensu* Longhurst, 1998). North Sea plankton shifted polewards as a result of the northward movement of a critical thermal boundary (CTB). The CTB, associated with high biological and ecological variance, is identified by the annual isotherm 9-10°C (Beaugrand *et al.*, 2008). If the reorganisation is too substantial (i.e. the subarctic influence disappears totally), all higher trophic levels depending upon the ecosystem directly or indirectly, are likely to decline (Kirby & Beaugrand, 2009).

Increasing sea temperatures may also affect fish directly, although less evidence is available for such impacts (Heath *et al.*, 2012), and this could affect the availability of alternative prey for seabirds. The most obvious alternative prey in the North Sea is the European sprat. For example, changes in the abundance of sprat may influence the breeding success of guillemots, kittiwakes and puffins (Lewis *et al.*, 2001; Wanless *et al.*, 2005). A recent study indicates that an increase or sustained probability of occurrence of sprat during the first half of the 21st century could partly compensate any reduction in North Sea sandeels (Lenoir et al., unpubl.). The decline in the probability of occurrence of sprat is predicted to remain moderate along Scottish coasts of the North Sea until 2050, which might help sustain seabird colonies albeit at lower numbers than at present. However, a much more intense warming might accelerate the decrease in the probability of occurrence of sprat. More research is required to evaluate the potential role of alternative prey in supporting seabird populations.

The one-year lag in the relationship between *C. finmarchicus* suitability (or equivalently, SST) and breeding success is assumed to reflect the dependence of many seabirds on 1-year-old fish to fledge young successfully. While kittiwakes and guillemots indeed feed their young extensively on 1-year-old sandeel, at least early in the season (Lewis

et al., 2001; Wilson *et al.*, 2004; Daunt *et al.*, 2008), puffins only do so to a limited extent (Harris & Wanless, 2011). Nevertheless, the observed relationship on the Isle of May was stronger with a one-year lag than without for all three species (Table 1); Frederiksen *et al.* (2006) argued that this was due to adults being dependent on 1-year-old fish to achieve sufficiently high body condition to enable successful breeding.

Many other mechanisms can prevent seabirds from achieving high breeding success in situations where physical conditions are suitable for *C. finmarchicus* (Fig. 4). Firstly, nutrient levels may be too low to support high abundance of *C. finmarchicus*, despite physical conditions being suitable as indicated by the NPPEN model. This is unlikely to be the case in the shelf waters off Northwest Europe, where primary productivity is generally high, at least during the spring bloom (Gazeau *et al.*, 2004). Secondly, competition from other abundant predators for *C. finmarchicus* may prevent large stocks of schooling fish suitable for seabirds from being maintained. The most obvious candidates are other schooling fish too large for most seabirds, e.g. Atlantic mackerel (*Scomber scombrus*) (Castonguay *et al.*, 2008; Langøy *et al.*, 2012), adult Atlantic herring (Prokopchuk, 2009). In recent years, stocks of mackerel in the Northeast Atlantic have increased and expanded their range northwards (ICES, 2011), and this has been suggested as a contributory cause of repeated breeding failures of seabirds in south Iceland (E.S. Hansen, pers. comm.), the Faroes and along the west coast of Norway. Blue whiting (*Micromesistius poutassou*) increased dramatically in the North Atlantic in the mid-2000s and has since declined again (Payne *et al.*, 2012); this mesopelagic schooling fish eats some copepods, but more typically larger pelagic crustaceans (Dolgov *et al.*, 2010; Langøy *et al.*, 2012), and it is probably too big and occurs too deep to be important food for seabirds. Thirdly, seabirds may face competition for forage fish from other natural predators and/or human fisheries. Potentially important predators on sandeels include adult herring (Frederiksen *et al.*, 2007a), mackerel, gadoids and marine mammals, including baleen

whales. Sandeels are targeted by a large-scale industrial fishery in the North Sea, and reduced

breeding success and adult survival of kittiwakes at the Isle of May in the 1990s have been

linked to the activity of this fishery off east Scotland (Fig. 4, see also Frederiksen *et al.*,

2004). In general, large-scale fisheries on forage fish have been linked with widespread

impacts on seabirds and other dependent predators in many ecosystems worldwide (Cury *et

al.*, 2011; Smith *et al.*, 2011). Finally, variation in wind and currents may affect spawning

and/or prevent advection of fish larvae from spawning areas to feeding areas where they

become available for large seabird populations (Sætre *et al.*, 2002). This phenomenon has

been implicated as the underlying cause of breeding failures of many seabirds in Shetland in

the late 1980s due to lack of sandeels (Wright & Bailey, 1993), and to some degree of puffins

at Røst in many years during the 1970s to 2000s due to lack of young herring (Durant *et al.*,

2003). In the case of Røst, seabird breeding success is probably largely determined by

conditions in the extensive shelf area upstream of the colony rather than by the theoretical

suitability of the local environment. Locally, non-nutritional aspects such as predation,

parasitism and adverse weather could also be important.

It is generally accepted that the distribution of *C. finmarchicus* in the North Atlantic is

the result of its thermal niche, along with advection from deep-water overwintering areas

onto continental shelves such as the North Sea (Speirs *et al.*, 2006; Helaouët & Beaugrand,

2007). Given this, it can be expected that the distribution will shift northwards as

temperatures increase through the 21st century (Reygondeau & Beaugrand, 2011), and if this

key species is not replaced by other zooplankton grazers suitable (in terms of distribution,

size, quality and quantity) as prey for small fish, seabird populations are expected to suffer

reduced breeding success, likely leading to declines in population size (this study). The most

likely replacement for *C. finmarchicus* as temperatures increase is its close relative, the

warm-temperate *C. helgolandicus* (Helaouët & Beaugrand, 2007; Møller *et al.*, 2012), which

has increased in abundance in the North Sea over recent decades as *C. finmarchicus* has decreased (Heath *et al.*, 2009). However, for several reasons *C. helgolandicus* does not appear to be a full replacement for *C. finmarchicus* in terms of ecosystem functioning, in particular the ability to sustain large stocks of schooling, planktivorous fish (Bonnet *et al.*, 2005): it is smaller, has a lower lipid content, and tends to occur at low densities early in spring when most fish larvae need access to abundant copepod prey (Beaugrand *et al.*, 2003). Taken together, these factors are likely to lead to a less efficient grazing food web when the system is dominated by *C. helgolandicus*, and thus a lower capability to support large populations of fish and dependent piscivores, including seabirds.

Widespread northward range shifts of fish species have already been documented in the North Sea and other parts of the Northeast Atlantic and linked to increasing temperatures (Perry *et al.*, 2005), and more such shifts are expected (Cheung *et al.*, 2011; Lenoir *et al.*, 2011). Sandeels are considered particularly vulnerable to climatic warming, due to their strict habitat requirements (Heath *et al.*, 2012). However, few of the species observed or expected to increase in this area are abundant planktivores which could sustain large seabird populations. The European anchovy *Engraulis encrasicolus* has increased in abundance in the North Sea (Petitgas *et al.*, 2012), but although this species is commonly eaten by seabirds in warm-temperate parts of the Northeast Atlantic (e.g. Navarro *et al.*, 2009), it appears never to have sustained seabird populations of the sizes seen in boreal waters (Barrett *et al.*, 2006).

In conclusion, based on the projected northward range shift of *C. finmarchicus*, the expected resultant declines in abundance of schooling pelagic fish such as sandeel and herring, and the lack of obvious replacements for these as seabird prey, it is likely that breeding populations of piscivorous seabirds in the boreal Northeast Atlantic will also shift northwards (cf. Russell, 2009; Harris & Wanless, 2011). Remnant populations may well remain in southern areas with particularly high prey availability, but the very large

populations currently present in e.g. Scotland and the Faroes seem likely to disappear. The speed of these range shifts, and their impact on total abundance of the seabird species involved, will depend on how likely these normally highly philopatric birds are to disperse to more northerly colonies (Matthiopoulos *et al.*, 2005), and whether habitat quality in these areas will improve, allowing large seabird populations to be sustained.

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Table 1 Significance and variation explained for the relationship between predicted suitability for *C. finmarchicus* and seabird breeding success at the Isle of May with and without a one-year lag (see also Fig. 4). At Røst, no relationships were significant. Significance levels were adjusted for temporal autocorrelation (Beaugrand, 2009). For kittiwakes, the amount of variation explained is for the whole model, including the effect of a sandeel fishery during 1990-1999.

Species	Study period	No lag		One-year lag	
		R^2	P_{ACF}	R^2	P_{ACF}
Kittiwake	1985-2010	60%	0.072	63%	$1.4 * 10^{-4}$
Guillemot	1982-2010	28%	0.14	30%	0.098
Puffin	1977-2010	33%	0.062	48%	0.027

Fig. 1. Linear correlations between mean annual sea surface temperature (SST) and hydro-climatic indices in the North Atlantic for the time periods 1953-1979 (left) and 1980-2006 (right). Top panels: correlations between annual SST and Northern Hemisphere Temperature (NHT) anomalies. Bottom panels: correlations between annual SSTs and the North Atlantic Oscillation (NAO) index. Positive correlations are shown in red and negative correlations in blue. A plus sign (+) indicates correlations significant at $P < 0.1$, after adjusting the degrees of freedom to account for temporal autocorrelation (see Materials and methods). The red asterisks in the top left panel indicate the location of the Isle of May and Røst (outside map frame).

Fig. 2. Historical environmental suitability (1960-2010) for *C. finmarchicus* predicted from the NPPEN model in four areas of the boreal Northeast Atlantic with large populations of breeding seabirds.

Fig. 3. Projected 21st century environmental suitability for *C. finmarchicus* predicted from the NPPEN model in four areas of the boreal Northeast Atlantic with large populations of breeding seabirds. Values shown are decadal means.

Fig. 4. Breeding success of three seabird species at the Isle of May and Røst, as a function of the environmental suitability for *C. finmarchicus* as predicted by the NPPEN model (see Materials and methods) in the previous year. Solid lines indicate significant linear regressions, and dashed lines near-significant trends ($P < 0.1$). For kittiwakes, the presence or absence of an industrial fishery for sandeels around the Isle of May is included in the model (cf. Frederiksen *et al.*, 2004).
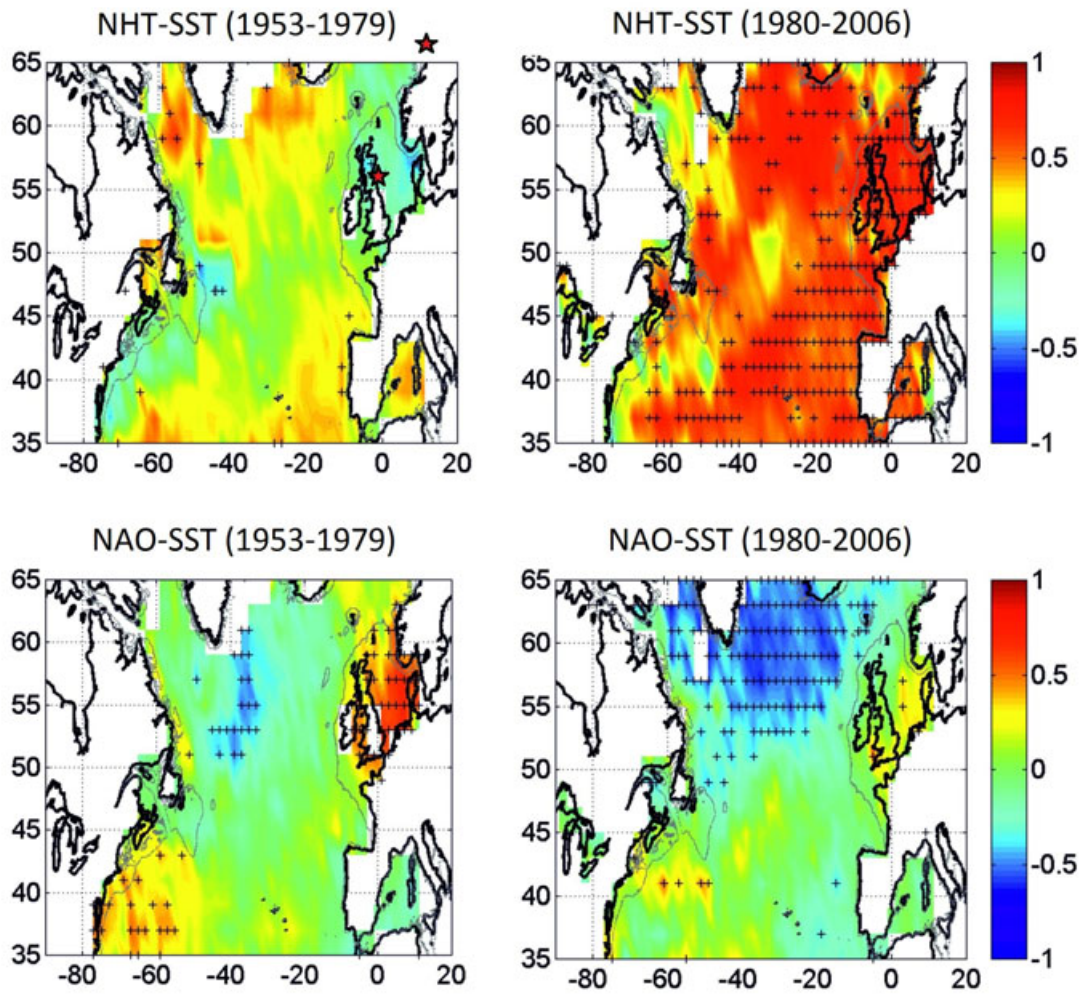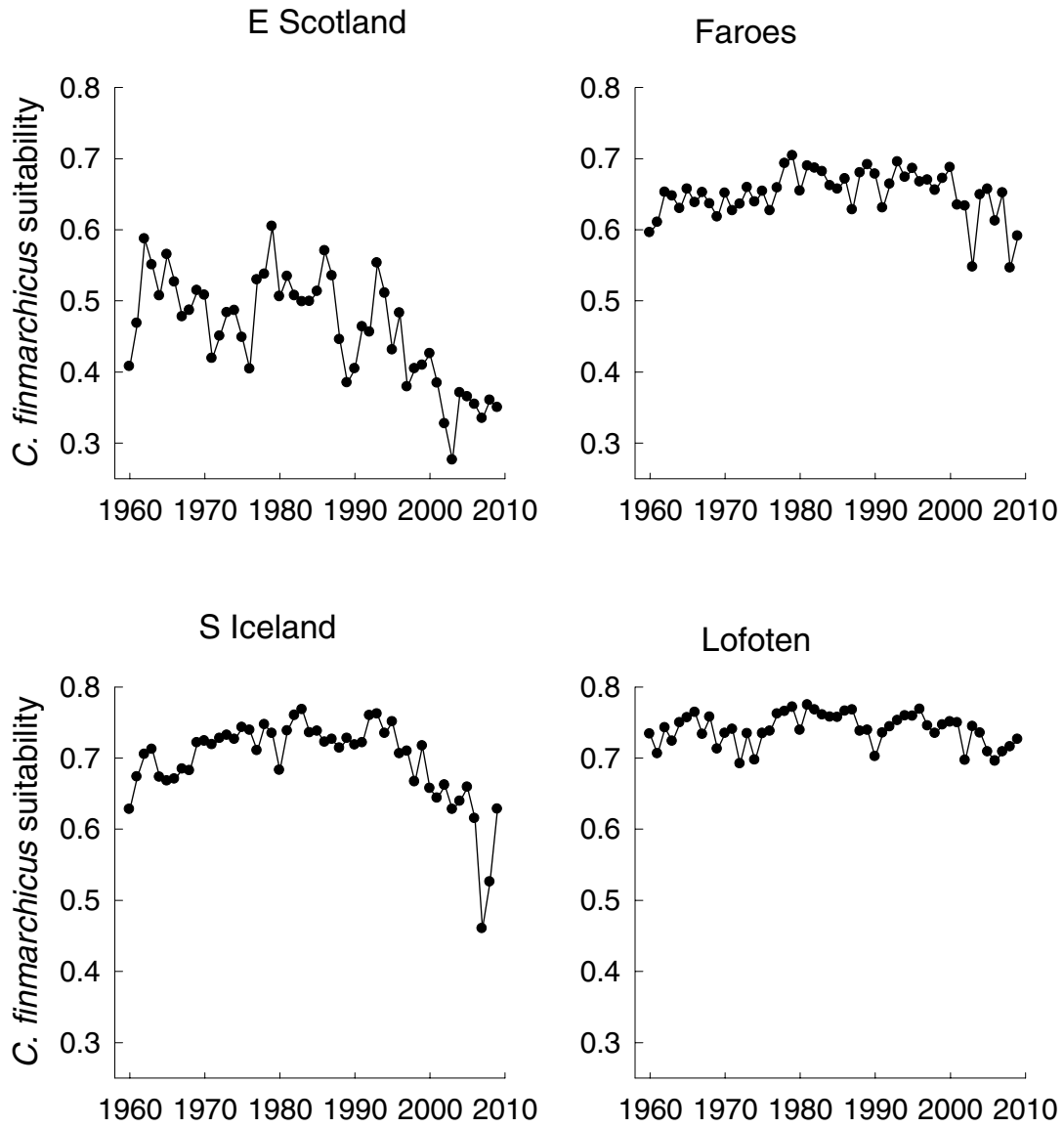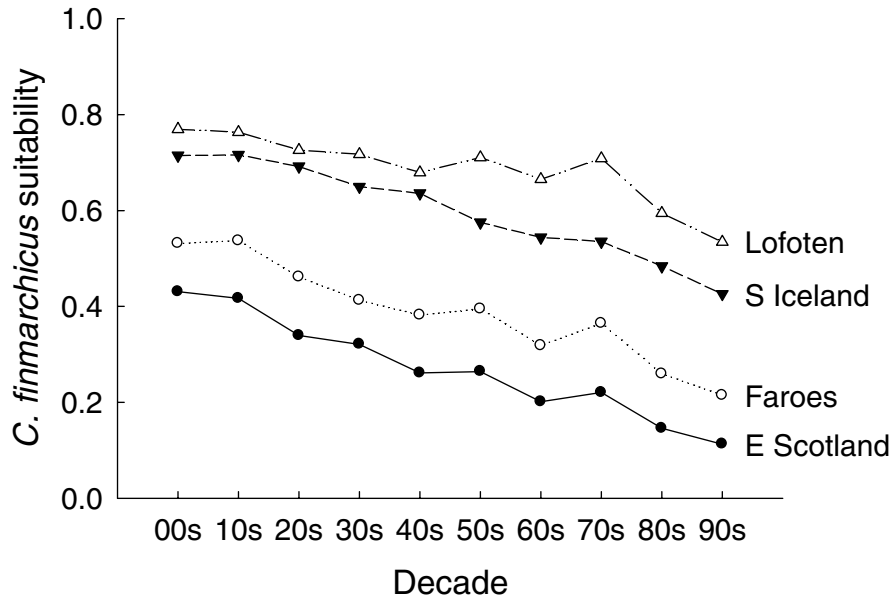
Fig. 1

NHT-SST (1953-1979) NHT-SST (1980-2006)

NAO-SST (1953-1979) NAO-SST (1980-2006)

Fig. 2.

Fig. 3.

Fig. 4.