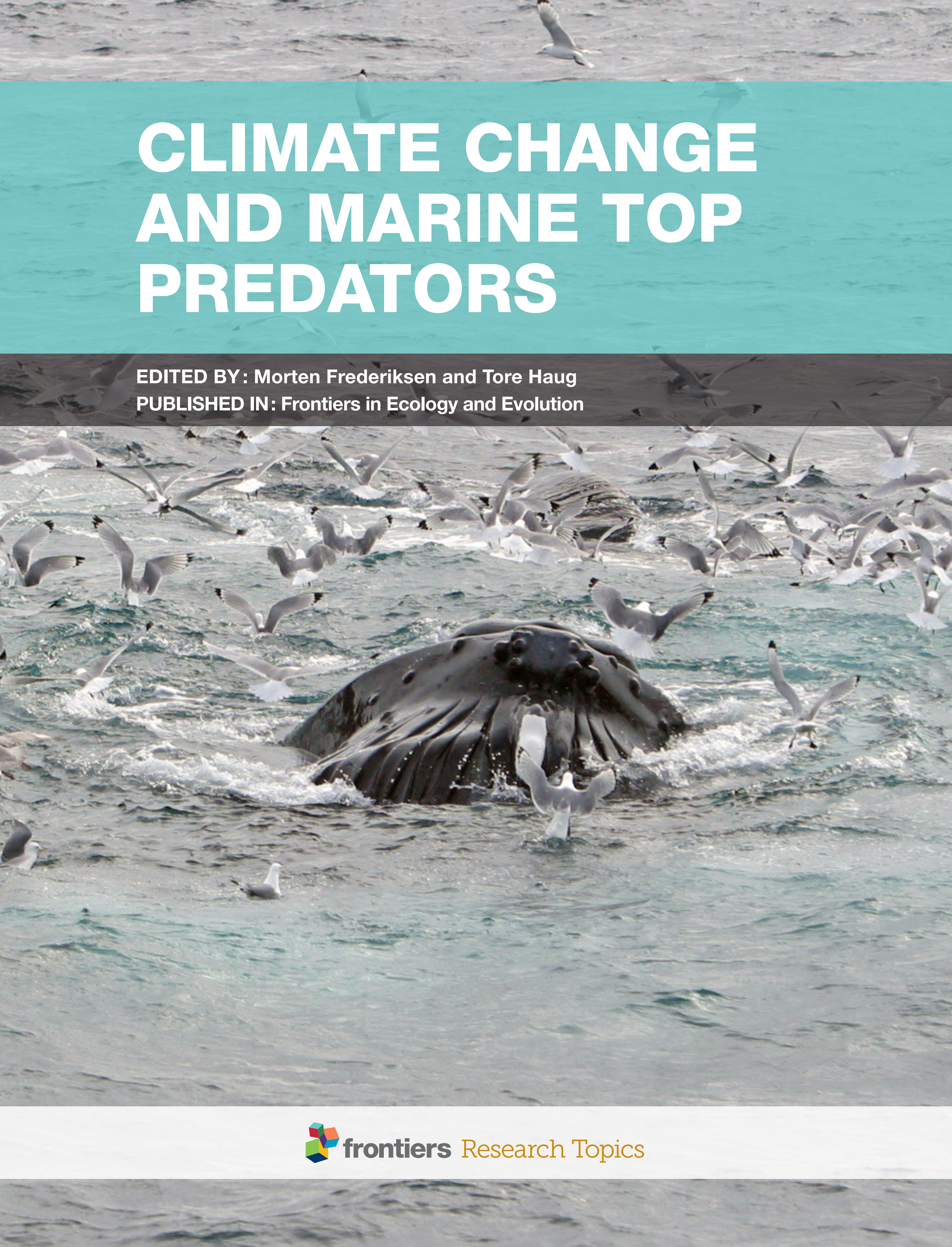

CLIMATE CHANGE AND MARINE TOP PREDATORS

EDITED BY: Morten Frederiksen and Tore Haug
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frontiers Research Topics

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CLIMATE CHANGE AND MARINE TOP PREDATORS

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Humpback whales and black-legged kittiwakes feeding on capelin in the Barents Sea (Photo: Kjell-Arne Fagerheim, Institute of Marine Research, Norway)

Climate change affects all components of marine ecosystems. For endothermic top predators, i.e. seabirds and marine mammals, these impacts are often complex and mediated through trophic relationships. In this Research Topic, leading researchers attempt to identify patterns of change among seabirds and marine mammals, and the mechanisms through which climate change drives these changes.

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Editorial: Climate Change and Marine Top Predators

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Climate is one of the main structuring forces in natural ecosystems (Richardson and Schoeman, 2004), and anthropogenic climate change is regarded as an important driver of changes in the range and abundance of species as well as community composition, not least in marine ecosystems (Poloczanska et al., 2013). There are two overall mechanisms by which climate change can affect range and abundance of a species (Thomas, 2010): direct physiological effects, and indirect trophic effects mediated by other species. Understanding to what extent and through which mechanisms climate change affects particular species is one of the main challenges facing ecologists. In this collection of papers, researchers take a variety of approaches to the study of climate change impacts on marine birds and mammals, ranging from documentation of large-scale patterns, through quantification of impacts on vital rates, to detailed mechanistic studies of changing behavior, and physiological effects.

The first paper in this collection (Oro, 2014) describes the challenges involved in studying the impacts of climate change on seabirds, and critically evaluates the existing literature. One of the central issues identified in this paper is that reliance on single climate indices for describing changes in complex ecosystems may result in biased predictions. The remaining papers both illustrate some of these challenges, and contain pointers to ways in which they can be overcome.

Measuring climatic variation on a scale that makes sense in relation to the study organism is complex. In a cross-disciplinary paper, Mesquita et al. (2015) illustrate how methods from climatology can help identify ecologically meaningful covariates of population change, in this case of common guillemots (*Uria aalge*) in northern Norway. Distinguishing impacts of climate from other drivers is important and often difficult. Crawford et al. (2015) examine changes in distribution of several seabirds in South Africa, and conclude that reactions to fisheries dominate those to climate.

Most climate-related seabird studies have focused on the breeding colonies, while relatively few have examined changes in staging or wintering populations. Two papers examine respectively wintering alcids off Massachusetts (Veit and Manne, 2015) and staging shearwaters in the Bay of Biscay (Louzao et al., 2015). Both show species-dependent relationships between large-scale climate and the occurrence of seabirds in these areas.

Climate warming may both enhance poleward expansion of temperate species from lower latitudes and change the distribution of resident species at higher latitudes. This may present challenges both for newcomers and residents. Cod (*Gadus morhua*) abundance has increased, and its range has extended northwards in the Barents Sea in recent years. One implication of this is a new overlap of feeding grounds with harp seals (*Pagophilus groenlandicus*) and minke whales (*Balaenoptera acutorostrata*), two other important top predators in the area. Bogstad et al. (2015) demonstrate that both these mammal species have exhibited declines in body condition in recent years, and competition for food with the increasing cod stock is suggested as a possible explanation. Significant changes in the distribution and abundance of several cetacean species during recent decades has been shown both in Icelandic and adjacent waters (Víkingsson et al., 2015) and in the Norwegian Sea (Nøttestad et al., 2015). Both papers illustrate that whale species have the capability to rapidly perform shifts in distribution and abundance patterns strongly associated with adaptive search behavior in relation to both changing levels of abundance of their prey and increased sea surface temperatures.

Two papers investigate the impact of changes in sea ice on vital rates and population trends of Adélie penguins (*Pygoscelis adeliae*). One study documents complex long-term trophic effects (Ballerini et al., 2015), while the other shows strong impacts of stochastic events, viz. very large icebergs blocking access to foraging areas (Dugger et al., 2014). In both cases, the impacts on demography and population dynamics were profound.

Climate-related changes in demography as well as population and range dynamics are mediated by behavioral and physiological mechanisms. Two long-term studies on colonial birds illustrate the complexity of these links between climate, behavior and demography. In common terns (*Sterna hirundo*), Szostek et al. (2015) find that arrival date and mass at the breeding colony were related to climatic conditions and food availability in wintering and staging areas, but that age groups differed in their reaction to climate. Reed et al. (2015) show that the probability of skipping breeding in common guillemots was higher after warm winters, and that individuals differed in both mean skipping propensity and their response to temperature.

Behavioral reactions of one species to climatic change may lead to cascading effects on other species. Prop et al. (2015) show that the occurrence of polar bears (*Ursus maritimus*) on land during summer in Svalbard and Greenland has increased as sea ice cover has decreased, and that this has led to increased predation on ground-nesting colonial birds. Staying with polar bears, loss of sea ice, and reduced access to prey is likely to result in prolonged fasting periods with subsequent increases of tissue concentrations of persistent organic pollutants. In a perspective paper, Jenssen et al. (2015) suggest increased focus on potential population effects of such increases in pollutant exposure, and to consider such effects in addition to the effects of climate-induced habitat loss.

Overall, these papers illustrate the complexities both of the ways that climate change can impact marine top predators, and of the approaches taken to study this important subject. Research in this field is progressing rapidly, and innovative collaborations with neighboring disciplines are increasingly being used to good effect. Among the remaining challenges, the prediction of future changes in populations and communities still looms large, and success in this endeavor will depend on continual development of new collaborative approaches.

AUTHOR CONTRIBUTIONS

MF and TH co-wrote this editorial.

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Seabirds and climate: knowledge, pitfalls, and opportunities

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As a physical driver of ecosystem functioning, it is not surprising that climate influences seabird demography and population dynamics, generally by affecting food availability. However, if we zoom in ecologically, seabirds are in fact very heterogeneous, ranging in size from very small to very large species (with a difference of more than two orders of magnitude in body weight), from planktivorous forms to predators of large fish and squid, from benthic to pelagic, from species with small foraging ranges to species feeding throughout the whole circumpolar region, and from resident species (at a spatial mesoscale) to trans-equatorial migrating seabirds that travel large distances across several oceanographic systems. Due to this high variability and the difficulty in obtaining direct reliable estimates of long-term food availability, global climatic indices have been extensively used in studying seabird demography and population dynamics. However, the use made by researchers of these indices has certain conceptual and methodological pitfalls, which I shall address in this review. Other factors, such as anthropogenic impacts (including oil-spills and interaction with fisheries), may further alter or confound the association between climate and seabird demography. These pitfalls and environmental noise, together with the inability to incorporate resilience, may bias our predictions regarding the future impact of global warming on seabirds, many of which have vulnerable populations.

Keywords: predictive models, resilience, methodological bias, evolution, global change, climate, seabirds

HISTORICAL BACKGROUND

A search performed in June 2014 using the words "climate & seabird" in the ISI Web of Science resulted in 946 items. Even though some of those items dealt with other marine organisms or were focused on some related issues (such as oceanographic processes), that result represents a large number of scientific contributions on the topic of how climate may influence seabird ecology. The influence of climate on marine organisms has been extensively studied in seabirds because, compared to most other species (except some marine mammals such as seals and sealions), their demography and population dynamics can be easily monitored in breeding colonies.

Up to the 90s, the changes in demographic parameters and population size in seabirds were explored mostly in relation to intrinsic features of the colonies such as their size or the presence of predators (Hunt et al., 1986). The effects of climate (mostly in the form of oceanographic indices) on seabird ecology were seldom analyzed in those years (Myres, 1979), and research efforts were addressed mostly to determining the distribution of seabirds at sea (Abrams, 1985). The influence of oceanographic features was outlined especially when extreme and anomalous events occurred (such as cyclones or El Niño-Southern Oscillation (ENSO) years (e.g., Blomqvist and Peterz, 1984; Graybill and Hodder, 1985), whereas some pioneering studies dealt with the relationship between climatic events and seabird mortalities (La Cock, 1986). In the 90s some papers started to highlight the potential impact of climate warming on seabirds (Burger, 1990; Brown, 1991; Duffy, 1993) and the role played by climate on bottom-up control mechanisms, food availability and its effects on seabird population dynamics (Crawford, 1991; Ainley et al., 1994). Nevertheless, it was not until the end of the 90s that the literature on climate and seabirds exponentially increased (Montevecchi and Myers, 1997; Guinet et al., 1998; Lyver et al., 1999) (see **Figure 1**) and that the first paper relating climate and adult survival of a seabird appeared using reliable and robust quantitative methods (Barbraud et al., 2000). That exponential phase was likely the result of the increasing interest of the scientific community about climate change in the ecological literature during those years, together with the appearance of new statistical tools and the improvement of computational power (**Figure 1**) (Green et al., 2005).

Given that previous papers have recently reviewed thoroughly the state-of-the-art knowledge on seabirds and climate (Schreiber, 2002; Barbraud et al., 2012; Sydeman et al., 2012; Jenouvrier, 2013; Quillfeldt and Masello, 2013), here I shall concentrate on more conceptual issues, knowledge gaps and pitfalls typical of the studies dealing with how climate influences the ecology of seabirds.

CLIMATE AND ITS INFLUENCE ON SEABIRDS

It is no surprise that bottom-up control in marine ecosystems exerted by oceanographic drivers, which is mostly controlled by

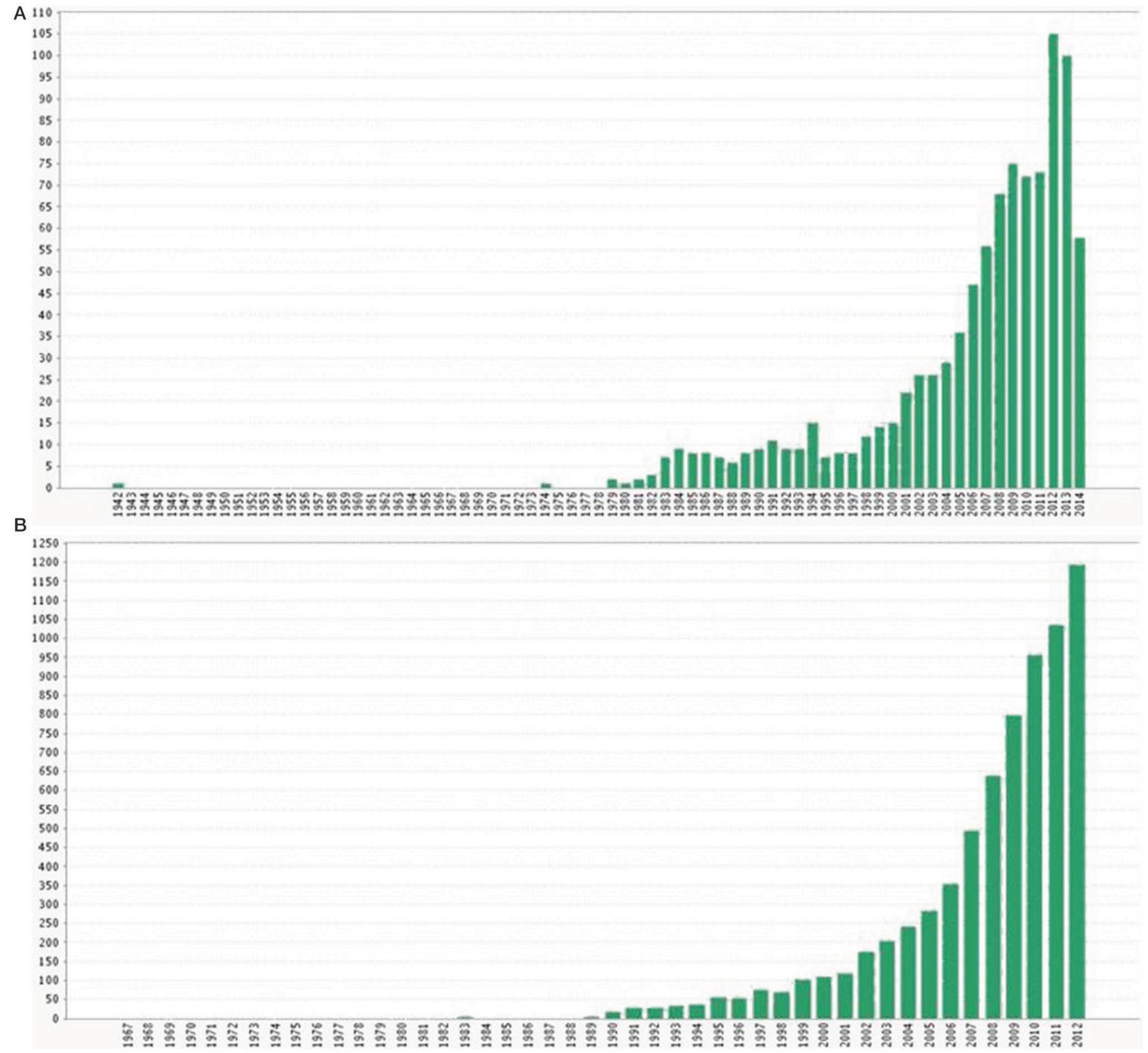

FIGURE 1 | Number of publications (including papers, reports, books, meetings and any scientific document available) using the ISI web of knowledge about a) climate and seabirds since 1942 to 2014 and (B) climate change and ecological studies since 1967 to 2012. Note that the 2014 value in panel **(A)** may represent half of the publications because the search was performed in June.

climate variables (e.g., wind, temperatures, air pressure) influence the ecology of marine top-predators such as seabirds. As it should be expected, seabirds respond to the variability in climate change and warming (e.g., Schreiber, 2002; Jenouvrier, 2013), and responses occur at both proximal (ecological) and ultimate (evolutionary) levels (Parmesan, 2006; Weimerskirch et al., 2012). The scientific literature has been sensitive to the warning message involving climate warming and papers dealing with seabirds have not been an exception (Votier et al., 2008a). Massive breeding failures following climate perturbations have attracted the attention of researchers, and records on El Niño events and its ecological consequences are a good example (e.g., Glantz, 2001; Velarde et al., 2004; Devney et al., 2009). In general, the literature shows that climate variability influences most ecological parameters analyzed, including range shifts (in breeding but mostly in foraging areas) and changes in both phenology and demographic parameters (including survival, dispersal, recruitment and breeding propensity). Back in the 80s, some papers already recorded events of adult seabird mortality overlapping with extreme climate years (La Cock, 1986). But more unexpected has been the range of papers that have found linear relationships between adult survival and climate variables, because adult survival should be a highly conservative parameter due to evolutionary canalization, typical of long-lived organisms including seabirds (Stearns et al., 1995; Gaillard and Yoccoz, 2004). One possible reason is that more powerful statistical tools, such as capture-recapture models, have allowed researchers to take advantage of the large number of long-term data bases collected in the last 40–50 years on seabird ecology (mainly population trends and individually marked monitoring). With these long time series researchers can detect more subtle associations between climate factors and demographic parameters like survival, that exhibit relatively low amounts of temporal variation. In fact, the amount of available long-term data on several species and populations of seabirds is amazing, compared to other marine or even terrestrial organisms (Grosbois et al., 2008; Sydeman et al., 2012). I found up to 49 papers (some of them corresponding to several species, morphs or colonies) assessing the potential impact of climate on adult survival using methods accounting for recapture probability (**Table 1**). Those papers included 36 different species (most of them Procellariiformes) and seldom considered time lags between the climate index and adult survival (24% of the cases). More than 77% of the 75 species*colonies studies found a relationship (linear in most cases) between climate and adult survival. Nevertheless, Grosbois et al. (2008) warned about several potential biases that could occur when assessing the effects of climate on survival, including the test of multiple covariates without correcting α-values of statistical significance (in cases where classical null hypothesis statistical testing is employed for inference purposes), collinearity between those covariates and survival, or the inclusion or not of lag times when testing for those effects (see below).

Charles Darwin was fascinated by the size of seabird colonies, formed by millions of individuals. After centuries of direct harvesting, introduced mammalian predators and destruction of suitable breeding habitat, most of those colonies have been decimated, and environmental stochasticity, including climate variation, has a greater impact on population changes than it did in the past, because population sizes are smaller and closer to the quasi-extinction thresholds than ever before. Nevertheless, ecological responses of seabirds facing climate variability suggest that they can have highly resilience responses, and this should be viewed as a buffer against decline or extinction (see below) (Forcada et al., 2008; Gremillet et al., 2012). Changes in seabird populations or demographic parameters associated with climate are often described as "alterations" and "reductions," with an implied warning message or value-judgment (Martínez-Abraín and Oro, 2013). Only when researchers can show that changes in seabird ecology associated with climate variability fall outside the range of inherent variability in biological parameters (at the level of both individuals and populations) should we be concerned about the fate of a population or a species due to climatic change. In fact, much less has been published on the influence of climate on population dynamics of seabirds (e.g., Frederiksen et al., 2004b; Jahncke et al., 2004; Forcada and Trathan, 2009; Burthe et al., 2014; Woehler et al., 2014) but even in those cases it is difficult to know which percentage of the variance in population size or density is explained by climate forcing compared to other factors such as competition, density-dependence, predation or dispersal (Bustnes et al., 2013).

PITFALLS AND GAPS OF THE CLIMATE-SEABIRD RESEARCH

Scientific generalizations are helpful because the message of the concept is clearer: climate warming is a scientific fact, and the resulting changes in the biosphere follow the same fast trend. I am not going to discuss here the particularities involving climate change (e.g., spatial heterogeneity in warming, consequences for other components such as precipitation, humidity, or atmospheric pressure); however, given that I use the general term "seabirds," it is difficult to avoid dealing with the variability across taxa. Seabird body sizes range from very small to very large forms (with a difference of more than two orders of magnitude in body weight); their diets range from planktivorous to predators of large fish and squid; their foraging habitats range from neritic to pelagic areas, there are species with small foraging ranges while others feed throughout the whole circumpolar regions; some are divers and some forage at the sea surface; some seabirds are resident species (at a spatial mesoscale) whereas others are trans-equatorial migrators, which travel large distances across several oceanographic systems. With this variability in life history strategies and ecology, we should expect that the impacts of climate on seabird ecology to vary across ecological parameters and species that are impacted by climate variation. For instance, Kitaysky and Golubova (2000) showed that climate change differentially influenced reproductive performance of sympatric alcid species depending on their foraging strategy (e.g., planktivorous vs. piscivorous). Other studies have also addressed the influence of environmental variation in some seabird communities and the specific effects on each species relative to their particular ecology (Sydeman et al., 2001; Sabarros et al., 2012). Even for the same species in different studies, results are not always similar (see **Table 1**), suggesting differences among populations (Tavecchia et al., 2008) or raising doubts about the suitability of selected climate indexes, the temporal window analyzed or the power of each data set to detect associations between climate and the seabird parameter of interest, especially when these associations are not statistically significant (Jenouvrier, 2013). For instance, some studies found that the influence of increased SST on adult survival was positive or negative depending on the study colony or the genetic morph (Harris et al., 2005; Reiertsen et al., 2012), and these are good examples of how little we still know about the mechanisms linking climate and vital rates (Forero et al., 2001). Finally, non-linear relationships between demographic parameters and climate indices can also result in differences between studies on the same species when different temporal windows are considered. For example, if adult survival is associated non-linearly with a climate covariate that changes through time, then performing the same analysis during two different time windows may yield different results.

It would be interesting (though very challenging) to have a global review available to understand what species and populations are more sensitive to climate variability, how important extreme climate events can be, how important a role intrinsic individual and state attributes (such as age, sex, breeding state, and physical condition) are playing, what temporal and

Table 1 | Studies assessing the effects of climate on seabird adult survival.

Species	Index	Effects on adult survival	Time lag	References
CHARADRIFORMES				
Least auklet	North Pacific Index	Yes	No	Jones et al., 2002
Cassin's auklet	SOI	Yes	No	Lee et al., 2007
Cassin's auklet	ENSO	Yes at four study colonies	No	Bertram et al., 2005
Cassin's Auklet, Rhinoceros Auklet and Tufted Puffin	Two extreme climate events: a strong El Nino event in 1997–1998 and an atmospheric blocking event	No for the two first species; yes only for females of the third species	No	Morrison et al., 2011
Atlantic puffin	NAO, SST	Yes in four out of five study populations	Both lagged and not-lagged indexes	Harris et al., 2005
Little auk	NAO, SST	Yes	Both lagged and not-lagged indexes	Hovinen et al., 2014
Audouin's gull	NAO	No	No	Tavecchia et al., 2007
Razorbill	Labrador Current temperature	Yes at one colony but not clear in the other	Both lagged and not-lagged indexes	Lavers et al., 2008
Brünnich's guillemot	Arctic Oscillation, SST	Very slight	Both lagged and not-lagged indexes	Smith and Gaston, 2012
Common guillemot	SST	Yes	Both lagged and not-lagged indexes	Reiertsen et al., 2012
Common guillemot, Brunnich's guillemot, razorbill, Atlantic puffin and black-legged kittiwake	NAO, SST	Yes except for razorbill	Both lagged and not-lagged indexes	Sandvik et al., 2005
Black-legged kittiwake	NAO, SST	Slight	Both lagged and not-lagged indexes	Frederiksen et al., 2004b
PROCELLARIIFORMES				
Cory's shearwater	SOI	Yes at all six study populations	No	Jenouvrier et al., 2009
Cory's shearwater	SOI, NAO, SST	Yes	No	Boano et al., 2010
Cory's shearwater	SST	Yes	No	Ramos et al., 2012
Cory's shearwater	SOI	Yes at two colonies	Variable depending on the covariate	Genovart et al., 2013
Indian yellow-nosed Albatross	SOI	No	No	Rolland et al., 2009a
Amsterdam albatross	DMI, SOID, SST	No	No	Rivalan et al., 2010
Amsterdam albatross, black-browed albatross, snow petrel	SST for albatrosses, sea- ice concentration for petrel	Only for black-browed Albatross	No	Barbraud et al., 2011
Wandering, sooty, yellow-nosed and black-browed albatross	SOI, SST	Only for black-browed Albatross	No	Rolland et al., 2010
Black-browed albatross	SST	Yes	No	Rolland et al., 2008
Black-browed albatross	SST	Yes	No	Pardo et al., 2013
Black-browed albatross	SOI, SST	Yes for inexperienced breeders, no for experienced	No	Nevoux et al., 2007
Black-browed albatross	SOI, SST	Yes for inexperienced breeders at the two study colonies	No	Nevoux et al., 2010a
Black-browed albatross	SOI, SST	Only for immatures, no for adults	No	Nevoux et al., 2010b
Black-browed albatross	SOI, SST	Yes for inexperienced and experienced breeders	No	Rolland et al., 2009b
White-chinned petrel	SOI	Yes	Both lagged and not-lagged indexes	Barbraud et al., 2008
Snow petrel	Extent of sea-ice, SST	Yes	No	Barbraud et al., 2000

(Continued)

Table 1 | Continued

Species	Index	Effects on adult survival	Time lag	References
Snow petrel	Air temperature, sea- ice concentration	No	No	Jenouvrier et al., 2005b[a]
Blue petrel	ENSO	Yes	Both lagged and not-lagged indexes	Barbraud and Weimerskirch, 2003
Blue petrel	Sea surface height	Only for inexperienced individuals	No	Barbraud and Weimerskirch, 2005
Mediterranean Storm Petrel	14 covariates	Yes	No	Soldatini et al., 2014
Monteiro's storm petrel	Chl-a, SST	Yes	No	Robert et al., 2012
Thin-billed prion	Winter sea ice concentration	Yes	No	Nevoux and Barbraud, 2006
Southern fulmar	SST, sea- ice concentration	Yes	No	Jenouvrier et al., 2003
Northern fulmar	NAO	Yes for females, not clear for males	No	Grosbois and Thompson, 2005
SPHENISCIFORMES				
Adélie penguin	SOI	Yes	No	Jenouvrier et al., 2006
Adélie penguin	Winter sea ice extent	Yes	No	Ballerini et al., 2009
Adélie penguin	Sea-ice concentration during breeding	No	No	Lescroël et al., 2009
Adélie penguin	7 sea-ice variables, SOI, SAM	Yes	No	Emmerson and Southwell, 2011
Yellow-eyed penguin	SOI	Yes	No	Peacock et al., 2000
King penguin	SOI, SST	Yes	Both lagged and not-lagged indexes	Le Bohec et al., 2008
Rockhopper penguin	SST	Yes	No	Dehnhard et al., 2013
Macaroni penguin	SST, ENSO, SAM	Yes	Both lagged and not-lagged indexes	Horswill et al., 2014
Emperor penguin	Air temperature-sea ice concentration	Yes	No	Barbraud and Weimerskirch, 2001
Emperor penguin	Air temperature-sea ice concentration	Yes	No	Jenouvrier et al., 2005b[a]
Emperor penguin	Sea ice concentration anomalies	Yes	No	Jenouvrier et al., 2012
SULIFORMES				
European shag	Winter gales	Yes	No	Frederiksen et al., 2008
Blue-footed Booby	SOI, SST	Yes	No	Oro et al., 2010

SOI, Southern oscillation index; NAO, North Atlantic oscillation index; DMI, dipole mode index; SAM, southern annular mode; SOID, Southern Indian Ocean dipole; SST, sea surface temperature.

[a] This study is duplicated because included two species of different orders.

spatial scales are most important, and how other biological processes (such as density-dependence, interference competition or predation) interact with climate (see also below). For instance, Ezard et al. (2007) suggested that to avoid drawing incorrect conclusions regarding variability in demographic or ecological parameters (such as breeding phenology) and/or the factors responsible for these perceived changes, researchers need to be sure and control for strong inherent sources of variation, such as age. These authors had a very detailed demographic data-set that is not always available in conventional studies, but these types of confounding biotic factors (i.e., age, sex) that should be taken into account when studying the effect of climate on seabird populations. An increasing number of studies showed that the effects of climate factors or pollutants on demographic parameters are state dependent (Nevoux et al., 2010a; Goutte et al., 2014). This also matches with life history theory since energetic costs and metabolism differ between breeding and non-breeding individuals, which may in turn affect their demographic performance.

Another open question on climate-seabird research might be: is survival of larger seabirds (such as albatrosses) less sensitive to climate variability than survival of smaller species such as storm petrels? Larger species tend to have higher survival than smaller species (Weimerskirch, 2002), so environmental canalization (Gaillard and Yoccoz, 2004), i.e., the process of buffering environmental stochasticity should be stronger in the former than in the later. However, a qualitative look at available results is not so clear (see **Table 1**), maybe because biological reasons (e.g., life-history pressures, type of foraging habitat, noise from other processes such as intra-guild predation, competition, anthropogenic impacts) or because of methodological biases (increase of survival estimates through time due to appearance of more reliable statistical tools, Weimerskirch, 2002) or differential criteria to select climate indexes. It seems that there is no association between adult survival and body mass in Procellariiformes when phylogeny is taken into account in a capture-recapture modeling framework (Abadi et al., 2014); this may also explain the discrepancies found in several studies (**Table 1**), although this remains to be investigated in other seabird families.

When assessing the global impact of climate on seabirds, it should also be important to include the potential effects of breeding habitat loss or gain (typical of Arctic and Antarctic seabirds, but also among ground coastal nesting seabirds due to sea level rise), and the additive effects of anthropogenic impacts (mainly fisheries and direct harvesting, but also invasive species and pollutants) (Barbraud et al., 2012; Lewison et al., 2012; Goutte et al., 2013). To have some universal and comparable measure of the impact of climate on different species and populations, Jenouvrier (2013) proposed the use of a thorough new index, the "population robustness to climate change," together with retrospective and prospective analysis of population models.

Another gap of the association between seabirds and climate is the low number of studies on tropical seabird species. Most of seabird-climate studies have been conducted in temperate or polar marine ecosystems, whose functioning is different from tropical regions, where many seabirds occur with often poor conservation status. Future studies should thus attempt understanding tropical seabird ecology and demography and the effects of climate if we want to have better understanding of seabird climate relationships.

THE IMPORTANCE OF SUITABLE TEMPORAL AND SPATIAL SCALES

The use of oceanographic indexes to test the influence of climate on seabird ecology has been quite common (Sydeman et al., 2012), and mainly covered three spatial scales: some of them were more local (mainly climate around the breeding sites such as sea surface temperature, wind speed, air temperature, sea level pressure), some other were more regional (e.g., the Western Mediterranean Oscillation index WeMOi), whereas other indexes were more global such as El Niño-Southern Oscillation index (ENSO), Southern Oscillation index (SOI), the Southern Annular Mode (SAM), or the North Atlantic Oscillation index (NAO). The use of different spatial scales is not clearly justified in all studies (e.g., Soldatini et al., 2014) and an understanding of the spatial use of marine habitat made by each species in each period of the life cycle is essential to test appropriate hypotheses on the effect of climate on seabird ecology (Frederiksen et al., 2004a; Scott et al., 2006). To that end, the improvement of technology in recent decades (e.g., Burger and Shaffer, 2008; Wakefield et al., 2009) has allowed researchers to increase their knowledge about migration routes (e.g., Guilford et al., 2009; Egevang et al., 2010), wintering areas (González-Solís et al., 2007; Frederiksen et al., 2012) and foraging areas also during reproduction (Gremillet et al., 2004; Guilford et al., 2008) and apply oceanographic indices at more appropriate temporal and spatial scales (Duffy, 1993; Weimerskirch et al., 2012).

Regarding the temporal window of the climate indexes used in each study, even though it has also been explained in most cases, it is not always coincident among studies either. This does not nullify the results of each individual study, but makes it harder to develop any common pattern from retrospective studies that encompass completely different snapshots in time. This is particularly worrying when analyzing survival, because this is the most sensitive parameter for seabird population dynamics, and it is crucial to understand what period of the whole year is more critically affecting this parameter. Some studies used only the temporal window of the breeding season (implying that conditions during breeding are more important for survival than conditions during winter, maybe through the costs of reproduction, what is against the expectations of life-history theory in long-lived organisms capable of reducing breeding effort in a given season if survival is threatened), whereas others used only climate conditions during winter (assuming that most mortality occurs in this period, Harris et al., 2005; Genovart et al., 2013), during the two periods separately (e.g., Barbraud and Weimerskirch, 2003) or even during the whole year as an integration of all year-round variability (Gordo et al., 2011). The temporal scale also defines the difference between weather and climate: the former consists of short-term (minutes to months) changes in the atmosphere, whereas the later is the average of weather over time and space. Some weather events (such as strong storms and tsunamis, Viera et al., 2006; Sherley et al., 2012) are not necessarily correlated with climate indexes and can introduce some noise when analysing their potential association with some ecological parameters, particularly short-term processes such as reproduction and hence breeding success (Schreiber, 2002).

In general, researchers need to be very careful to present results and conclusions, particularly from retrospective observational studies, because the study design and analytical approach used must be appropriate to properly answer research questions of interest. This is true for any spatial and temporal scales used, and positive results do not necessarily ensure that the index tested is the one explaining the most variance or alternatively that there is no effect on the parameter analyzed when negative results are reported. Little is known about the frequency of negative results that do not ever get published but the potential bias against these studies by journal reviewers and editors might bias a meta-analysis or any general review of the global effects of climate on seabirds (Sydeman et al., 2012). A general recommendation to properly select the most suitable indices at both temporal and spatial scales would be first partitioning the life cycle into breeding and non-breeding seasons, and then researchers should identify the foraging ranges used by the study species in each of those seasons and test for climate effects over the corresponding spatial scales.

THE MECHANISMS LINKING CLIMATE VARIATION TO SEABIRD POPULATION CHANGE

Since most climate studies are based upon correlational evidence, the mechanistic processes linking climate variation to seabird ecology remain in most cases unclear, especially when global indexes are used (e.g., Breton et al., 2008; Sydeman et al., 2009). Typically, the first parameters to be affected when environmental conditions change are reproductive success because climate influence oceanographic conditions and food available for breeding, which is the main driver of fertility in the absence of predation (Oro et al., 1999; Schreiber and Burger, 2002; Frederiksen et al., 2006). Even though population change in seabirds is in theory less sensitive to changes in breeding success, this parameter, which influence recruitment rates, is often the vital rate that exhibits the most variation and it certainly constitutes an important factor that can affect population fluctuations. Sometimes the association between climate and breeding success is either direct in the form of heat strokes and catastrophic events such as volcanic eruptions, gales or tsunamis (Viera et al., 2006; Finkelstein et al., 2010; Sherley et al., 2012), or indirect, i.e., mediated by parasitism or diseases (Gaston et al., 2002; Cooper et al., 2009; Rolland et al., 2009a). That association should be strong in seabirds, because they are long-lived organisms and selection pressures have shaped conservatism in the energy devoted to reproduction: when environment is harsh, individuals invest less or may refrain from breeding and very low breeding success or even failures are commonly recorded for a number of species (La Cock, 1986; Frederiksen et al., 2006). However, there are other drivers that influence breeding success such as predation, food subsidies obtained from anthropogenic activities (mainly fisheries) and stochasticity in the links between climate and food-webs (Oro et al., 1996; Regehr and Montevecchi, 1997; Frederiksen et al., 2006).

The same correlation nature of studies linking climate variability with adult survival hinders the mechanisms involved, which are far from being well understood. This is particularly true when the process invoked is food availability through bottom-up control in food webs, because at the population level, adults should not jeopardize their own survival (i.e., the most conservative parameter in long-lived organism) when environmental conditions are bad and trade-offs such as survival *in lieu of* reproduction should be observed (but see Olsson and van der Jeugd, 2002; Oro and Furness, 2002). Studies suggesting direct mortality caused by harsh marine conditions during winter (e.g., gales, hurricanes) (Frederiksen et al., 2008; Boano et al., 2010; Genovart et al., 2013) are clearer examples of the potential mechanisms linking climate and survival. Population fluctuations should be more sensitive to changes in adult survival in accordance with the theory of life-histories and the evolutionary canalization of adult survival, but this association is not always clear (Harris et al., 2005).

In general, the mechanisms involved in the association between climate and vital rates (e.g., breeding success, survival, recruitment, dispersal) can be associated directly with climate (extreme values of temperature, precipitation, winds) or indirectly, through climate effects on a critical resource (e.g., food, nest sites, wintering grounds) or an interacting biological component of the ecosystem (e.g., parasites, predators). Indirect effects are often harder to distinguish in that association because the complex nature of biological interaction in food webs.

In addition, time lags in climate indexes relative to survival and population change, for example, appear reasonable when climate effects on adult survival are mediated by the food-web, because seabirds are top-predators, and some delay between climate, physical forcing and a large part of the food chain is to be expected (Thompson and Ollason, 2001; Arnott and Ruxton, 2002; Lloret et al., 2004; Martín et al., 2012). Furthermore, this delay may depend on the species, with some taxa feeding on relatively low trophic levels (e.g., fish larvae), whereas some species feed on higher food web prey (e.g., squid). However, the range of time-lags recorded between climate and adult survival has been variable among studies or not tested at all (**Table 1**, see also Jenouvrier, 2013) and the confounding effects of time, cohort and age on survival and recruitment sometimes make it difficult to assess the reliability of results. Correlations between climate covariates and population fluctuations are also analyzed either with time lags or without lagged associations. In the former case, researchers assume that those covariates influence mainly fertility and the effects on population numbers are reflected some years later, owing that seabirds do not reach sexual maturity for several years until recruitment (Cook et al., 2014). In some other cases, climate covariates of the previous year were tested, and researchers assume that conditions prior to breeding were more important by influencing adult survival, breeding propensity and immigration (Jenouvrier et al., 2003; Frederiksen et al., 2008; Irons et al., 2008; Devney et al., 2009; Lauria et al., 2012). The absence of time lag in the response of seabirds to climate variability may be reasonable in some situations, even when the process invoked is food availability, because availability of food depends on its abundance, accessibility, and distribution, which can be directly influenced by climate. Jenouvrier et al. (2005a) found that climate may have a direct or a lagged effect on population dynamics depending on environmental stochastic conditions. Some studies showed that climate have a simultaneous effects both direct and lagged because each demographic parameter are affected differently by climate (Erikstad et al., 2013; Sandvik et al., 2014). Finally, the existence of non-linear relationships between climate and seabird ecological parameters has seldom been explored (e.g., Durant et al., 2004; Jenouvrier et al., 2005a; Ballerini et al., 2009; Regular et al., 2009), despite the importance of identifying tipping points and thresholds when buffering capacity (i.e., both behavioral and demographic) is overcome.

PREDICTING THE FUTURE IMPACTS OF CLIMATE ON SEABIRDS

What is our capacity to forecast the effects of climate change on seabird abundance, distribution and viability? Several now relatively old papers anticipated the importance of predicting how climate would affect marine food webs and top-marine predators (Crawford, 1991). However, climate is just one driver among environmental-change agents and our ability to modify climate, compared to some other components of environmental change (e.g., pollutants, habitat fragmentation, fisheries interactions), is very limited. In addition, climate has a strong inertia, so it is difficult to apply conservation and management actions even if we are able to build reliable predictions for some extreme cases with detailed demographic information (e.g., some penguin, petrel and albatross species typical of Polar regions). Predictions are challenging because they rely on models built using retrospective data (i.e., "past" relationships) and thus include considerable uncertainty regarding future trajectories (Hulme, 2005; Sutherland, 2006). In addition, the best predictive models rely on large amounts of high quality demographic data, and sophisticated quantitative approaches. Yet, generating general predictions is difficult because of the inherent ecological variability amongst species, ecosystems (Chambers et al., 2011) and even among individuals (Lescroël et al., 2009, 2010; Lescroel et al., 2014) and populations (Tavecchia et al., 2008; Dias et al., 2010). These predictions, if they are local, can also be biased by dispersal processes (e.g., Woehler et al., 2014), because seabirds are very vagile, even species considered as highly philopatric (Genovart et al., 2007). Despite those constraints, population models together with tools for time-series analysis have yielded very promising results when long-term data sets and detailed estimations of demographic parameters were available (Jenouvrier et al., 2009, 2012, 2005a). Thus, research on the effects of climate on seabirds (or on any other organism and ecosystem) should be focused to building solid scientific evidence on predicted rates of population change, meta-population dynamics, and changes in species distribution given the present rates of warming (Sydeman et al., 2012). Testing hypotheses about the effects of climate on seabird ecology (e.g., diet, behavior, and phenology) is a first step toward making predictions regarding climate effects on population trajectories and to understanding the mechanisms linking patterns and processes, but this is just the first step. In general, we should move to a research devoted more toward forecasting the effects of global change (not only climate, but considering the synergetic effects of several agents of global change (e.g., Votier et al., 2008b; Finkelstein et al., 2010; Rolland et al., 2010; Lebreton, 2011), and to offer evidence that can help managers develop a roadmap of conservation actions (Jenouvrier, 2013). However, we need to collect the foundational information regarding links between demographics and climate, and the mechanisms that link them as we must have robust estimates of vital rates to build predictive models, and this constitutes a big challenge. In general, there is more potential to manage the impacts of other global change agents such as overharvesting (Jahncke et al., 2004; Becker and Beissinger, 2006), bycatch in fisheries (Bunce et al., 2002; Barbraud et al., 2008; Rolland et al., 2008; Ramos et al., 2012), habitat deterioration (Lindenmayer and Fischer, 2013), pollution (Croxall et al., 2012) or invasive species (Nogales et al., 2004; Ruffino et al., 2009; Major et al., 2013) than there is for managing climate (Rogelj et al., 2013), so this can be an indirect way of battling the impacts of climate warming.

Finally, population predictions must take into account the resilience of species to environmental change including extreme events, which are predicted to increase in frequency. For example, Hass et al. (2012) forecasts the impact of increasing hurricanes on the viability of the already endangered black-capped petrel *Pterodroma hasitata*, and predicted that this increase in hurricane frequency could nearly double the expected number of wrecked petrels over the next century, placing the species at greater risk of extinction by acting upon already much reduced populations due to human action (e.g., harvesting, bycatch, loss of breeding habitat). In addition Gremillet et al. (2012) showed that foraging behavior plasticity in little auks *Alle alle* maintained fitness levels across a wide range of sea surface temperatures, which may buffer them against at least the initial impacts of climate change. Several ecological parameters (e.g., vital rates, distribution, and foraging ranges) have been observed to shift as a result of changes in climate in several seabird species, but relatively little is known about the potential for changes in other demographic mechanisms to buffer these shifts. I can hypothesize that changes in recruitment rates, breeding propensity and increased fertility, as well as the role of immigration in source-sink systems at local population level, all have the potential to offset potential declines in survival for example, in relation to climate change. Some of these compensatory mechanisms have been already found in harvested populations of fish and ungulates (Lebreton, 2005; Servanty et al., 2011).

At the scale of geological times, seabirds have a long evolutionary history. Bone remains of a *Phaeton* tropicbird have been recently found in Morocco preserved from the Ypresian Age, in the lower Eocene, ca. 48×10^6 years ago (Bourdon et al., 2008). In geological- time scales, seabirds have experienced changes in climate, including warming and cooling periods, and extreme events. The previous interglacial period ($1.2–1.3{*}10^5$ years BP) was substantially warmer than the present one; about 2°C in the North Temperate Zone and 5°C in the Arctic, and it may have been the warmest period since the onset of the Pliocene (Fedorov et al., 2013). Some species have likely shown more plasticity to adapt to such changes and to anthropogenic factors acting in synergy with climate change, and we have to identify what species would be more sensitive to the current rate of climate change. A major difference between the so-called Anthropocene with previous geological periods is major habitat alteration due to the growth of human population (breeding habitat destruction, introduced predators, pollutants) with these factors acting in synergy with climate. Therefore, plasticity may be not enough to adapt to climate change given these additional factors for which many seabird species were not previously exposed and selected for. For instance, Igual et al. (2007) showed that Cory's shearwaters, due to their limited behavioral plasticity and heavy evolutionary loads, did not perceive the presence of invasive predators signaling differences in predation risk and in turn of breeding success.

Climate has in itself the features of a paradigmatic complex system: emergent properties that cannot be explained by the sum of its components. So the study of its influence on seabird ecology is far from being straightforward because climate has many emergent properties that cannot be explained solely by the sum if its own components, to a large extent because of its random structure, and additionally because many other factors can be involved, including extrinsic (e.g., predators in the case of small and medium-sized species, prey density, competition) and intrinsic (e.g., density-dependence, age-structure, sex) factors.

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Adélie penguins coping with environmental change: results from a natural experiment at the edge of their breeding range

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We investigated life history responses to extreme variation in physical environmental conditions during a long-term demographic study of Adélie penguins at 3 colonies representing 9% of the world population and the full range of breeding colony sizes. Five years into the 14-year study (1997–2010) two very large icebergs (spanning 1.5 latitude degrees in length) grounded in waters adjacent to breeding colonies, dramatically altering environmental conditions during 2001–2005. This natural experiment allowed us to evaluate the relative impacts of expected long-term, but also extreme, short-term climate perturbations on important natural history parameters that can regulate populations. The icebergs presented physical barriers, not just to the penguins but to polynya formation, which profoundly increased foraging effort and movement rates, while reducing breeding propensity and productivity, especially at the smallest colony. We evaluated the effect of a variety of environmental parameters during breeding, molt, migration and wintering periods during years with and without icebergs on penguin breeding productivity, chick mass, and nesting chronology. The icebergs had far more influence on the natural history parameters of penguins than any of the other environmental variables measured, resulting in population level changes to metrics of reproductive performance, including delays in nesting chronology, depressed breeding productivity, and lower chick mass. These effects were strongest at the smallest, southern-most colony, which was most affected by alteration of the Ross Sea Polynya during years the iceberg was present. Additionally, chick mass was negatively correlated with colony size, supporting previous findings indicating density-dependent energetic constraints at the largest colony. Understanding the negative effects of the icebergs on the short-term natural history of Adélie penguins, as well as their response to long-term environmental variation, are important to our overall understanding of climate change effects in this and other species facing both rapid and persistent environmental change.

Keywords: Adélie penguin, breeding productivity, chick mass, climate change, environmental variation, nesting phenology

INTRODUCTION

Climate change effects on species' demographic parameters are increasingly evident across a broad range of taxa (Walther et al., 2002; Parmesan, 2006; Jenouvrier, 2013). This is especially evident at the poles, where massive changes in the extent and volume of glaciers and sea ice have occurred throughout geologic time, greatly altering the availability of habitat required for vertebrates to exist (for the Antarctic, see e.g., Emslie et al., 2007; Thatje et al., 2008). In recent decades, environmental changes attributable to anthropogenic climate change are more rapid and extensive than at any time in at least the past 1400 years (Kinnard et al., 2011; Stammerjohn et al., 2012). Species adapted to life in polar regions have had to adjust to such dramatic changes in the past, ostensibly by adjusting behavior, phenology, and ultimately distribution (Emslie et al., 2007; Thatje et al., 2008). However, the degree to which environmental change can be absorbed by a species' phenotypic coping mechanisms before long-term population changes occur remains largely unknown (reviewed in Barbraud et al., 2012). The unprecedented rate and magnitude of climate change occurring now provides an opportunity to assess species' capacity to adapt (Lescroël et al., 2014). At the same time, other environmental changes and their interactions with the direct effects of climate change have the potential for more rapid and consequential impacts on species' distributions and population dynamics than climate change alone (Warren et al., 2001; Jongsomjit et al., 2012; Jenouvrier, 2013). In particular, understanding the limits of the natural history and demographic attributes of ice-obligate species like the Adélie penguin (*Pygoscelis adeliae*) is of importance given the rapid increase in sea ice extent and persistence in the Ross Sea sector of the Southern Ocean over the past 30 years, particularly given these changes are in stark contrast with the Antarctic Peninsula sector and the Arctic Ocean (Stammerjohn et al., 2012).

Adélie penguin natural history has been well-studied Antarctic-wide (Ainley, 2002) with recent research focused on long-term temporal and spatial patterns in abundance and demographics (Jenouvrier et al., 2005; Dugger et al., 2006, 2010; Lynch et al., 2012a; Lyver et al., 2014), foraging ecology (e.g., Watanuki et al., 2002; Ainley et al., 2003, 2004; Ballard et al., 2010a; Lescroël et al., 2010, 2014), and breeding biology (Ainley et al., 1983; Emmerson and Southwell, 2008; Hinke et al., 2012). In summary, it appears that population responses of Adélie penguins to environmental drivers can vary temporally and spatially, with contrasting responses of vital rates to patterns of sea ice extent and/or concentration (Croxall et al., 2002; Forcada and Trathan, 2009; Ainley et al., 2010; Lynch et al., 2012a; Hinke et al., 2014). For example, increased summer sea ice concentrations near breeding colonies can result in decreased reproductive success (Ainley, 2002; Emmerson and Southwell, 2008) and foraging efficiency (Lescroël et al., 2014), but survival is lowest when winter sea ice concentrations are either very high or very low (Ballerini et al., 2009). Decreased summer sea ice extent 6 years previous can lead to increased populations (Jenouvrier et al., 2005), while extensive winter sea ice has been linked in a 5-year lag to decreased subadult survival (Wilson et al., 2001). The existence of polynyas (areas of persistent open water or low ice concentration within the larger sea ice field) is critical in affecting penguins' access to the ocean and thus, to food resources, because their presence reduces commuting time to foraging areas, thereby decreasing foraging effort and energy expenditure (Ballance et al., 2009; Ainley et al., 2010; Ballard et al., 2010a). Polynyas ultimately influence the distribution and persistence of Adélie penguin breeding colonies (Ainley, 2002; Arrigo and van Dijken, 2003) and the McMurdo Sound and Ross Sea polynyas are important to the distribution, persistence and size of the Ross Island penguin colonies that we study. Therefore, factors that disrupt or block these adjacent open water areas can have significant impacts on this species (Emslie et al., 2003; Ballard et al., 2010a; Lescroël et al., 2014).

During former millenia, changing ice conditions have caused major re-distributions of Adélie penguins in the Ross Sea, likely with associated effects on genetic diversity (Millar et al., 2012). Indeed, high rates of micro-evolution between ancient (∼6000 years ago) and modern populations have been documented for Adélie penguins (Shepherd et al., 2005), consistent with low emigration rates and high natal philopatry exhibited during periods of relatively stable environmental conditions (Ainley, 2002; LaRue et al., 2013). This is in contrast to overall genetic homogeneity documented for modern populations, and surprising for a species with such a large geographic distribution and general life history traits that should favor genetic differentiation (Roeder et al., 2001). However, millennia-scale environmental changes resulting in the southernmost portion of the Ross Sea being re-occupied only in the past ∼1100 years (Emslie et al., 2003, 2007), large population sizes, extensive population re-distribution, and increased exchange between populations during periods of high environmental variation (Dugger et al., 2010), is likely responsible for this genetic homogeneity (Roeder et al., 2001; Shepherd et al., 2005).

Adélie penguin breeding populations are presently disappearing from areas in the Antarctic Peninsula that have been occupied for 500–800 years, beginning with onset of the Little Ice Age (Emslie, 2001). Thus, distributional shifts are once again occurring and have been linked to the rapid climate change in the region, including warming temperatures, increasing precipitation, and the disappearance of sea ice (Ducklow et al., 2007; Schofield et al., 2010; Lynch et al., 2012a) and associated penguin prey species (Sailley et al., 2013). In addition, the short breeding season associated with polar ecosystems results in a relatively inflexible breeding phenology (e.g., onset of laying, peak laying or hatch date) with limited opportunities for penguins to adjust to these rapid changes in foraging and nesting habitat at low latitudes (Hinke et al., 2012; Lynch et al., 2012b).

We have a 14-year time series (1997–2010) on demographics and breeding/foraging effort derived from three Adélie penguin colonies that vary in size by multiple orders of magnitude, within a 4-colony metapopulation in the Ross Sea (see Ainley, 2002; LaRue et al., 2013; Lyver et al., 2014; **Figure 1**). The objectives of this study were to use these data to determine the effect of typical seasonal variation in the sea ice environment at multiple spatial scales (i.e., Ross Sea sector of the Southern Ocean, the Ross Sea itself, and foraging areas adjacent to nesting colonies; **Figure 2**) on three important natural history parameters of Adélie penguins: breeding productivity, chick mass, and nesting chronology. After 5 years of this long-term study were completed, two giant icebergs grounded, one of which essentially constituted a fence 1.5 latitude degrees long (170 km in length; **Figure 1**), and dramatically altered local habitat conditions (Arrigo et al., 2002). This provided a "natural experiment" with which to evaluate smaller vs. extreme environmental perturbations that could alter important factors regulating colony size and persistence. During the middle third of the study period, the large icebergs brought extreme conditions by altering sea ice concentration (or cover; SIC), polynya formation, primary productivity and circulation (Arrigo et al., 2002; Robinson and Williams, 2012). In addition, because the icebergs were grounded and rose well above sea level, they created a physical barrier between the easternmost colony on Ross Island and the western colonies (**Figure 1**). The sea ice trapped by the icebergs during spring and summer when it usually breaks out, precluded development of the McMurdo Sound Polynya, and forced the penguins nesting at the western McMurdo Sound colonies to forage through a limited number of cracks in the sea ice or walk 50–70 km to reach open water. More importantly, the icebergs physically occupied the entire western marginal ice zone of the Ross Sea Polynya, one of the most ecologically prominent features of the region (Arrigo et al., 2002; Ballard et al., 2012; **Figure 1**), further reducing the availability of preferred foraging habitat (SIC <15%; Ballard et al., 2010b; Lescroël et al., 2014). Thus, the presence of these icebergs provided a unique opportunity to investigate the impact of a severe, short-term habitat change on an ice-obligate species during a time

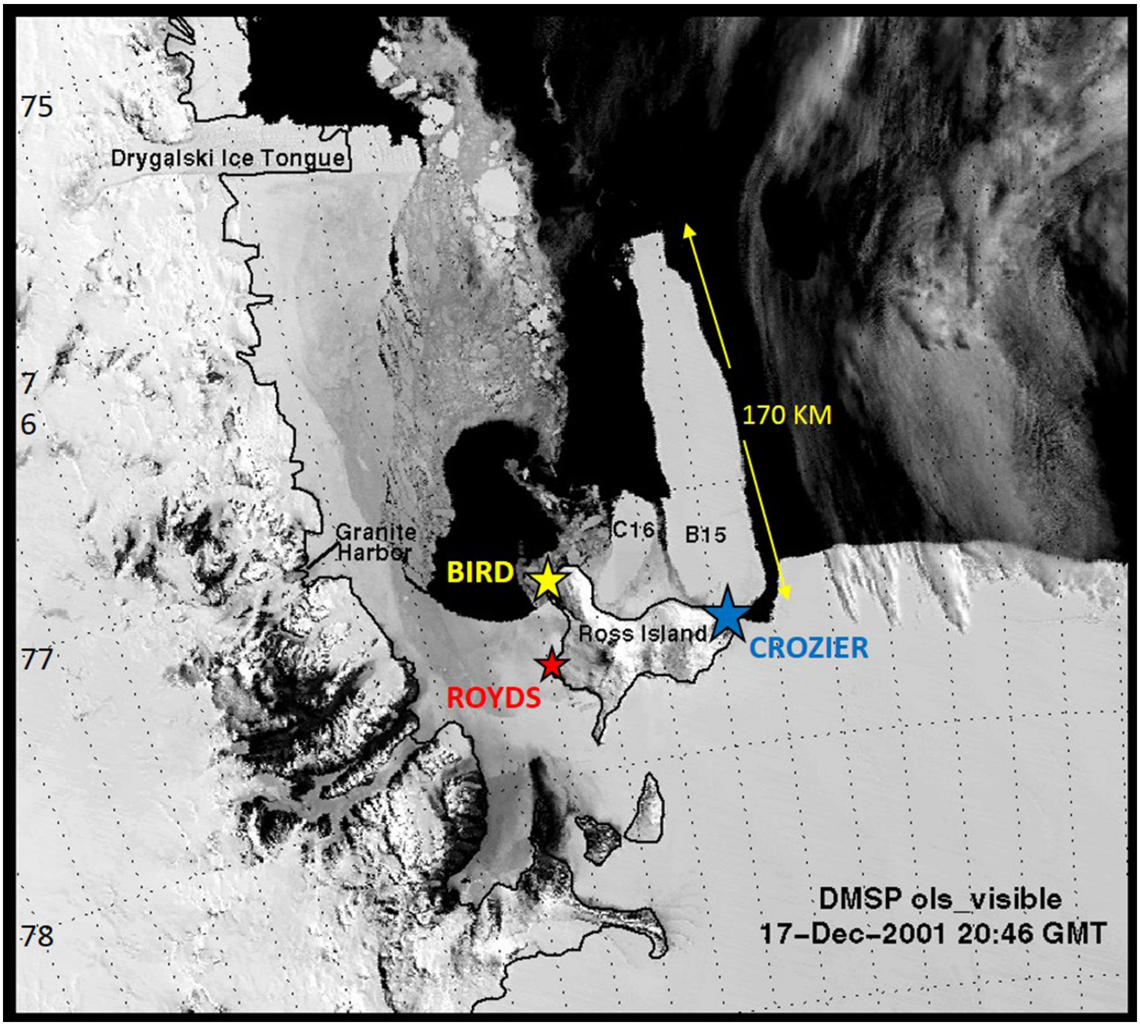

FIGURE 1 | Southern Ross Sea, Antarctica, and the locations of three Adélie penguin breeding colonies on Ross Island where reproductive performance parameters were collected from 1997 through 2010. Colonies vary in size by orders of magnitude, with Cape Royds the smallest (mean size: 2865), Cape Bird intermediate (mean size: 43,321), and Cape Crozier the largest (mean size: 153,623). The positions of the giant icebergs (B15 and C16) in December 2001 are also indicated.

when large-scale climate change was altering the region, including sea ice extent, duration of the sea ice season and polynya formation (cf. Parkinson, 2002; Zwally et al., 2002; Ainley et al., 2005, 2010; Stammerjohn et al., 2008, 2012). In addition, these data may help us to understand the mechanisms behind breeding colony formations and extirpations that have occurred infrequently in association with varying degrees of sea ice persistence in the region as the West Antarctic Ice Sheet withdrew from the Ross Sea during the Holocene (Emslie et al., 2003, 2007). These colonies were abandoned and then re-established at least twice during this time: 5000–4000 and 2000–1100 years B.P. (Emslie et al., 2003, 2007).

MATERIALS AND METHODS

Measures of reproductive performance, including breeding productivity, chick mass, and nesting chronology, were collected from three Adélie penguin colonies on Ross Island during 1997 through 2010 (Cape Royds, Bird, and Crozier). These colonies represent 9% of the global population as well as the full range of sizes of Adélie penguin colonies (cf. Lynch and LaRue, 2014), varying by multiple orders of magnitude (mean size, 1981–2012: Cape Royds: 2865, Cape Bird 43,321, and Cape Crozier 153,623 prs; most recent counts, 3083, 75696, and 272340, respectively; LaRue et al., 2013, 2014; Lyver et al., 2014). Access to food resources and intra- and inter-specific competition for food (Ainley et al., 2004, 2006; Ballance et al., 2009) are factors influencing the size-structure of the colonies in this meta-population. Nesting chronology was determined from the monitoring of marked nests at each colony, generally in association with data collection for other studies ($n > 30$ per site, per year; Ballard et al., 2001; Lescroël et al., 2009).

Breeding productivity (number of chicks per pair) was estimated from (1) ground counts of the number of occupied territories in a sample of subcolonies at each site (20–40 depending

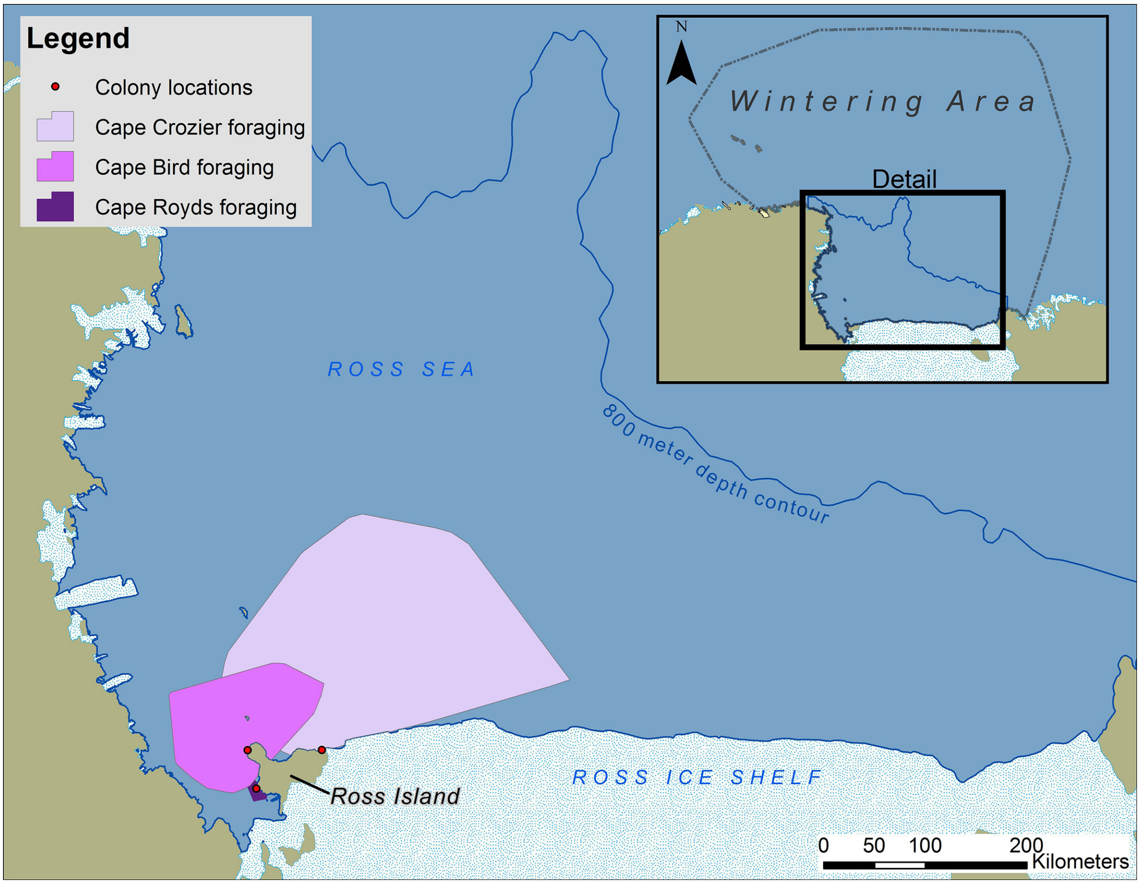

FIGURE 2 | Wintering, migration and foraging areas of Adélie penguins nesting at three colonies on Ross Island Antarctica, during 1997–2010.

on colony and year) conducted during late incubation (late November/early December) each year; and (2) counts of the number of chicks at each of these same subcolonies in mid-January. An overall mean number of chicks per pair for the entire sample of subcolonies was generated for each colony annually, and used as the dependent variable for modeling.

We determined mean chick mass (gr) from ~50 chicks measured 5 weeks after peak hatch date at each colony each year (Ainley, 2002; Whitehead et al., in review). For nesting chronology, we could not estimate onset of laying, since penguins arrived at some of our colonies and began laying eggs before we had access to field camps. However, mean annual hatch dates were determined each year from >30 nests monitored in reference subcolonies at each colony. A long-term mean peak hatch date was calculated from annual peak hatch dates (1997–2010), and a "relative peak hatch date" was then generated by subtracting each year's peak hatch date from the long term mean for that colony. This resulted in a "relative" peak hatch date each year where positive values were later than mean peak hatch date and negative values were earlier than mean peak hatch date. We standardized the peak hatch dates by colony long-term means, because the onset of laying differed by as much as 14 days between Crozier (closest colony to wintering areas) and Royds (most southern Adélie penguin colony in the world).

Estimation of sea ice conditions was based on monthly means taken from weekly passive imagery using the Special Sensor Microwave/Imager (SSMI, Cavalieri et al., 1996/2008), as follows: at the large scale, (a) sea ice concentration or cover (SIC; % of ice in a given ocean area) in wintering areas and (b) SIC along migration routes in the Ross Sea (both delineated by Ballard et al., 2010b; see **Figure 2**); and, at the meso-scale, (c) distance to polynya edge in McMurdo Sound during the breeding season and (d) SIC within foraging areas adjacent to each colony during December (**Table 1**; **Figure 2**). To generate annual estimates of net primary production (NPP) for the Ross Sea, SIC was calculated from SSM/I imagery using the Polynya Signature Simulation Method (PSSM) algorithm (Markus and Burns, 1995) which computes sea ice presence/absence at 6.25 km resolution.

In addition to SIC, the icebergs called B-15A and C-16 calved from the Ross Ice Shelf in March 2000, and by January 2001 had lodged against Ross Island between Capes Crozier and Bird, projecting 180 km north (1.5 latitude degrees; **Figure 1**). The icebergs moved out of the area in July 2006, so 1997–2000 and 2006–2010 were considered "not impacted" by the cumulative effects of the icebergs, and years 2001–2005 were considered "iceberg" years (Lescroël et al., 2009, 2014; Ballard et al., 2010a). In addition, the McMurdo Sound Polynya (adjacent to Cape Royds and Bird), failed to develop at least once in the years before

Table 1 | Acronyms and brief descriptions of environmental covariates used to model relative peak hatch date, annual productivity (chicks per pair), and mean chick mass at 5 weeks post-hatch for Adélie penguins breeding at Cape Royds, Cape Bird and Cape Crozier on Ross Island during 1997–2010.

Acronym	Description
Year	Categorical variable representing general annual variation in time series.
Colony	Categorical variable representing 3 breeding colonies on Ross Island.
ColSize	Continuous variable for the number of breeding pairs as counted from aerial photographs taken at the onset of incubation each year (∼Dec. 1st).
Iceberg	Categorical variable representing presence/absence of iceberg. Iceberg was present during 2001–2005 breeding seasons and absent during 1997–2000, and 2006–2010 seasons.
IceCover	Categorical variable denoting presence or absence of extensive sea ice in the McMurdo Sound that precluded typical formation of McMurdo Sound polynya. Ice cover was present during 1999, 2001–2002, 2004–2005, and 2008, and absent in 1997–1998, 2000, 2003, 2006–2007, 2009–2010.
DistIce	Continuous variable for the weekly distance (km) to ice edge from each colony, averaged by month during the breeding season. We investigated November (DistIce_N), December (DistIce_D) and January (DistIce_J) monthly means.
RSice	Continuous variable for weekly % ice cover in the entire Ross sea averaged for November (RSice_N), October (RSice_O), and both October and November (RSice).
WAice	Continuous variable for weekly % ice cover for Adélie penguin wintering areas averaged for October (WAice_O) and October and November (WAice).
FA_Dec	Continuous variable for colony-specific weekly % ice cover averaged for December for foraging areas adjacent to Adélie penguin colonies.
NPP	Primary production in the Ross Sea during 1997–2010.

the iceberg (owing to reduced winds), but during iceberg years when it was very windy (2003) it did form normally. So in addition to the iceberg covariate, which incorporated the physical presence of the icebergs, we looked at the effects of extensive SIC (in foraging areas) alone (hereafter referred to as IceCover; **Table 1**). Under this scenario, the 6 years during which sea ice remained in McMurdo Sound through chick rearing included 1999, 2001–2002, 2004–2005, and 2008.

Annual estimates of net primary production (NPP) for the Ross Sea were calculated by integrating daily estimates of NPP over the growing season from October 17- March 21. For this purpose, the Ross Sea was defined as the geographic area from 60 to 79°S and 160°E to 155°W. Daily estimates of NPP (Tg C day-1) were calculated by spatially integrating daily maps of NPP over the area of open water. Daily NPP maps (mg C m-2 day-1) were produced using satellite-derived chlorophyll *a* (Chl *a*), sea surface temperature, and sea ice cover using the algorithm detailed in Arrigo et al. (2008). Chlorophyll *a* concentrations were calculated for the years 1997 through 2002 from SeaWiFS Level 2 (4 km resolution) ocean color data (Reprocessing R2010.0), using the OC4v4 algorithm (O'Reilly et al., 1998). For October 2002 through March 2012, Chl *a* concentrations were calculated from MODIS Aqua Level 2 (1 km resolution) ocean color data (Reprocessing R2012.0), using the OC3M algorithm (O'Reilly et al., 2000). Five-day averages were used for calculating NPP. Sea surface temperature used to calculate NPP was taken from the Daily Reynolds Optimally Interpolated SST (OISST) Version 2 product (Reynolds et al., 2002), from NOAA (www.ncdc.noaa.gov/oa/climate/research/sst/oi-daily.php).

Estimates of colony size, i.e., number of breeding pairs, were obtained from Lyver et al. (2014), and were based on counts derived from annual aerial photographs taken during late incubation (∼December 1st) each year, concurrent with the ground counts described above. Using these data, we were able to include colony size directly as a continuous variable, rather than a more general categorical effect in models.

A variety of *a priori* models that reflected hypothesized relationships between reproductive performance and these environmental covariates, including colony size, were developed specific to each dependent variable (Supplementary Material). For example, we hypothesized that breeding productivity each year would most likely be influenced by factors that affected breeding propensity (i.e., the probability that a bird breeds each year) such as arrival date at the colony, and also foraging conditions during the breeding season adjacent to each colony. Therefore, the number of chicks per pair was modeled in relation to SIC on wintering areas and also for the Ross Sea in general during October and November, as we expected high SIC during this time to delay birds returning to breed. We hypothesized that delayed arrival from wintering areas each spring would likely affect adult body condition and delay onset of breeding (i.e., as measured here with relative peak hatch date).

In contrast, we predicted negative effects on chicks produced per pair and chick mass of SIC in foraging areas adjacent to each colony and/or distance to ice edge (polynya edge) in McMurdo Sound when chicks were being fed through December. We also expected a link between primary production in the Ross Sea and chick mass, with higher productivity resulting in heavier chicks. Due to differences in intraspecific competition as a function of colony size, we also predicted heavier chicks at the smaller colonies (Royds and Bird) compared to the largest (Crozier).

Finally, similar to breeding productivity, we expected nesting chronology to be most strongly related to large-scale SIC during spring migration, with higher SIC resulting in later relative peak hatch dates at each colony. Thus, we generated models linking relative peak hatch date to SIC on wintering areas and on migration routes during October and November. SIC and sea ice extent at the large scale are strongly correlated (Zwally et al., 2002).

For each of the reproductive parameters (breeding productivity, chick mass, and nesting chronology) we used general linear models (SAS Proc Mixed; SAS Institute, Inc, 2008) to investigate the effects of continuous SIC covariates, primary production, and colony size, as well as categorical variables denoting years when icebergs or extensive SIC in McMurdo Sound were present. We investigated each of these covariates as a single additive effect and also 2-factor models containing colony or colony size, and iceberg presence or SIC as additive and interactive effects if those covariates received strong support as single-factor effects (Supplementary Material). We also included an intercept-only model and model containing general annual variation for comparison (Supplementary Material). We used an information-theoretic approach including differences in model AIC$_c$ compared to model with lowest AIC$_c$ ($\triangle AICc$), AIC$_c$ weights, and model coefficients (betas:β) to determine strength of evidence for models and specific effects within models (Burnham and Anderson, 2002). For the top models in each analysis we used a variance decomposition approach to determine the amount of variance explained by the best model (e.g., Franklin et al., 2000; Olson et al., 2004). We used changes in residuals generated by Proc Mixed in SAS (SAS Institute, Inc, 2008) in relation to the intercept-only model to separate the contribution of parameters in the model to overall variance in the dependent variable.

RESULTS

Breeding productivity was strongly affected by colony and iceberg presence with the best model indicating that these effects were additive (Model 1, Supplementary Material). The iceberg had a strong negative effect on breeding productivity as predicted ($\hat{\beta} = -0.60$, $SE = 0.08$, 95% CI: −0.44 to −0.76), and the effect was strongest at Royds (**Figure 3**); a pattern consistent with the second best model that included an interaction between iceberg presence and colony (Model 2, Supplementary Material). The top-ranked model containing the additive effects of iceberg and colony, explained 59.9% of the total variance in penguin productivity (Model 1, Supplementary Material). Thus, in conjunction with initial overall declines in breeding populations at all 3 colonies in relation to the presence of the iceberg (Lyver et al., 2014), on average, ∼2500, 36,000, and >125,000 fewer chicks per year were produced at Royds, Bird and Crozier, respectively, during the 5 years the icebergs were present.

If models including the iceberg effect and colony or colony size were not considered in our *a priori* model set, then the top models would have included significant positive effects of SIC in winter areas during October (Model 6; $\hat{\beta} = 0.07$, $SE = 0.02$, 95% CI: 0.04–0.11). Moreover, the negative effects of the average weekly distance (km) to the ice edge/polynya edge in November (Model 8; $\hat{\beta} = -0.007$, $SE = 0.002$, 95% CI: −0.003 to −0.011) and December (Model 7; $\hat{\beta} = -0.009$, $SE = 0.002$, 95% CI: −0.005 to −0.014) on penguin productivity would have received more support (Supplementary Material). A positive relationship between SIC on wintering and migration areas in October and the number of chicks produced per pair was contrary to what we hypothesized if high SIC delayed spring arrival or decreased breeding propensity, which could decrease productivity. We did predict that chick mass would increase with decreased distance to the ice edge/polynya edge during the breeding season, and as a consequence more chicks may survive, thereby increasing overall productivity.

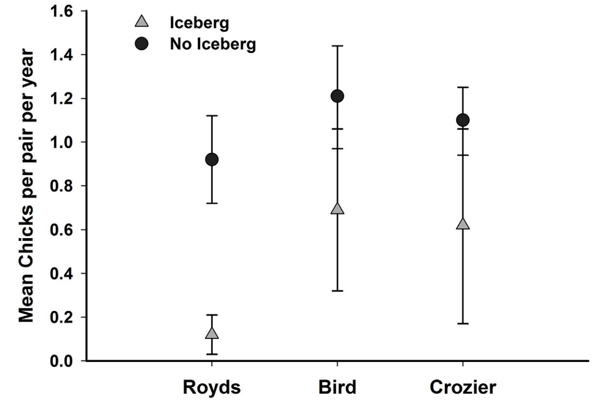

FIGURE 3 | The mean number of Adélie penguin chicks per pair (with 95% confidence limits) produced at Capes Crozier and Royds on Ross Island, Antarctica when icebergs were present (2001–2005) and when icebergs were not present (1997–2000, 2006–2010).

Chick mass was lower at all 3 colonies when the iceberg was present, but interestingly, there was also a strong negative linear relationship between chick mass and colony size (Model 1, Supplementary Material; **Figure 4**), consistent with Whitehead et al. (in review). Chicks averaged 347 gr ($SE = 98.6$) heavier during non-iceberg years, but mass decreased 3 gr ($SE = 0.6$) with every 1000 breeding pair increase in colony size (**Figure 4**). The top model containing additive effects of both colony size and the iceberg effect received 77% of the AIC$_c$ weight and explained 46.5% of the total variance in chick mass during this study. None of the other covariates received any support as evidenced by low AIC$_c$ model weights (Supplementary Material), and even if the iceberg effect was not considered, the effect of colony size far outweighed the impact of any other covariate for these data.

When all years of available data were used in the nesting chronology analyses, relative peak hatch date was slightly earlier (0.46 days) during non-iceberg years, than during iceberg years (Model 1; iceberg absent: $\hat{\beta} = -1.422$, $SE = 0.89$, 95% CI: 0.36 to −3.20; Supplementary Material). This top model only explained 3.4% of the total variance in relative peak hatch date, and confidence limits on this coefficient included zero, so the iceberg had only a weak effect on this parameter. However, this data set included outliers for Cape Royds and Crozier during the 2009 season, when mean peak hatch dates at both colonies were >1 week later than is typical because of a large asynchrony in timing of return to the breeding colonies. This was unrelated to the iceberg, or any apparent environmental conditions we investigated, but resulted in a peak of birds arriving with typical timing and another peak of birds arriving much later. If data from 2009

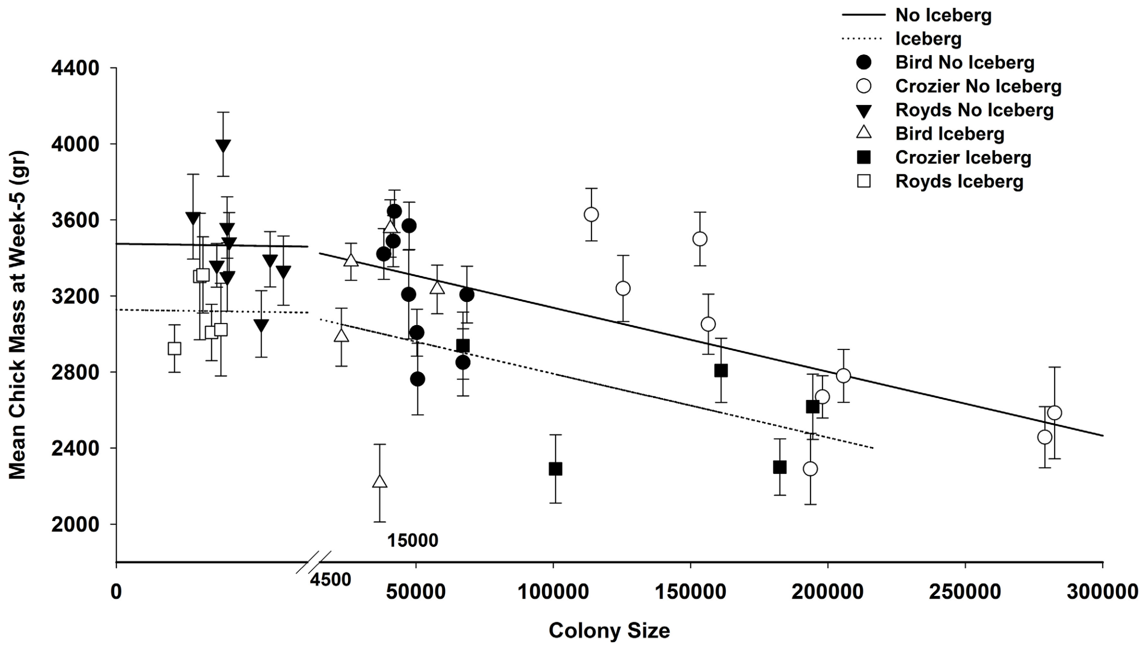

FIGURE 4 | Predicted mean mass (gr; with 95% confidence limits) of chicks at 5 weeks post-peak hatch date from best model plotted against colony size, for Adélie penguin at Cape Royds, Bird, and Crozier on Ross Island, Antarctica when icebergs were present (2001–2005) and when icebergs were not present (1997–2000, 2006–2008).

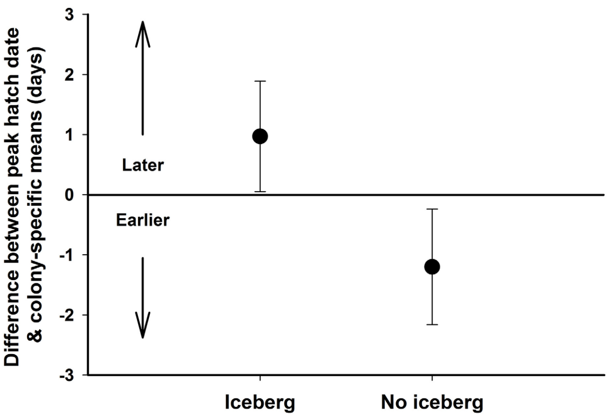

FIGURE 5 | The mean difference (with 95% confidence limits) between peak hatch date and colony-specific means for Adélie penguin s breeding at Cape Royds, Bird, and Crozier on Ross Island, Antarctica during years when the icebergs were present (2001–2005) and when there were no icebergs, excluding 2009 (1997–2000, 2006–2008, 2010).

were excluded, the iceberg effect was stronger (Model 1; AIC_c $wt = 0.78$; Supplementary Material), with the best model containing the iceberg effect explaining 17.3% of the total variance, and a coefficient with confidence limits that did not include zero ($\hat{\beta} = -2.12$, $SE = 0.69$, 95% CI: -0.74 to -3.49). Excluding 2009, mean relative peak hatch dates were nearly 2 days earlier during years when the iceberg was not present (**Figure 5**).

When all years were considered, only the model with the iceberg effect (Model 1) ranked higher than the intercept-only model (Model 2, Supplementary Material), indicating that none of the other covariates considered could explain much variation in relative peak hatch date if the iceberg effect was not considered. However, if 2009 was excluded, and the iceberg effect was not considered, then the mean weekly SIC for Adélie penguin wintering areas during October would have been the top model (Model 2, Supplementary Material). The direction of the effect is as anticipated, with more ice on wintering areas in October resulting in a later relative peak hatch date, with the confident limits on the coefficient just barely overlapping zero ($\hat{\beta} = -0.20$, $SE = 0.11$, 95% CI: 0.02 to -0.42). This indicates that although the effect of conditions during spring migration on breeding phenology in this study were weak, the relationship may be worth exploring in more detail with a longer time series.

DISCUSSION

The variation among measures of reproductive performance observed during years the icebergs were present was generally outside the range of variation seen in more typical years, with fewer chicks produced, lower chick mass, and delayed nesting chronology observed during iceberg years. Chick mass was also strongly negatively correlated with breeding population size (see also Whitehead et al., in review), lending support to previous findings suggesting that density-dependent energetic constraints exist at the largest colony (Ballance et al., 2009). When we excluded the effects of the iceberg perturbation, we also found weak support for the effect of SIC in October (spring migratory period) on breeding chronology (when 2009 was excluded) and some indication that distance to the ice or polynya edge during chick-rearing affected the number of chicks per pair produced each year. However, none of the other environmental covariates had substantial effects on the population parameters we investigated even if the effect of the icebergs was not considered. The positive relationship between peak hatch date and SIC is consistent with sea ice extent being greater as well (Zwally et al., 2002), resulting in penguins wintering farther north than "normal" (cf. Ballard et al., 2010b), which could delay their arrival on breeding colonies in the spring and reduce breeding propensity, ultimately affecting colony size (Wilson et al., 2001).

Despite the fact that the levels of summer primary production, exhibited extreme variation in the Ross Sea during this study (5.7–49.6 Tg C year^{-1}) and was especially affected by the large icebergs, we were surprised that there was no effect on the penguin reproductive parameters we measured. Changing primary productivity, and correlated chlorophyll concentrations, have been found to affect the ecosystem in general (Schofield et al., 2010) and penguins in particular (Lynch et al., 2012a; Cimino et al., 2013) especially along the western coast of the Antarctic Peninsula, where climate change has been amplified. Chlorophyll concentration has been used as a proxy for food availability in many studies of seabirds and other upper level marine predators, however, the actual link between chlorophyll level and prey availability has rarely been made, and is likely very complex (e.g., Grémillet et al., 2008; Ainley et al., 2009; Suryan et al., 2011). Our results suggest that considering such a link should be done with caution and might be applicable only at larger spatial and temporal scales. At the scale of the entire Ross Sea there is a disproportionate contribution to total Southern Ocean productivity and an exemplary robust food web (cf. Arrigo et al., 1998; Ballard et al., 2012; Smith et al., 2014), perhaps mitigating any potential effects of more local variability in productivity.

The decline in reproductive performance during iceberg years had large effects on colony population size, particularly for the smallest colony in this meta-population. The three Ross Island colonies vary in size by multiple orders of magnitude and these large differences have affected natural history parameters, particularly in light of density-dependent and competitive effects on foraging effort and efficiency in this metapopulation (Ainley et al., 2004, 2006; Ballance et al., 2009). Additionally, the impacts of rare (in terms of a species' life span), but extreme environmental perturbation can be important for regulating population size (Drake, 2005; Frederiksen et al., 2008; Van de Pol et al., 2010), with extreme events predicted to have relatively larger effects on smaller populations compared to large ones, in part explaining why large Adélie penguin populations are large and small ones are small (Ballard, 2010). Indeed, the Royds breeding population decreased from 3600–3900 pairs before 2001 to ∼2200 pairs by 2006; in contrast, the Crozier population increased from about 155,000 to >175,000 pairs during the iceberg years, and is now estimated to be over 270,000 breeding pairs (LaRue et al., 2014; Lynch and LaRue, 2014; Lyver et al., 2014). In addition, negative effects on productivity in particular are consistent with the decreased foraging efficiency (Ballard et al., 2010a; Lescroël et al., 2010, 2014) and increased inter-colony movement rates we observed for breeding adults (Dugger et al., 2010; LaRue et al., 2013) during this natural experiment. Movement rates of breeding adults between colonies increased in response to the presence of the icebergs, particularly emigration from Royds, the colony with the lowest productivity during those years (Dugger et al., 2010).

The variability inherent in demographic traits and life history characteristics are of particular interest given changing climate regimes, with gathering evidence indicating that some species lack the ability to adapt to the environmental variation they now face, with population declines and/or changes in distribution often the result (McLaughlin et al., 2002; Both et al., 2006; Lescroël et al., 2014). In fact, it has been suggested that Adélie penguins at the latitude of the Antarctic Peninsula region (northern edge of range) are less able to adjust their breeding chronology to warming temperatures, at least compared with Adélie penguins throughout their range (Ainley, 2002; Emmerson et al., 2011) and when compared to sympatric penguin species at the southern edge of their respective ranges (Hinke et al., 2012; Lynch et al., 2012b). However, in Tèrre Adélie, East Antarctica, Adélie penguins were found to change their laying date (later) but not arrival date in response to gradually changing ocean variables (Barbraud and Weimerskirch, 2006), and within the 18 latitude degrees in which Adélie penguins nest, spring arrival and laying vary by latitude (Ainley, 2002). For long-distance migratory birds in temperate climates, a disconnect between arrival on breeding grounds and the subsequent onset of reproduction, and peak food resources required to lay eggs and/or raise chicks has been reported (Visser et al., 1998, 2004; Both and Visser, 2001; Both et al., 2006). This disconnect has been linked directly (Both et al., 2006) and indirectly (Both et al., 2010) to population declines of these migratory species. At the northern limits of the Adélie penguin distribution (62–64S), sea ice disappearance has been linked to population declines (Ducklow et al., 2007; Schofield et al., 2010; Lynch et al., 2012a), with decreases in prey availability as a function of sea ice also a factor (cf. Trivelpiece et al., 2011; Sailley et al., 2013). Other climate-related changes have been linked to changes in breeding phenology in these same areas, but there is currently no evidence indicating that changes in food abundance are responsible for changes in timing of reproduction or breeding success at these northern colonies (Hinke et al., 2012). Decreasing krill availability as cetaceans recover from whaling off East Antarctica, could explain the apparent shifts in date of laying (getting later) by Adélie penguins there (cf. Barbraud and Weimerskirch, 2006; Ainley et al., 2007, 2010), but it is generally unclear what demographic mechanisms (i.e., changes in survival, movements, or reproductive success) are driving the changes.

In the southern Ross sea, the southernmost edge of the species' breeding range (77–78S), Adélie penguins are likely very limited in their ability to shift breeding phenology because the summer season is very short relative to the time required to lay eggs and raise chicks to fledging (∼85 days; Taylor, 1962; Ainley, 2002). In addition, the Ross Island metapopulation has by far the longest migration for this species, a function of the distance between the southernmost location of the breeding colonies and the northern location of the outer pack ice, where the species winters because there is adequate light and suitable SIC (Ballard et al., 2010b; Ainley and Ballard, 2011). This species' ability to fast during portions of the breeding season helps them extend the time available to breed in southern Antarctica (Ainley, 2002), but arrival on the breeding grounds and the onset of breeding is triggered by day length (Ainley, 2002) and extending chick rearing later into the season would disrupt fall migration phenology and molt (Ainley, 2002; Ballard et al., 2010b). Our results show that the physical presence of the icebergs, which led to loss of polynya access for western Ross Island colonies and loss of the marginal ice zone for Crozier, had negative short-term consequences on this species' productivity at a population level, despite the fact that some individuals were able to cope with this environmental variation (Lescroël et al., 2010, 2014). In addition, given the delayed maturation of this species (~3–7 years age at first reproduction; Ainley, 2002), long-term effects on demography and breeding population size are still being realized, several years after the iceberg "experiment" terminated; indeed the Royds colony continued to decrease (down to ~1800 pairs), five years after return to typical polynya presence patterns (Lyver et al., 2014). For Adélie penguins in the Ross Sea, changes in breeding phenology, movements away from colonies most severely affected by the icebergs (Dugger et al., 2010), retention of birds on a colony where nesting habitat increased (LaRue et al., 2013), and selection for breeders who can forage most efficiently in the face of environmental stress (Lescroël et al., 2010, 2014) may reflect responses that can ameliorate short-term and even extreme environmental variability for this species (but see below).

This species has coped with multiple glacial advances in the past, and these long-term environmental changes resulted in substantial changes to breeding distributions lasting thousands of years (Emslie et al., 2007; Millar et al., 2012). If environmental conditions represented by the presence of icebergs during this study are analogous to increased SIC associated with the last "cooling" period that occurred ~900 years ago, severe declines in reproductive success may be one mechanism that facilitated breeding distribution changes documented during those geologic time periods (Emslie et al., 2007). Despite the fact that sea ice is currently increasing in the Ross Sea region owing to increasing winds (Thompson and Solomon, 2002; Russell et al., 2006; Stammerjohn et al., 2008, 2012), future conditions (next 50 years) are predicted to be quite different than conditions previously encountered by the species, as sea ice will eventually disappear on a much accelerated temporal scale (Ainley et al., 2010; Smith et al., 2014). The environmental conditions observed during this study when the icebergs were present (higher SIC), may appear anomalous to what we might expect given that the Antarctic climate generally is warming (Ainley et al., 2010). However, while the Ross Ice Shelf (West Antarctic Ice Sheet, WAIS) is believed to have been relatively stable over the last 100 years (Bentley, 1998), with calving events of large icebergs occurring every 30–40 years on average (Arrigo et al., 2002), calving rates have been high at times (within a geologic/glaciological context), as the WAIS retreated since the Last Glacial Maximum 20k years ago years (Conway et al., 1999; Emslie et al., 2007). In addition, warming climates might be expected to facilitate a future increase in calving rates and decrease overall ice shelf stability (Arrigo et al., 2002), as has been the case for ice shelves in the extreme northern part of Antarctica in recent years (Pritchard et al., 2009; Mulvaney et al., 2012). Thus, major calving events like the one we report on here are not new to Adélie penguins, and the conditions they experienced during the iceberg years illustrate the short-term environmental extremes and resulting population-level effects on reproductive performance that they must cope with at the most southern portion of their range. On a longer time scale, these southern colonies are at the forefront of range expansion in the face of WAIS retreat (with the accompanying hazard of large icebergs), while also coping concomitantly with increased distances from wintering areas in pack ice to the north (Ballard et al., 2010b).

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fevo.2014.00068/abstract

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Predicting responses of the Adélie penguin population of Edmonson Point to future sea ice changes in the Ross Sea

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Atmosphere-Ocean General Circulation Models (AOGCMs) predict changes in the sea ice environment and in atmospheric precipitations over larger areas of Antarctica. These changes are expected to affect the population dynamics of seabirds and marine mammals, but the extent of this influence is not clear. We investigated the future population trajectories of the colony of Adélie penguins at Edmonson Point, in the Ross Sea, from 2010 to 2100. To do so, we incorporated the relationship between sea ice and demographic parameters of the studied colony into a matrix population model. Specifically, we used sea ice projections from AOGCMs and a proxy for snowfall precipitation. Simulations of population persistence under future climate change scenarios showed that a reduction in sea ice extent (SIE) and an increase in precipitation events during the breeding season will drive the population to extinction. However, the population growth rate estimated by the model was lower than the population growth rate observed during the last decades, suggesting that recruits from other colonies maintain the observed population dynamics at Edmonson Point. This local "rescue" effect is consistent with a metapopulation dynamic for Adélie penguins in the Ross Sea, in which neighboring colonies might exhibit contrasting population trends and different density-dependent effects. In the hypothesis that connectivity with larger source colonies or that local recruitment would decrease, the sink colony at Edmonson Point is predicted to disappear.

Keywords: climate change, environmental stochasticity, IPCC, matrix population models, metapopulation dynamics, population growth, seabirds

INTRODUCTION

In the Southern Ocean, the disappearance of the sea ice habitat associated with climate change threatens the viability of seabird and marine mammal populations (Fraser et al., 1992; Jenouvrier et al., 2005, 2009, 2012; Barbraud and Weimerskirch, 2006; Siniff et al., 2008; Forcada and Trathan, 2009; Ainley et al., 2010; Trivelpiece et al., 2011) because their life cycles and life-history strategies evolved in response to a sea ice habitat that was stable and predictable over large spatial and temporal scales (Forcada et al., 2008). The Adélie penguin (*Pygoscelis adeliae*) is one of the species that has been affected the most by changes in sea ice extent (SIE) and sea ice concentration (SIC) linked to increased air and sea temperature (Ainley, 2002; Ainley et al., 2010). This species uses sea ice as a resting platform in the winter period (Ainley, 2002). Sea ice is also the habitat for Adélie penguins' principal preys, such as the krill (*Euphausia* spp.) and the Antarctic silverfish (*Pleuragramma antarcticum*).

Satellite data on sea ice characteristics are available for Antarctic since late 1970s (Cavalieri et al., 2003). They show a decrease in SIE, SIC, and duration of the winter sea ice season in the western Antarctic Peninsula region (Kwok and Comiso, 2002; Zwally et al., 2002; Stammerjohn et al., 2008, 2012) and an increase in SIE and in the size of the Ross Sea polynya (an area of permanent open water within the sea ice) in the Ross Sea sector of the Southern Ocean (Parkinson, 2002; Zwally et al., 2002; see also Ainley et al., 2010).

These changes in the sea ice habitat affected the Adélie penguin populations (Ainley et al., 2010). Census of Adélie penguin breeding populations began around 1950s (Croxall et al., 2002) and showed a decrease in the size of Adélie penguin population along the Western Antarctic Peninsula and the Scotia Sea region, but an increase in the Ross Sea sector (Smith et al., 1999). The negative trend of penguin populations in the Western Antarctic Peninsula/Scotia Sea region has been thought to be a consequence of the loss of sea ice habitat caused by the rapid increase of air and sea temperature (Fraser et al., 1992; Smith et al., 1999; Ducklow et al., 2007; Hinke et al., 2007; Forcada and Trathan, 2009; Lynch et al., 2012). In addition to the negative effects of decreased SIE, penguin populations in the Western Antarctic Peninsula/Scotia Sea region have also been affected by the increased snowfall and water melt runoff (Trivelpiece and Fraser, 1996). The opposite positive trend in the Ross Sea is presumably the consequence of the increase in SIE and the size of the Ross Sea polynya that supposedly facilitated access to breeding colonies on land (Ainley et al., 2005, 2010). These contrasting trends in Adélie penguin population dynamics at different geographic locations in the Southern Ocean are explained by a habitat optimum model (Fraser and Trivelpiece, 1996; Smith et al., 1999) that relates population growth to the frequency of years with extensive winter sea ice. According to the model, either too much or too little winter SIE and SIC negatively affect penguin population growth (Fraser and Trivelpiece, 1996; Smith et al., 1999; Ainley et al., 2010). Winter SIE affects survival rates (Wilson et al., 2001; Jenouvrier et al., 2006; Ballerini et al., 2009; Emmerson and Southwell, 2011), and summer sea ice conditions close to breeding colonies influence breeding success (Olmastroni et al., 2004a; Emmerson and Southwell, 2008).

Global climate models developed by the Intergovernmental Panel on Climate Change (IPCC; Meehl et al., 2007) predict a decline of SIE and SIC all over Antarctica by the end of the century, even in the Ross Sea where SIE has so far increased (Ainley et al., 2010). Climate models also predict a robust increase in snowfall precipitations in Antarctica in the coming century with the possibility of intensification of extreme atmospheric events (Meehl et al., 2007; Turner et al., 2009). The majority of the studies on Adélie penguin population dynamics and sea ice are based on census of total population size (cfr. Fraser et al., 1992; Smith et al., 1999; Wilson et al., 2001; Ainley et al., 2005; Forcada et al., 2006; Hinke et al., 2007). However, studying the whole life cycle and the effects of a changing environment on vital rates is essential to understand the mechanisms that allow birds to respond to climate change (Ådahl et al., 2006; Jenouvrier, 2013; Oli, 2014).

Here, we used demographic data collected at the individual level during the breeding seasons 1994–2004 at the colony of Edmonson Point, Central Victoria Land coast, Ross Sea (**Figure 1**), to build a matrix population model (Caswell, 2001) for the Adélie penguin. First, we compared the growth rate projected from the demographic model to the growth rate measured from ground census. Then we used the model to project population growth using future projections of SIE obtained form IPCC-class climate models (Jenouvrier, 2013). To investigate cross-seasonal effects (Ward et al., 2005) we also built environmental scenarios that are based on the assumed causation between unusually harsh weather conditions at the breeding site (Olmastroni et al., 2004a) and increased mortality in the following winter despite "good" sea ice conditions (Ballerini et al., 2009).

MATERIALS AND METHODS

STUDY POPULATION AND DEMOGRAPHIC DATA

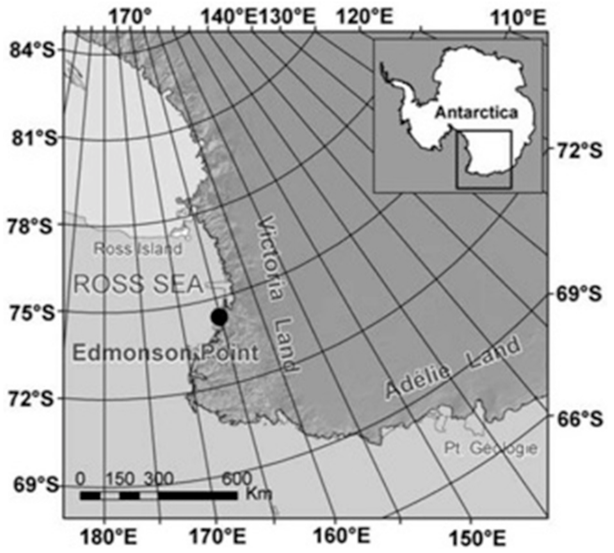

FIGURE 1 | The Adélie penguin colony of Edmonson Point is located on an ice-free area at 74° 20 S, 165° 08 E, along the Victoria Land coast, Ross Sea, Antarctica.

The colony of Edmonson Point (74°21′ S–165°10′ E) is situated in the Wood Bay, a large embayment covered by fast ice (persistent sea ice that keeps in place for several years), along the Victoria Land cost in the Ross Sea (**Figure 1**). Edmonson Point has been a nesting site for Adélie penguins since 3000 BP (Baroni and Orombelli, 1994). Today the colony is composed of several (10–13) breeding groups (hereafter "subcolonies") where population size was assessed by ground counts in 13 seasons during the period 1993–2009 (Olmastroni et al., 2000; Pezzo et al., 2007; this study). From 1994 to 2004 two of the subcolonies have been the focus of an intensive study of individual-based information on marked animals and nests (Supplementary Material, Table A1; Olmastroni et al., 2000). Each year, birds implanted with passive transponders (TIRIS tag) were reobserved in the study area through an Automatic Penguin Monitoring System and through manual observations (Olmastroni et al., 2000). Their capture histories were used to get estimates of age- and time-dependent survival probabilities for this population (Ballerini et al., 2009). Nests were monitored daily from the beginning to the end of the breeding season to calculate annual values of clutch size, hatching success and creching success (Pezzo et al., 2007) according to the CCAMLR Ecosystem Monitoring Program (cfr. SC-CCAMLR, 2004). Daily observations of breeding nests also allowed estimation of the percentage of eggs and chick mortality due to weather factors (Olmastroni et al., 2004a) and skua predation. The demographic parameters measured during the study period were used to create a time-invariant and a time-dependent dataset used in the demographic analyses.

LIFE CYCLE AND MATRIX POPULATION MODEL

We combined the available survival (Ballerini et al., 2009) and fecundity parameters (Pezzo et al., 2007) collected at the colony of Edmonson Point into a closed, pre-breeding, age-structured model for the Adélie penguin (**Figure 2**). The model considers females only and the projection interval is from November at year t to November at $t+1$. Following Ballerini et al. (2009), the model has five age classes. New individuals result from the combination of breeding propensity (*bp*), female fecundity (*f*) and survival during the first year of life (*s*0). Fecundity (*f*) is defined as the product of clutch size (*cs*), hatching success (*hs*) and fledging success (*fs*). Age-at-first reproduction varies in the Adélie penguin (Ainley, 2002), but precise estimates are not available for penguins at Edmonson Point, where all breeding birds were assumed to be 4+ (Ballerini et al., 2009). Transitions between age-classes are represented by a structured matrix population model, **A,** that includes fecundity and survival estimates for each age class considered (Caswell, 2001) as:

$$\mathbf{n}(t+1) = \mathbf{A}(t)\,\mathbf{n}(t) \tag{1}$$

where $\mathbf{n}(t)$ is a vector with the number of birds for each age at time t and the matrix $\mathbf{A}(t)$ projects the population from t to $t+1$. The population growth rate (λ) was calculated as the dominant eigenvalue of the matrix **A**, while the stable age distribution, **w,** is the dominant right eigenvectors of **A.** In the initial population vector $\mathbf{n}(1)$ the number of individuals in each age class was scaled according to the stable age distribution **w** obtained from **A** with average parameters over the study period.

FITNESS LANDSCAPE

The population growth rate (λ) estimated by the matrix model was lower than the population growth rate derived from ground census (see Results). Previous studies indicated that the values of breeding success (0.76 chicks/nest, Pezzo et al., 2007) and first-year survival (0.34, Ballerini et al., 2009) estimated for the colony of Edmonson Point are lower than in other penguin populations. But while the value of breeding success is robust because obtained from individually monitored nests and from ground census, first-year survival might be underestimated (Ballerini et al., 2009). First-year survival for the population of Edmonson Point was estimated based on resightings of marked birds in the intensive study area. While Adélie penguins have strong return rates to their natal colony (Sheperd et al., 2005), it is possible that birds marked as chicks in the intensive study area settled as breeders in other subcolonies of Edmonson Point. A search for tagged birds outside of the intensive study area helped identify only a few breeders (Olmastroni, personal observation). Capture-mark-recapture models used to estimate survival rates at the colony of Edmonson Point (Ballerini et al., 2009) confound permanent emigration with mortality. Thus, any bird breeding outside the intensive study area will be considered as dead and negatively bias the juvenile survival rate. To take into account this likely underestimation in survival rates in the first year (Ballerini et al., 2009), we used the time-invariant dataset to perform a fitness landscape analysis to identify the value of first-year survival that determines a population growth rate (λ) equal to 1. The analysis showed that, all other parameters being constant, first-year survival *s0c* should be 0.71 (**Figure 3**). This value, $s0c = 0.71$, was used to correct the formula for first-year survival (see Section Projections of Population Growth).

STOCHASTIC SEA ICE FORECASTS

SIE and SIC are highly correlated and they can affect penguins in several ways and at different spatial scales (see Ainley et al., 2010). For the population of Adélie penguins of Edmonson Point, breeding success is not correlated to large-scale sea ice variables (Ballerini, 2007), while survival is correlated to SIE anomalies (SIEA) during winter (June, July, August, and September) in the Ross Sea (Ballerini et al., 2009). SIEA are proportional anomalies in SIE, relative to the mean from 1979 to 2010 calculated over a large sector of the Ross Sea (from 150 to 230°E). This includes the ice edge area where Adélie penguins from Edmonson Point are thought to overwinter in the Ross Sea (Wilson et al., 2001; Ballerini et al., 2009; Ballard et al., 2010).

Observed SIE from 1979 to 2010 were obtained from passive microwave satellite imagery provided by the National Snow and Ice data Center, using the NASA team sea ice algorithm (Cavalieri et al., 1996, http://nsidc.org/data). Forecasts of SIE from climate models were extracted from 20 models available as part of the

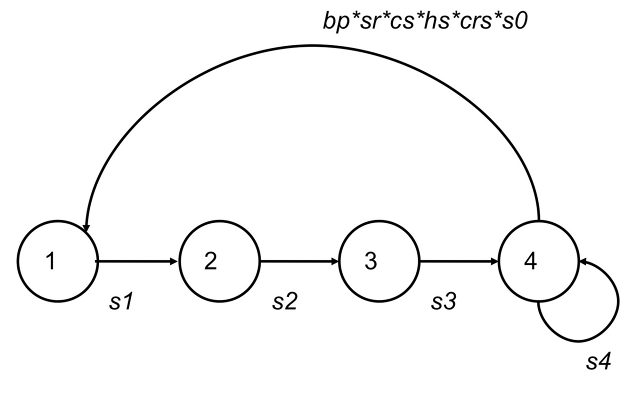

FIGURE 2 | Adélie penguin life cycle graph. s_i is the probability that an individual in stage *i* survives from time *t* to time $t+1$; *bp* is the probability, conditional on survival, that an individual in stage *i* breeds; *sr* is the assumed sex-ratio at birth; *cs* is clutch size; *hs* is the probability of an egg to hatch; *crs* is the probability of a chick to survive until the crèche stage. The graph corresponds to the matrix population model (Equation 1) (see Methods section).

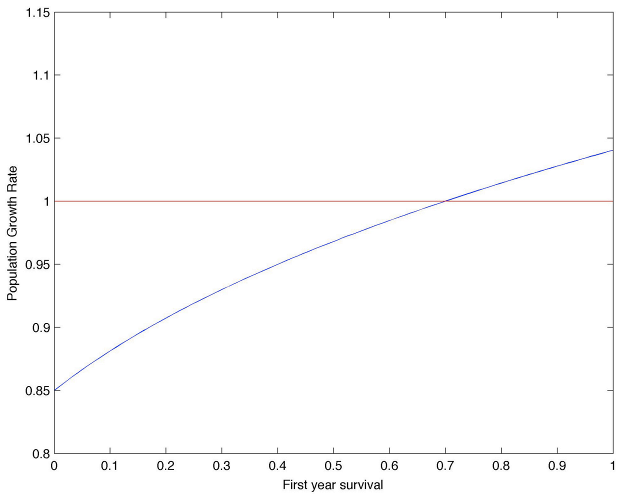

FIGURE 3 | Fitness landscape analysis. Population growth rate, λ, as a function of first-year survival, s0c.

WCRP CMIP3 multi-model dataset from 1900 to 2100 (see Meehl et al., 2007 and http://esg.llnl.gov/portal).

AOGCMs differ in their ability to reproduce sea ice conditions in Antarctica (Lefebvre and Goosse, 2008; Ainley et al., 2010). Thus, from an initial set of 20 climate models, we selected those for which the statistical properties of the distribution of SIEA output agree well with the observations from 1979 to 2010, in terms of both the median and the standard deviation of the SIEA distribution following the approach developed by Jenouvrier et al. (2012).

The comparison of the statistical properties of the distribution of SIEA was performed for the months of June, July, August, and September. For each month, we first compared the medians, selecting model m if

$$Q_1 \leq X_m \leq Q_3 \tag{2}$$

where X_m is the median of the SIEA output of model m and Q_1 and Q_3 are the first and third quartile of the distribution of observations. Second we compared the standard deviation of SIEA, selecting model m if

$$0.5^* s_{xo} \leq s_{xm} \leq 0.5^* s_{xo} \tag{3}$$

where s_{xm} and s_{xo} are the standard deviation of SIEA from the climate model m and from observations, respectively. Five models were selected for which Equations (2) and (3) applied for the 4 months. Then, we used the monthly data to create a single average value for winter SIEA and compared this value with average winter values from observations with Equations (2) and (3). The five models selected in the first phase were selected also in the second phase (Supplementary Material, Table A3).

The selected climate models were then forced with a middle range emissions scenario (SRES A1B, IPCC, 2000). This scenario assumes a future socio-economic development depending on fossil and non-fossil energy sources in balanced proportions. Under this scenario, the CO_2 level doubles by 2100, from 360 to 720 ppm.

To generate stochastic SIEA forecasts, we first obtained output for SIEA in the winter period. From this output, we computed smoothed means *x(t)* and smoothed covariance matrices *C(t)*, using a Gaussian kernel smoother with smoothing parameter $h = 2$. We then generated stochastic SIEA vectors by drawing *x(t)* as an iid sample from a normal distribution with mean *x(t)* and covariance matrix *C(t)*.

PROJECTIONS OF POPULATION GROWTH

We used stochastic sea ice forecasts from the IPCC models that were selected to force the survival rates in the Adélie penguin population model. Survival probabilities were expressed as a function of SIEA in the Ross Sea using the functional relationship determined for this population by Ballerini et al. (2009):

$$\begin{aligned} Phi\_age = \text{invlogit}\,(&alpha\_age + beta\_age^* \text{ SIEA} \\ &+ beta\_age^* \text{ SIEA}^2) \end{aligned} \tag{4}$$

Where *Phi_age* is the survival rate for the five age classes in the population model in **Figure 2**, while *alpha_age* and *beta_age* are the age-specific coefficients of the relationship between survival and sea ice determined with mark-recapture models (Ballerini et al., 2009). We took into account the systematic bias in first-year survival by setting:

$$\begin{aligned} Phi\_age0 = \text{invlogit}\,(&alpha\_age0 + beta\_age0^* \text{ SIEA} \\ &+ beta\_age\, 0^* \text{ SIEA}^2) + s0c - 0.34 \end{aligned} \tag{5}$$

where $s0c = 0.71$ is the value of first-year survival derived from the fitness landscape analysis and 0.34 is the value of first-year survival, $s0$, from the time-invariant dataset.

We projected the population under three scenarios. The first scenario considers stochastic SIE forecasts from five IPCC models to generate a sequence of demographic rates from 2010 to 2100 in the projection matrix. The initial population vector was built with the average equilibrium population structure from the time-invariant population model. To evaluate uncertainties in climate, we used 200 stochastic forecasts from each of the five AOGCMs. The other two scenarios include SIE forecasts but also account for an increased frequency of extreme atmospheric events during the breeding season. In 2002/03, unusual strong winds and snowfall resulted in longer foraging trips during the guard stages and lead to reduced survival rates for breeders. This catastrophic breeding season was proposed to be responsible for an additional 7% in the adult mortality during the winter 2003 (Ballerini et al., 2009). Therefore, we included these extreme events by randomly sampling a matrix where adult survival, $s4$, expressed as a function of stochastic sea ice forecasts is then depressed by 7%. We considered a frequency of one catastrophic event every 14 years (as observed during the study period) for Scenario 2 and a frequency of one every other year (hypothetical scenario of an increasing frequency) for Scenario 3.

RESULTS

PENGUIN POPULATION GROWTH AT EDMONSON POINT: EVALUATION OF THE DEMOGRAPHIC MODEL

In the period 1993–2009, the Adélie penguin colony at Edmonson Point increased in size passing from 1473 to 2712 breeding pairs (Supplementary Material, Table A2). During the period 1994–2004 the relative size of the subcolonies that compose the colony of Edmonson Point varied strongly, some breeding groups disappeared while others increased in size. In the two subcolonies intensively studied, the number of breeding pairs decreased, ranging from 390 occupied nests in 1994 to 249 occupied nest in 2004 (**Figure 4A**). This corresponds to 3.1% annual decline in observed population size in the local study area. The long-term population growth rate (λ) calculated from the time-invariant population model indicates a 6.3% annual decline of the study population, thus predicting an annual reduction in population size that is twice as much as the observed growth rate (from ground census). The λ from the time-dependent matrix model underestimates annual population growth every year with the exception of the year from the breeding season 2000 to breeding season 2001 (**Figure 4B**).

STOCHASTIC SEA ICE FORECASTS AND POPULATION PROJECTIONS

Most AOGCMs projected declines in the total Antarctic SIE in the Ross Sea for the period 1979–2010 (Supplementary Material,

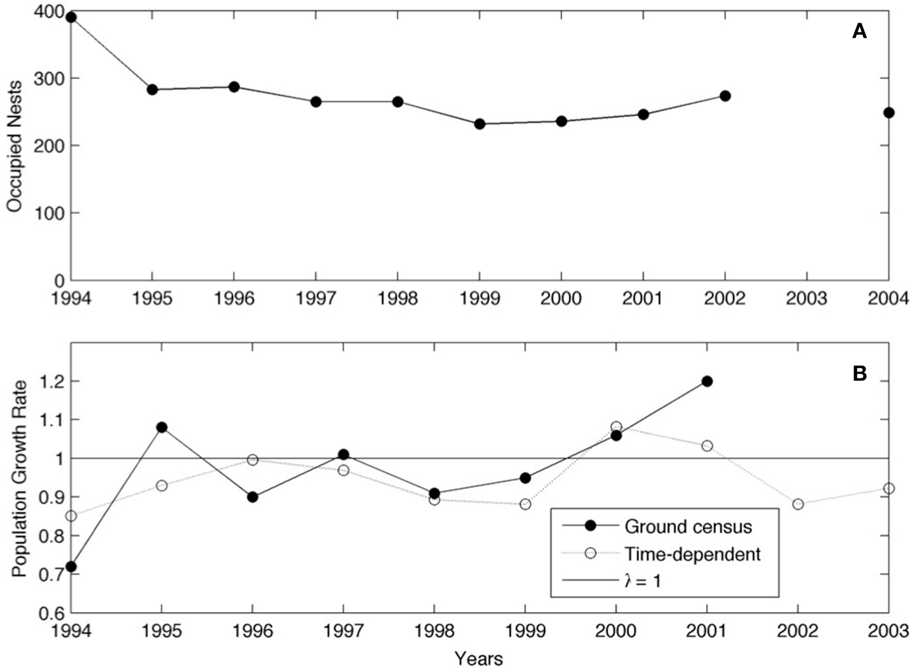

FIGURE 4 | Annual counts of population size (A) and yearly values of the population growth rate, λ, (B) in two subcolonies at Edmonson Point. Values of λ calculated from ground census of the breeding population (solid circles) and by the matrix population model (open circles) are indicated. Note that "breeding season 1994" indicates the breeding season 1994/95, while "winter 1995" indicates the period between the breeding season 1994 and the breeding season 1995.

Figure A1), contrary to the observed trend (Stammerjohn et al., 2012). However, simulated and observed trends are generally consistent with natural variability and trend discrepancies may not necessarily indicate a model bias, especially within a short time window (Mahlstein et al., 2013; Hobbs et al., 2014). Among the 20 AOGCMs, five were retained for which the median and the standard deviation of the simulated SIEA distribution agreed with observations (**Figure 5**; Supplementary Material, Table A3, Figures A1, A2). The retained models are cccma-cgcm3-1-t63, giss-aom, inmcm3-0, miroc3-2-hires and gfdl_cm2_0. The last two models were also retained by Ainley et al. (2010), who predicted changes in penguin sea ice habitat around all Antarctica using several key climate variables (wind stress, Antarctic Circumpolar strength and boundary, seasonal cycle of sea ice around Antarctica and annual mean ice thickness). Differently from the first three models, these two models, miroc3-2-hires and gfdl_cm2_0, predict a transient increase in SIE in the Ross Sea, possibly linked to the ozone hole, before SIE decreases (Ainley et al., 2010).

The five AOGCMs that were retained were used to get stochastic SIE forecasts in the Ross Sea, which in turn were used to drive survival probability in the population projections (population projections for all the AOGCMs, including the ones that were not selected, are available in the Supplementary Material, Figure A2). All population projections from the retained AOGCMs predicted a dramatic decline of the breeding population down to extinction (**Figures 6, 7; Table 1**). However, there are differences in the speed of decline among the five AOGCMs. Model ccma-cgcm3-1-t63 predicts the fastest decline, with fewer than 300 breeding pairs in 30 years whereas model inmcm3-0 predicts a probability of extinction of only 0.12 after 30 years (**Table 1**). Model giss-aom predicts an extinction probability equal to 1 after 39 years. The two models selected also by Ainley et al. (2010), model miroc3-2-hires and model gfdl_cm2_0, project a probability of extinction equal to 1 after 37 and 41 years, respectively.

When the proxy for extreme atmospheric events is included in the simulations, extinction will occur sooner (**Figures 7B,C; Table 1**). A catastrophic event every other year would dramatically increase the probability of extinction, which is equal to 1 in 2024 with models cccms-cgm3-1-t63 and giss-aom. Model inmcm3-0 predicts the slowest decline of the population under a scenario of one catastrophic event every 14 years but it still predicts a probability of extinction of 1 after 29 years.

DISCUSSION

By linking a population model to climate change projections, we projected that the Adélie penguin population at Edmonson Point will be functionally extinct within 40 years. Based on a qualitative analysis of penguin response to climate change projected by a set of AOGCMs, Ainley et al. (2010) predicted that 75% of Adélie penguin colonies (70% of breeding population) north of 70°S are projected to decrease or disappear when global temperature will have increased by 2°C above pre-industrial levels (2025–2052). Edmonson Point is located far south (74°21′S) and although our results are worrisome for the persistence of Adélie penguins, we have to acknowledge that the population seems to be part of a

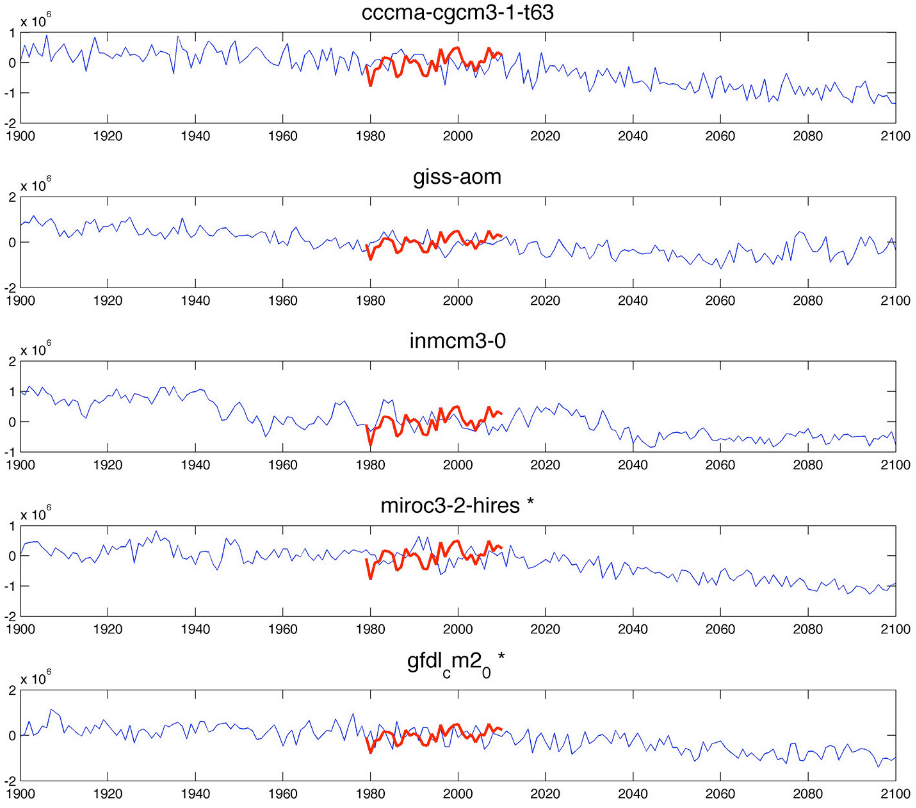

FIGURE 5 | Comparison of Ross Sea sea ice extent values derived from satellite observations (red line) and Ross Sea sea ice values derived from the AOGCMs that were retained (blue line). Models miroc3-2-hires and gfdl_cm2_0 were two of the four best models for the Ross Sea in Ainley et al. (2010).

metapopulation in which local breeding areas are connected by dispersal of breeding individuals (Ainley et al., 1995; Sheperd et al., 2005). Whether or not the metapopulation will persist is, as-yet, unknown.

METAPOPULATION DYNAMICS

Adélie penguin breeding populations all over Antarctica are organized in cluster of colonies, each cluster constituting a metapopulation with large *source* colonies contributing immigrants to smaller *sink* colonies (Ainley et al., 1995; Ainley, 2002). Dispersal rates are low among adults (1% during average years to 3.5% under extreme environmental in southern Ross Sea, Dugger et al., 2010) while dispersal among new breeders depends on stochastic events (Sheperd et al., 2005; La Rue et al., 2013). The Terranova Bay metapopulation is composed of two large colonies, Adélie Cove and Inexpressible Island (with 11 234 and 24 450 breeding pairs, respectively, Lyver et al., 2014) and of the smaller colony of Edmonson Point (Ainley et al., 2005). Data on migratory rates between these colonies do not exist. However, the demographic data from Edmonson Point suggest that this colony is not a closed system (Ainley et al., 2005) and that immigration might be crucial in determining its population dynamics. Adélie penguins show a high fidelity to the breeding site and we speculate that the Edmonson Point population is composed of a pool of established breeders that come back to breed at the colony year after year, and of a pool of new breeders that immigrate from nearby colonies each year. New breeders would come from the larger colonies of the Terranova Bay metapopulation where space for breeding is limited and/or where summer competition for food can be high (Ainley et al., 2004). It is possible that the colony of Edmonson Point is sustained also by birds from colonies further south in the Ross Sea. In the breeding season 2014, in fact, five birds marked with flipper bands at Cape Royds and Cape Bird, Ross Island, were observed breeding at Edmonson Point (Olmastroni, personal observation). Immigration of new breeders from nearby colonies could explain why the colony of Edmonson Point increased in size during the study period (Lyver et al., 2014; this work) even if breeding success and first-year survival were low in comparison to other locations in the Ross Sea (Pezzo et al., 2007) and not enough to sustain population growth.

Sink populations are usually situated in low quality habitats (Pulliam, 1988). Extensive fast ice (about 20 km) rests in place in front of Edmonson Point almost every year (Olmastroni et al., personal observation), thus making it energetically more costly for penguins to search for food, as they are obliged to walk instead of swimming to reach their foraging grounds (Clarke et al., 1998; Olmastroni, 2002). Longer foraging trips might cause lower delivery rates of food to chicks, thus negatively impacting the breeding success (Clarke et al., 2002; Olmastroni et al., 2004b). Delivery rates to chicks might also be limited by food competition with Adélies from the other colonies of the Terranova Bay metapopulation and with emperor penguins from the nearby colony of

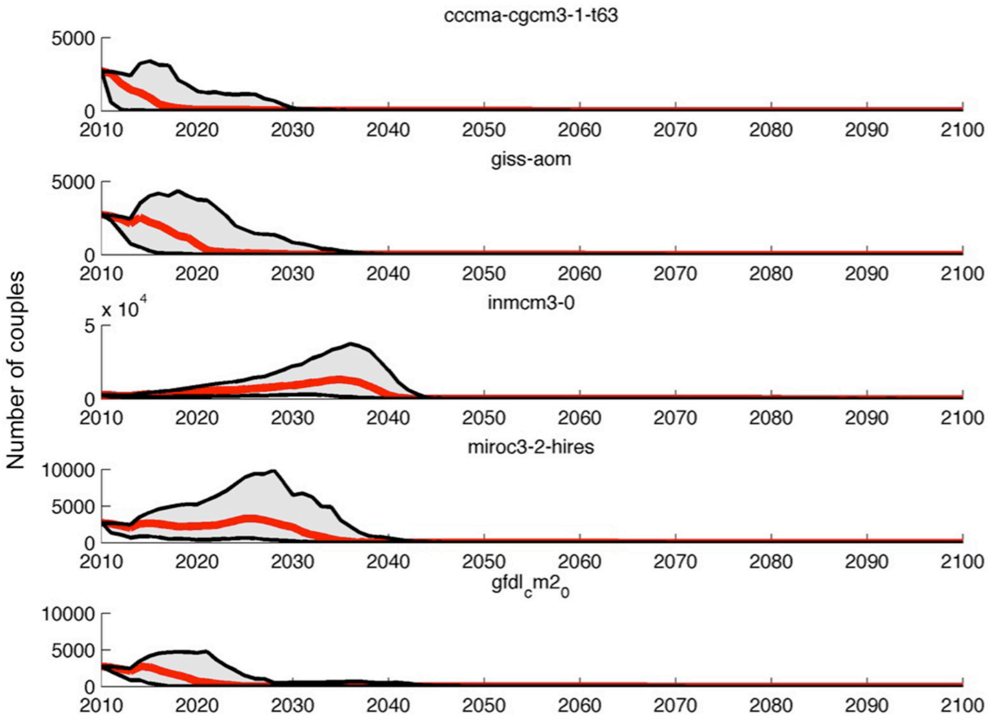

FIGURE 6 | Projections of the Adélie penguin population at Edmonson Point based on stochastic sea ice extent anomalies forecasts from five AOGCMs. For each AOGCM, the median population trajectory (thick red line) and the 95% envelope (gray area), from 200 stochastic simulations are shown.

Cape Washington (almost 12 000 breeding pairs, Barber-Meyer et al., 2007; but see Ainley et al., 1995). Finally, breeding success is strongly limited at Edmonson Point by predation of eggs and chicks by the South polar skua (*Catharacta maccormicki*). With a ratio skua pairs/penguins pairs of 1:20, the highest recorded along the Victoria Land coast (Pezzo et al., 2001), about 52% of eggs and chicks are predated each year (Olmastroni and Pezzo, unpublished data, average over 5 years).

The population growth rate calculated from the matrix population model is negative almost every year, indicating that the colony is not self-sustaining. While adult survival measured at Edmonson Point (Ballerini et al., 2009) is in the range of variability of other Adélie penguin populations that are not declining (cfr. Jenouvrier et al., 2006; Lescroël et al., 2009; Emmerson and Southwell, 2011), apparent juvenile survival (Ballerini et al., 2009; Emmerson and Southwell, 2011) and breeding success are lower than in other populations (Ainley, 2002 and studies herein; Pezzo et al., 2007). For these reasons, we speculate that the colony of Edmonson Point is a sink population sustained by neighboring colonies, and that the estimates of juvenile survival might be biased. Indeed, dispersal may be limited among adults but may be higher among juveniles (La Rue et al., 2013). Therefore, to project population response, we corrected for this systematic bias by tuning our population model so that the growth rate projected during the observation period matches a stable population (see fitness landscape analysis). Model tuning is a common strategy in climate modeling, so that the properties of climate models are adjusted in various ways to best match the known state of the Earth's climate system. Typically, the tuning is performed over uncertain and non-observable parameters related to processes not explicitly represented in the models (Mauritsen et al., 2012).

POPULATION PROJECTIONS

The population of Edmonson Point is projected to decline at a rapid rate, especially if extreme snow events are accounted for. The population is projected to be functionally extinct as soon as 13 years and as late as 40 years, depending on the climate models used to project SIE and on the frequency of simulated extreme weather events at breeding.

Differences among models in the SIE simulation outputs are due to uncertainties in the representation of climate processes within the models (Lefebvre and Goosse, 2008; Turner et al., 2013). In order to account for this structural uncertainty, we selected a model subset by comparing climatological aspects of the simulated SIEA to the observed climatology in term of median and standard deviation of the SIEA distributions during the study period (Jenouvrier et al., 2012; Jenouvrier, 2013; Jenouvrier et al., 2014). Because the climate variable included in our population model is SIEA and our aim is to project population trajectories given future SIEA projections, we believe this is a robust approach.

When using SIE forecasts from the five AOGCMs, all simulations of population dynamics predict extinction of the population of Edmonson Point in the next 40 years. However, different climate models imply different future sea-ice projections. For example, model miroc3-2-hires and model gfdl_cm2_0 predict a

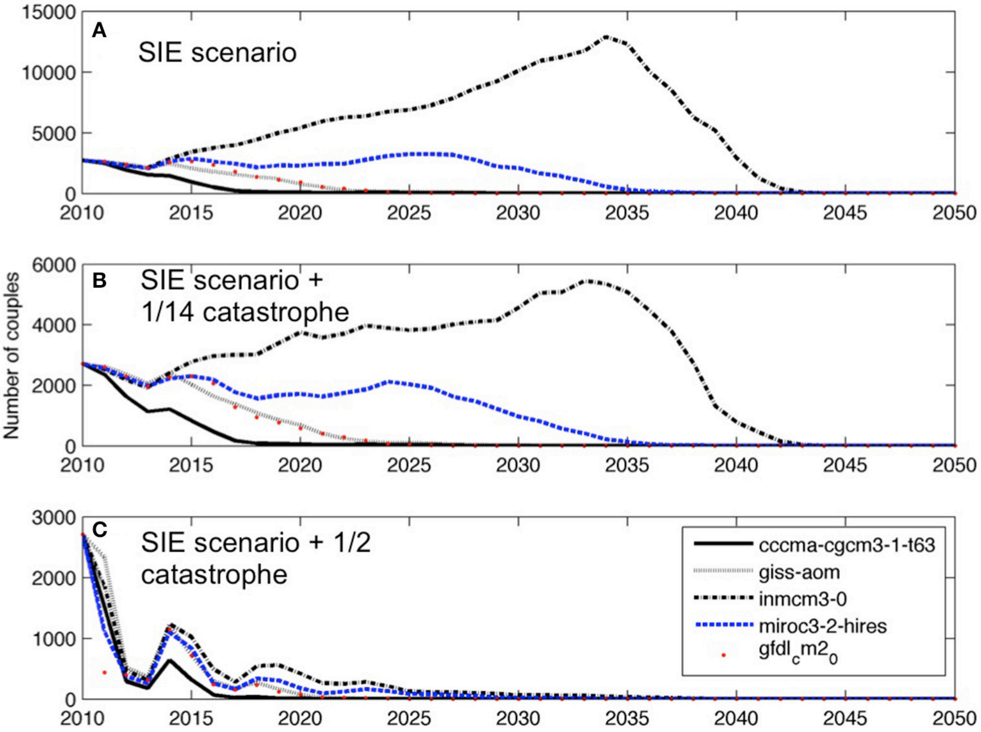

FIGURE 7 | Projections of the Adélie penguin population at Edmonson Point based on stochastic sea ice extent anomalies forecasts from five AOGCMs (A), considering a catastrophic weather event at breeding with a frequency of 1 over 14 years (B), and considering a catastrophic weather event every other year (C). For each AOGCM, the median population trajectory from 200 stochastic simulations is shown.

temporary increase in SIE in the Ross Sea in the next decades, although a general decrease in the long run. A temporary increase in winter sea ice implies a displacement further north of the ice edge, which is thought to negatively impact juvenile survival over the winter period by reducing the access to food resources (Wilson et al., 2001). For a similar reason, extreme winter SIE is also associated with reduced adult survival (Ballerini et al., 2009). All AOGCMs agree in predicting a decline of SIE by the mid of this century (Ainley et al., 2010). Reduced SIE means a displacement toward the south of the ice edge, possibly at latitudes where there is no light in the winter. This can impact over-winter survival by increasing competition for the narrow suitable winter habitat with enough light for penguins to successfully forage (Ballard et al., 2010).

Adélie penguins from Edmonson Point most likely share the same wintering grounds as birds from the other colonies along Victoria Land (Wilson et al., 2001; Ballard et al., 2010). Since survival in the Adélie penguin is affected by winter SIE and SIC (Wilson et al., 2001; Jenouvrier et al., 2006; Ballerini et al., 2009), it is likely that changes in SIE will affect survival rates of penguins from Adélie Cove and Inexpressible Island too. If this hypothesis is true, survival rates of penguins from other colonies will likely decline because sea ice is projected to shrink everywhere in Antarctica (Ainley et al., 2010). This can affect the immigration fluxes toward Edmonson Point and the persistence of the metapopulation in the Ross Sea. Future work entails projecting Adélie penguin population responses throughout the entire species range, by including dispersal scenarios and different functional relationships between climate and demography along a latitudinal gradient (Jenouvrier et al., 2014).

The responses of seabird populations to large-scale environmental changes will depend on the sensitivity of their demographic parameters to the physical processes and on how the changes in demographic parameters are expressed at the population level (Ådahl et al., 2006). Since survival has a strong impact on population growth, the expected reduction in SIE and increase in snowfall are likely to negatively impact the population dynamics of Edmonson Point. According to the matrix population model, these changes in the physical environment will determine an increase in the speed of decline of the population of Edmonson Point. The ability of Adélie penguins to respond to global environmental changes will depend on their ability to modulate the breeding strategy in the summer and on the availability of suitable habitat in the winter (cfr. Ainley et al., 2010).

The plastic responses of Adélie penguins to the their changing environment are being increasingly studied (Lynch et al., 2012; La Rue et al., 2013; Dugger et al., 2014; Lescroël et al., 2014). While it has been found that Adélie penguins can adapt their foraging efficiency to abrupt changes in SIC during the summer period (Lescroël et al., 2014), it is less clear how much they can modify their breeding phenology and breeding strategy (Barbraud and Weimerskirch, 2006; Dugger et al., 2010, 2014; Lynch et al., 2012). Adélie penguins are long-range migrant species that evolved their breeding strategy in response to an environment that varied over

Table 1 | Probability of extinction of the Adélie penguin population of Edmonson Point at time $t = 10, 20, 30$, and 40 years after 2010, for five AOGCMs and three environmental scenarios.

	AOGCMs				
	cccma-cgcm3-1-t63	**giss-aom**	**inmcm3-0**	**miroc3-2-hires**	**gfdl_cm2_0**
PROB EXTINCTION $t = 10$					
Scenario 1	0.81	0.26	0.01	0.03	0.27
Scenario 2	0.82	0.29	0.11	0.18	0.38
Scenario 3	0.99	0.91	0.81	0.89	0.95
PROB EXTINCTION TIME $t = 20$					
Scenario 1	0.93	0.86	0.01	0.06	0.94
Scenario 2	0.97	0.93	0.13	0.28	0.98
Scenario 3	1	1	0.97	0.99	1
PROBAB EXTINCTION TIME $t = 30$					
Scenario 1	1	0.98	0.12	0.9	0.96
Scenario 2	1	1	0.32	0.96	0.98
Scenario 3	1	1	1	1	1
PROBAB EXTINCTION TIME $t = 40$					
Scenario 1	1	1	1	1	0.99
Scenario 2	1	1	1	1	1
Scenario 3	1	1	1	1	1

Scenario, stochastic sea ice; scenario 2 = stochastic sea ice + proxy snowfall every 14 years; scenario 3 = stochastic sea ice + proxy snowfall every other year (see the Methods Section for more details).

much longer geological time scales than the current temporal scale of climate change (Fraser and Trivelpiece, 1996; Emslie et al., 2007; Forcada et al., 2008; Thatje et al., 2008; Li et al., 2014). AOGCMs predict an increased probability of extreme atmospheric events (Ainley et al., 2010), such as the heavy snowstorm that caused extensive mortality of eggs and chicks in 2003 (Olmastroni et al., 2004a). The possibility of microevolutionary adaptive responses (Sheperd et al., 2005) is probably limited in species with a long generation time (Rosenheim and Tabashnik, 1991) such as the Adélie penguin. In these species, the maximization of fitness is likely to rely on phenotypic plasticity or short-term individual responses to the environment (Forcada et al., 2008). If the frequency of "catastrophic" climatic events at Adélie penguin breeding sites increases and happens in a time interval equal to the generation time, there will not be a generation with a high fitness and the population will go extinct (Forcada et al., 2008; Melbourne and Hastings, 2008). So the responses of Adélie penguins to changing environment will depend, in part, on their ability to change their breeding phenology and breeding strategy.

Possible future changes in the Ross Sea food web (Smith et al., 2007, 2014), could potentially exacerbate the direct effects of changes in habitat availability on the viability of Adélie penguins populations. The principal prey species for Adélie penguins, krill and Antarctic silverfish, depend on the sea ice for successful completion of their life cycles. Disappearance of prey species in response to reduced sea ice habitat is thought to be one of the causes of reduction of penguin populations in the western Antarctic Peninsula region (Schofield et al., 2010; Trivelpiece et al., 2011; Sailley et al., 2013). Understanding the effects of climate change is further complicated by alterations to the Antarctic food web due to harvesting activities (Trivelpiece et al., 2011; Lyver et al., 2014). Lyver et al. (2014) suggest that the rapid increase in population size in the southern colonies of the Ross Sea since 2001 was, at least in part, due to competitive release of Antarctic silverfish following the commercial removal of the Antarctic toothfish (*Dissostichus mawsoni*).

As a conclusion, we detected and quantified the actual and future decrease of a small Adélie penguin colony that is probably part of a larger metapopulation. We concluded that this colony is a sink population, not limited by breeding sites availability but by inter-specific processes such as high predation. This population is sustained by immigration from larger colonies of the metapopulation. A decreasing trend of such sink population might be seen as a "spy light" indicating a possible future decrease of the whole metapopulation, including the source colonies. Causes of this potential general decline have to be investigated both among global drivers affecting adult survival, such as sea ice conditions over large areas, and among local drivers, such as stochastic weather events, greatly affecting breeding success.

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authors revised the final manuscript and agreed to be accountable for it.

SUPPLEMENTARY MATERIAL

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A changing distribution of seabirds in South Africa—the possible impact of climate and its consequences

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In the southern Benguela ecosystem off South Africa, there were recent shifts to the south and east in the distributions of three forage resources (anchovy, sardine, rock lobster), which probably were influenced by environmental change although fishing too may have played a part. In this study, we review information on trends in distributions and numbers of eight seabirds breeding in South Africa. For five species that feed predominantly on anchovy, sardine or rock lobster, their populations off northwest South Africa decreased markedly. For three of these species, which exhibit behavioral inertia and have restricted foraging ranges when breeding (African penguin, Cape cormorant, bank cormorant), there were large decreases in their overall populations in South Africa. Conversely, for two showing more plasticity and able to range over wide areas or move between breeding localities (Cape gannet, swift tern) there were increases. It is thought that movement of forage resources away from the northern islands led to a mismatch in the distributions of breeding localities and prey of dependent seabirds off western South Africa and to attempts by several species to establish colonies on the southern mainland closer to food resources. There also were shifts to the south and east in the distributions of three seabirds that do not compete with fisheries for prey (crowned cormorant, white-breasted cormorant, kelp gull), suggesting some environmental forcing, but decreases of these species off northwest South Africa were less severe and populations in South Africa remained stable or increased in the long term. It is likely, because many fishing plants are located in the northwest, that there was increased competition between seabirds and fisheries for prey as forage resources moved south and east. Potential interventions to mitigate the adverse impacts of distributional changes for seabirds include allocations of allowable catches of shared forage resources at regional levels, closures to fishing around impacted seabird colonies and establishment of new colonies nearer to the present location of food.

Keywords: behavioral inertia, Benguela ecosystem, competition with fisheries, distributional change, environmental forcing, forage resources, mainland breeding, seabirds

INTRODUCTION

Marine ecosystems are being affected by climate change worldwide. Often such change is pronounced at high latitudes, where its impact on associated fauna is readily apparent. For example, reductions in stable old ice, increases in unconsolidated ice and lengthening of the melt season in the Arctic Ocean have reduced the availability and quality of denning habitat in pack ice for polar bears (*Ursus maritimus*) and caused an increase of bears denning in coastal habitat, thereby altering their distribution (Fischbach et al., 2007). In the West Antarctic Peninsula, there have been poleward shifts in ice extent and local declines of ice-dependent Adélie penguins (*Pygoscelis adeliae*) (Trivelpiece et al., 2011; Lynch et al., 2012), which contrast with increases and a southward range extension of Gentoo penguins (*P. papua*) that do not depend on ice (Lynch, 2013). At lower latitudes changes in distributions of marine fauna also may be pronounced (Cheung et al., 2009), but sometimes the reasons for these and altered population trends are not as clearly understood. Thus, eight potential causes were postulated for circumpolar decreases of sub-Antarctic rockhopper penguins (*Eudyptes chrysocome* and *E. moseleyi*) (BirdLife International, 2010).

Off South Africa, in the southern Benguela ecosystem there have been recent changes in the distributions and population sizes of several animals, including seabirds (e.g., Whittington, 2004; Crawford et al., 2007, 2014b; Kirkman et al., 2012; Crawford, 2013) and three forage species that are important prey for seabirds: anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*) and rock lobster (*Jasus lalandii*) (van der Lingen et al., 2006; Blamey et al., 2015). From 1984 to 1995 most (61 ± 21% by mass standard deviation) spawning anchovy were located west of Cape Agulhas (**Figure 1**), whereas from 1996 to 2005 this proportion halved to 31 ± 11% (information in Roy et al., 2007). From 1994 to 1998 most (74 ± 17% by mass) spawning sardine were west of Cape Agulhas, but this decreased by two-thirds to 26 ± 12% from 1999 to 2007 (information in Coetzee et al., 2008). Catches of sardine similarly showed a marked shift to the south and east; their center of gravity was near Dassen Island in 1997 but off Mossel Bay, east of Cape Agulhas, in 2005 (Fairweather et al., 2006; **Figure 1**). During the 1990s there also was a notable change in the proportions of South African catches of rock lobster taken to the north and south of Dassen Island (**Figure 1**). Before the 1990s most of the catch was taken to the north, subsequently most was taken to the south with this proportion attaining 70% by 2010 (Blamey et al., 2012). The changed distribution of catches of rock lobster reflects an altered distribution of the species and an eastward expansion of its range to the Stony Point region (**Figure 1A**) and beyond (Tarr et al., 1992; Cockcroft and MacKenzie, 1997; Cockcroft et al., 2008).

There is accumulating evidence that an altered environment, possibly driven by climate change, is driving these changes (e.g., Gammelsrød et al., 1998; Roy et al., 2007; Cockcroft et al., 2008). However, ultimate causes of environmental change remain difficult to attribute, and it is unknown to what extent it may be reversible (Hutchings et al., 2009; Moloney et al., 2013). Furthermore, it is frequently difficult to disentangle the influence of the environment from anthropogenic impacts, such as fishing (e.g., Coetzee et al., 2008). However, in the Benguela ecosystem several studies have demonstrated relationships between the abundance of prey and numbers of breeding seabirds or their demographic parameters, such as breeding success and survival (e.g., Crawford et al., 2006, 2007, 2011; Crawford, 2007; Sabarros et al., 2012; Sherley et al., 2013, 2014). Therefore, it may be expected that factors influencing the distribution of prey species, and hence its regional availability, will impact on seabirds.

In the South African situation, African penguin (*Spheniscus demersus*), Cape gannet (*Morus capensis*), Cape cormorant

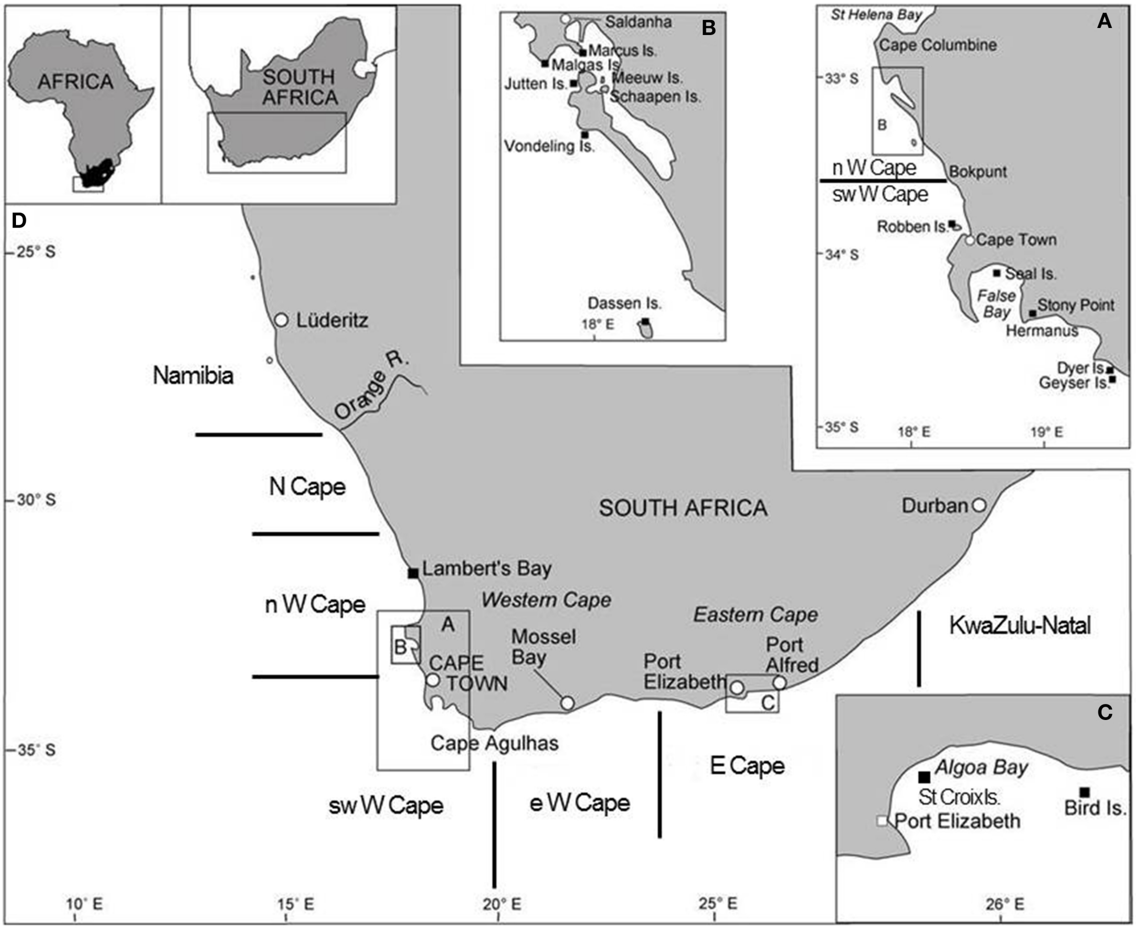

FIGURE 1 | Map of South Africa showing several of the important seabird breeding localities (amended from Crawford et al., 2014b). Boundaries of the five South African regions considered in this study are indicated.

(*Phalacrocorax capensis*), bank cormorant (*P. neglectus*) and swift tern (*Thalasseus bergii*) compete with fisheries for food, whereas other seabirds, including white-breasted cormorant (*P. lucidus*), crowned cormorant (*Microcarbo coronatus*) and kelp gull (*Larus dominicanus*), show little or no such competition (Hockey et al., 2005). A comparison of these two groups of seabirds may provide insight into the relative importance of factors driving change in their distributions and populations (Crawford et al., 2008d). Therefore, in this paper we review published and unpublished information on recent change in the distributions and population sizes of these eight seabirds, similarities and differences in their responses to recent environmental change, possible causes of different responses and potential means to mitigate adverse impacts of change.

METHODS

Good information is available for two or three periods between the mid-1970s and the mid-2010s (late 1970s/early 1980s, late 1990s/early 2000s, late 2000s/early 2010s) on the numbers of the above-mentioned eight species of seabird breeding in South Africa and their distributions (see **Table 1** for sources of data). The information for white-breasted cormorant, which is sometimes considered a race of the great cormorant *P. carbo* (BirdLife International, 2014), refers only to that portion of the South African population that breeds on the coast and excludes the KwaZulu-Natal coast in the east of the country. Except for white-breasted cormorant, each of the eight seabirds is endemic to the Benguela upwelling system off southwest Africa, although for swift tern and kelp gull only at a sub-specific level (Crawford, 2013). For all species, the counts or estimates of numbers breeding in each period were made using similar methods to those employed in the first period.

For African penguins, numbers of nests in use were counted. A nest was considered to be in use if it contained fresh eggs or chicks, if it was defended by a non-molting adult bird or, because breeding by African penguins is not always synchronous, if it showed recent signs of use, e.g., through the presence of substantial quantities of fresh guano or nesting material (Crawford et al., 2011). Numbers of chicks in crèches were divided by two, the usual clutch size, to estimate the number of nest sites they represented, with remainders taken to represent an additional site, e.g., crèches of five and six chicks would both be taken to represent three nests (Shelton et al., 1984). As is the case for cormorants (see below), because not all eggs hatch and broods may be reduced (e.g., Sherley et al., 2012a), this is likely to underestimate the actual number of nests represented by chicks in crèches and hence lead to a conservative estimate of the overall number of birds breeding. Furthermore, brood reduction may vary depending on conditions during breeding. However, the contribution of nests assumed from counts of chicks in crèches to the overall estimate of numbers breeding was small (<10%, usually <5%).

Table 1 | Overall numbers of eight seabirds breeding coastally in South Africa's Northern, Western and Eastern Cape provinces during the late 1970s/early 1980s, late 1990s/early 2000s and late 2000s/early 2010s (sources of information are indicated).

Species	Period of count	Number breeding (1000 pairs)	Source
African penguin	1978–1979	55.2	Shelton et al., 1984
	2000	48.6	Underhill et al., 2006; Crawford et al., 2009b
	2013	17.3	Crawford et al., 2011, 2014b
Cape gannet	1978	78.8	Crawford et al., 1983
	2001	145.5	Crawford et al., 2007
	2013	101.6	Crawford et al., 2014b
Cape cormorant	1977–1981	106.5	Cooper et al., 1982
	2009–2013	65.8	Supplementary Material
Bank cormorant	1978–1980	1.5	Cooper, 1981; Crawford et al., 1999
	1995–1997	1.2	Crawford et al., 1999
	2011–2013	0.8	Supplementary Material
White-breasted cormorant	1977–1981	1.1	Brooke et al., 1982
	2008–2012	1.3	Crawford et al., 2013b
Crowned cormorant	1977–1981	1.7	Crawford et al., 1982b
	2008–2012	1.9	Crawford et al., 2012
Swift tern	1984	4.7	Cooper et al., 1990
	2000	6.3	Crawford, 2009
	2013	10.1	Crawford et al., 2014b
Kelp gull	1976–1981	10.1	Crawford et al., 1982a
	1999–2004	20.5	Whittington et al., in press
	2008–2013	17.4	Whittington et al., in press

No comparative information for the intermediate period is available for Cape, white-breasted or crowned cormorants.

For Cape gannets, numbers breeding at colonies were estimated from the product of the area occupied by breeding birds and the mean density of nests (Crawford et al., 2007). The extent of the area occupied by breeders was measured on aerial photographs, taken vertically, using an Ibas interactive image-analysis system, or by walking around the colony with a Global Positioning System (GPS) (Crawford et al., 2007, 2014b). Measurements of the densities of nests at colonies were undertaken toward the end of the breeding season by placing four poles, each 2 m long, on the surface of the ground, so as to form a square of 4 m^2. The numbers of whole nests and part nests within the square were counted. The overall number of nests in the square was taken to be the number of whole nests plus half the number of part nests (Crawford et al., 2007).

For the four species of cormorant, counts were made of active nest sites, which were defined as paired birds defending a site, sites showing evidence of recent nest-construction, and nests with eggs, chicks or adults. When unattended chicks were found in crèches away from nests, their number was divided by the approximate mean clutch size of the species (two for bank cormorant, three for the other cormorants) to estimate the number of nest sites they represented, because nests at which these chicks were reared would not have been counted (Crawford et al., 2008a, 2012, 2013b, 2014b). Remainders were taken to represent further sites. For Cape, white-breasted and crowned cormorants, the highest count at each breeding colony during a 5-year period was taken and the selected counts were then summed to produce the total count for the period. The same process was carried out for bank cormorants but for periods of 3 years. This was done because not all colonies are visited each year and some only sporadically (Cooper, 1981; Cooper et al., 1982; Crawford et al., 1999). Cape and bank cormorants often show strong fidelity to breeding sites, whereas fidelity of white-breasted and crowned cormorants to sites is weaker (Crawford et al., 1994). This may lead to inflated estimates of numbers of the latter two species but under-counting at colonies also may occur. These biases are discussed more fully in Crawford et al. (2012, 2013b).

For swift terns, numbers of birds incubating eggs or with small chicks were counted with the aid of tally counters and binoculars. Large colonies were divided into smaller portions to facilitate counting (Cooper et al., 1990). Counts of chicks unattended by parents were added to those of breeding birds to estimate the number of pairs breeding, the mean size of swift tern clutches in southern Africa being approximately one (Crawford et al., 2002).

Counts of breeding kelp gulls were made from vantage points using binoculars after gulls had settled at nests, or by walking tightly spaced grids and marking nests (Crawford et al., 1982a; Whittington et al., 2006, in press). Counts took place during the breeding season and at the main colonies they were usually conducted from late October–early November, when birds at most nests were incubating eggs (Crawford et al., 1982a). Kelp gulls incubating eggs are generally easier to count than those that have yet to lay or are guarding chicks, because they remain longer at nests and soon settle at nests after being disturbed. Chicks are able to leave nests shortly after hatching and their cryptic plumage and behavior makes them easy to overlook (Crawford et al., 1982a). Therefore, recently used nests of kelp gulls also were counted.

Based on information in the indicated references, during periods of relative stability of populations the coefficients of variation for annual estimates of overall numbers of birds breeding at well-monitored colonies were 0.16 ($n = 8$) for African penguin, 0.10 ($n = 12$) for Cape gannet, 0.14 ($n = 21$) for Cape cormorant, 0.32 ($n = 14$) for swift tern (Crawford et al., 2014b), 0.07 ($n = 13$) for bank cormorant (Crawford et al., 2008a), 0.15 ($n = 17$) for white-breasted cormorant (Crawford et al., 2013b), 0.11 ($n = 14$) for crowned cormorant (Crawford et al., 2012) and 0.06 ($n = 5$) for kelp gull (Crawford et al., 2009a).

In order to examine changes in the distributions of breeding by the eight seabirds since the late 1970s/1980s, the eastern and southern coasts of South Africa were divided into five regions and the numbers of each seabird breeding in each region were plotted for periods for which information was available. The five regions were the same as those used by Crawford et al. (2013b) and similar to those used by Whittington et al. (in press), viz. the Northern Cape, the north, southwest and east sectors of the Western Cape and the Eastern Cape (**Figure 1**). In South Africa, seven of the eight species considered breed exclusively in these regions (Hockey et al., 2005). The white-breasted cormorant breeds too in KwaZulu-Natal, but numbers breeding coastally in that province are only available for 2008–2012 (Crawford et al., 2013b).

Following Whittington et al. (in press), changes between periods were also examined in the proportions of the eight seabirds breeding at maritime islands (including rocks and stacks surrounded by the ocean) and on the mainland (including islands in salt-works and estuaries) as seabirds on the mainland are subject to additional threats, such as predation by mainland carnivores (e.g., Crawford et al., 2011). Two sites that were formerly islands but subsequently joined to the mainland (Bird Island at Lambert's Bay in 1959 and Marcus Island in 1976) were considered mainland sites because the earliest counts considered here commenced in 1976.

Differences in numbers of seabirds nesting in the five geographical regions of the South African coastline and at maritime islands and on the mainland during the three periods considered (late 1970s/early 1980s, late 1990s/early 2000s, late 2000s/early 2010s) were investigated using the χ^2-test. In order to control for multiple testing, a false discovery rate adjustment was made to the probabilities (P_i) obtained for species i for both the regional and island vs. mainland comparisons. Species were ranked in the order of ascending probability values and P_i were deemed significant at the 5% level ($q = 0.05$) for all $P_i \leq (i/N).(q/c(N))$, where $N = 8$ and c(N) is the sum from $i = 1$ to N of 1/i (Benjamini and Yekutieli, 2001).

RESULTS

Numbers of African penguins, Cape cormorants and bank cormorants in South Africa all showed a substantial decline from the late 1970s/early 1980s to the late 2000s/early 2010s (**Table 1**). There were large decreases in African penguins around South Africa, but the decrease in the Eastern Cape was proportionally less than in the Western Cape so that in 2013 it held marginally more penguins than the Western Cape (**Figure 2**). Most of the South African population of Cape cormorants breeds in the north and southwest sectors of the Western Cape, with <1300 pairs breeding in any other region (Supplementary Material). Between 1977 and 1981 and 2009 and 2013 there was a large decrease in numbers in the north Western Cape and a slight increase in the southwest of this province (**Figure 2**). New colonies were formed in the southwest Western Cape at Robben Island in 2004 and Stony Point in 2010 and in the east Western Cape at Knysna Heads in 2008 and all had subsequent rapid growth. In South Africa, numbers of bank cormorants decreased throughout the species' breeding range (**Figure 2**), which is west of Cape Agulhas (Cooper, 1981). The proportion of bank cormorants breeding in the southwest Western Cape increased from 41 to 43% during the 1900s to 48% from 2011 to 2013.

The overall populations of crowned and white-breasted cormorants breeding around the west and south coasts of South Africa (Northern, Western and Eastern Cape provinces) were stable between 1977 and 1981 and 2008 and 2012 (**Table 1**). For both species, there were decreases in numbers breeding in all three regions west of Cape Agulhas, except for a large increase of crowned cormorants in the north Western Cape (**Figure 2**). Up until 1982, crowned cormorants were only known to breed west of Cape Agulhas, but in 2003 they extended breeding to the east sector of the Western Cape, where numbers increased from four pairs in 2003 to 33 pairs in 2012 (Whittington, 2004; Crawford

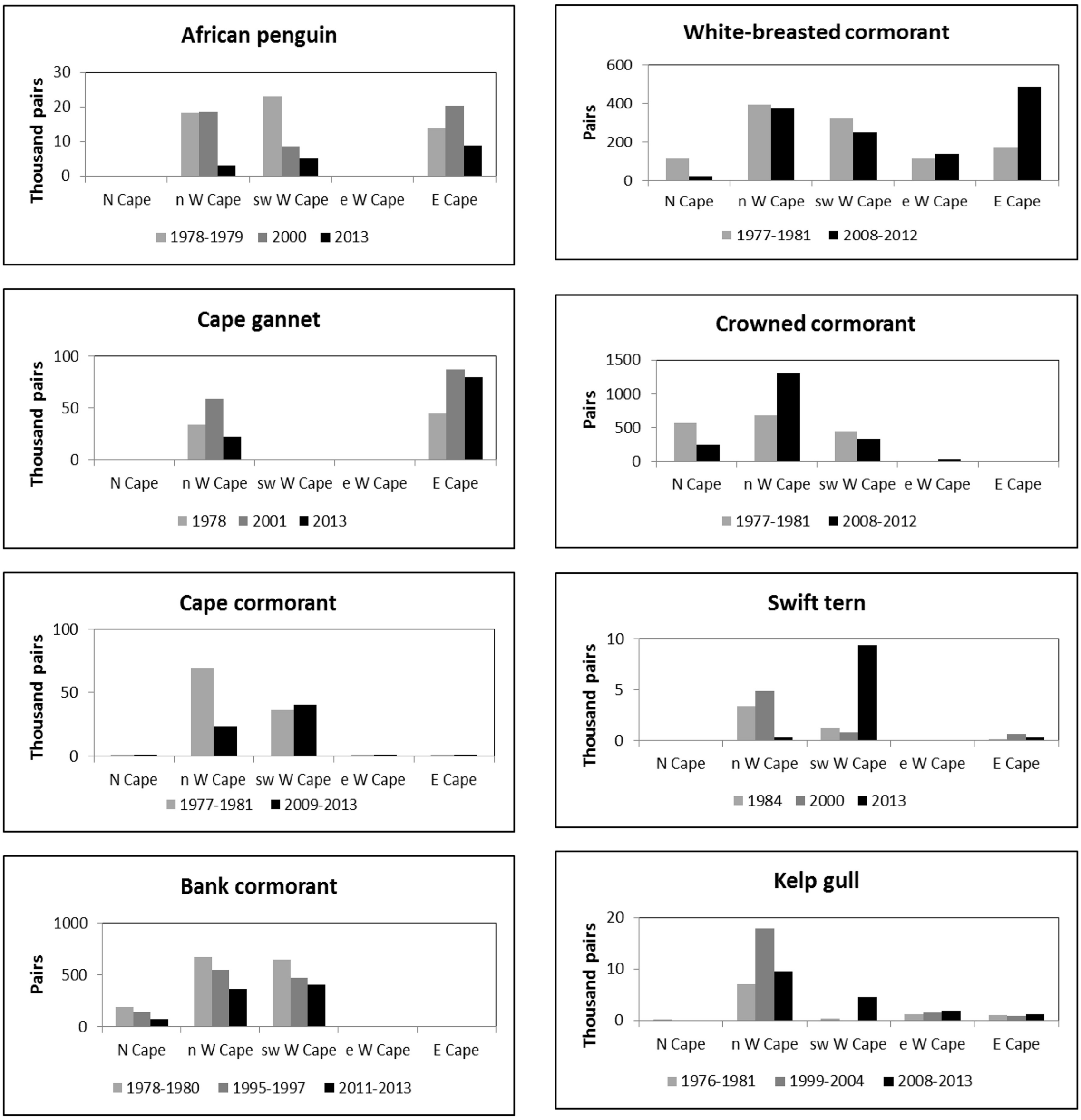

FIGURE 2 | Numbers of eight seabird species breeding coastally in five regions of South Africa's west and south coasts in different periods in which entire populations were estimated.

et al., 2012). East of Cape Agulhas numbers of white-breasted cormorants breeding coastally increased between 1977 and 1981 and 2008 and 2012 (**Figure 2**; Crawford et al., 2013b).

The number of Cape gannets in South Africa increased between 1978 and 2001 but decreased in 2013 (**Table 1**). The species breeds at only three islands in South Africa, two of which are in the north Western Cape and the third in the Eastern Cape. Numbers increased in both regions between 1978 and 2001, but then decreased in the Western Cape (**Figure 2**). Swift terns increased rapidly in South Africa in the present century, with numbers more than doubling to peak at 14,000–16,000 pairs between 2008 and 2011 (Crawford et al., 2014b); then about 10,100 pairs bred in 2013 (**Table 1**). After 2005, numbers in the north Western Cape decreased markedly and most birds now breed in the southwest sector of this province (**Figure 2**). The South African population of kelp gulls more than doubled between 1976 and 1981 and the turn of the 21st century but have since fallen again (**Table 1**). After the turn of the century, numbers decreased in the north Western Cape but increased in each of the three regions farther south and east (**Figure 2**).

Between the three periods there were significant changes in the regional distributions of all eight seabird species (**Table 2**). After the late 1970s/early1980s, there were significant changes in numbers of seven seabirds breeding at maritime islands and on the mainland, the exception being white-breasted cormorants (**Table 2**). The proportions of birds breeding on the mainland increased for African penguin, bank cormorant, crowned cormorant and kelp gull and decreased for Cape gannet, Cape cormorant and swift tern (**Figure 3**).

DISCUSSION

Four of the seabirds considered in this paper (African penguin, Cape gannet, Cape cormorant, and swift tern) compete with the South African purse-seine fishery for anchovy and sardine, their main prey items (e.g., Crawford and Dyer, 1995). In South Africa, a fifth seabird (bank cormorant) feeds mainly on rock lobster, which is also targeted by a commercial fishery (Hockey et al., 2005; Cockcroft et al., 2008). Crowned cormorants eat mostly small, inshore fish species, notably Clinidae, that are not harvested by humans and do not contribute to the diets of fish that are (Crawford et al., 2012). White-breasted cormorants and kelp gulls are opportunistic feeders that do not compete substantially with fisheries for food and whose key prey species are not important dietary items for the main fish species harvested by humans (Crawford et al., 1987, 1991, 2013b; Steele, 1992; Whittington et al., 2006). Therefore, the prey of white-breasted and crowned cormorants and kelp gulls will not have been severely impacted by fisheries or have increased substantially as a result of fishing activities.

Off South Africa, the distributions of anchovy, sardine and rock lobster shifted south and east during the 1990s and early 2000s (Blamey et al., 2015). Similarly, for each of the four seabirds that feed mainly on anchovy and sardine, there were large recent decreases in the proportions of birds breeding off northwest South Africa (Northern Cape and north Western Cape) in the 1990s and/or 2000s (**Figure 2**; Crawford et al., 2014b). The proportion of bank cormorants breeding off northwest South Africa also decreased, but only by ca. 6%.

The causes of the altered distributions of anchovy, sardine and rock lobster off South Africa are not fully understood. The eastward shift of anchovy spawners was attributed to improved conditions for spawning by this species to the east of Cape Agulhas (Roy et al., 2007). Differential growth and exploitation of sub-stocks of sardine occurring east and west of Cape Agulhas may have caused the shift in the distribution of this species, but environmentally mediated changes cannot be discarded (Cockcroft et al., 2008; Coetzee et al., 2008). The shift in the distribution of rock lobsters in the 1990s coincided with a decrease in lobster somatic growth rates and a major increase in the number and severity of lobster walkouts induced by low oxygen concentrations to the north of Dassen Island, indicating some underlying environmental cause (Cockcroft, 2001; Cockcroft et al., 2008).

Recent eastward extensions in the breeding ranges of two seabirds that are inshore feeders and do not compete with fisheries for food, crowned cormorant and Hartlaub's gull (*L. hartlaubii*), suggest some change in the environment (Whittington,

Table 2 | Results of χ^2-tests used to examine the significance of changes in numbers of seabirds breeding in different regions and at maritime islands as opposed to the mainland.

	Change in numbers breeding in different regions			Change in numbers breeding on maritime islands vs. the mainland		
	χ^2	*df*	$P < 0.05$	χ^2	*df*	$P < 0.05$
African penguin	8319	4	Yes	6071	2	Yes
Cape gannet	100354	2	Yes	101778	2	Yes
Cape cormorant	13002	4	Yes	10755	1	Yes
Bank cormorant	16	4	Yes	14	2	Yes
Crowned cormorant	351	3	Yes	14632	1	Yes
White-breasted cormorant	222	4	Yes	5	1	No
Swift tern	26521	4	Yes	10209	2	Yes
Kelp gull	730753	8	Yes	1846	2	Yes

For each comparison, it is indicated whether or not differences in numbers breeding in different regions/habitats were significant at the 5% level after undertaking a false discovery rate adjustment.

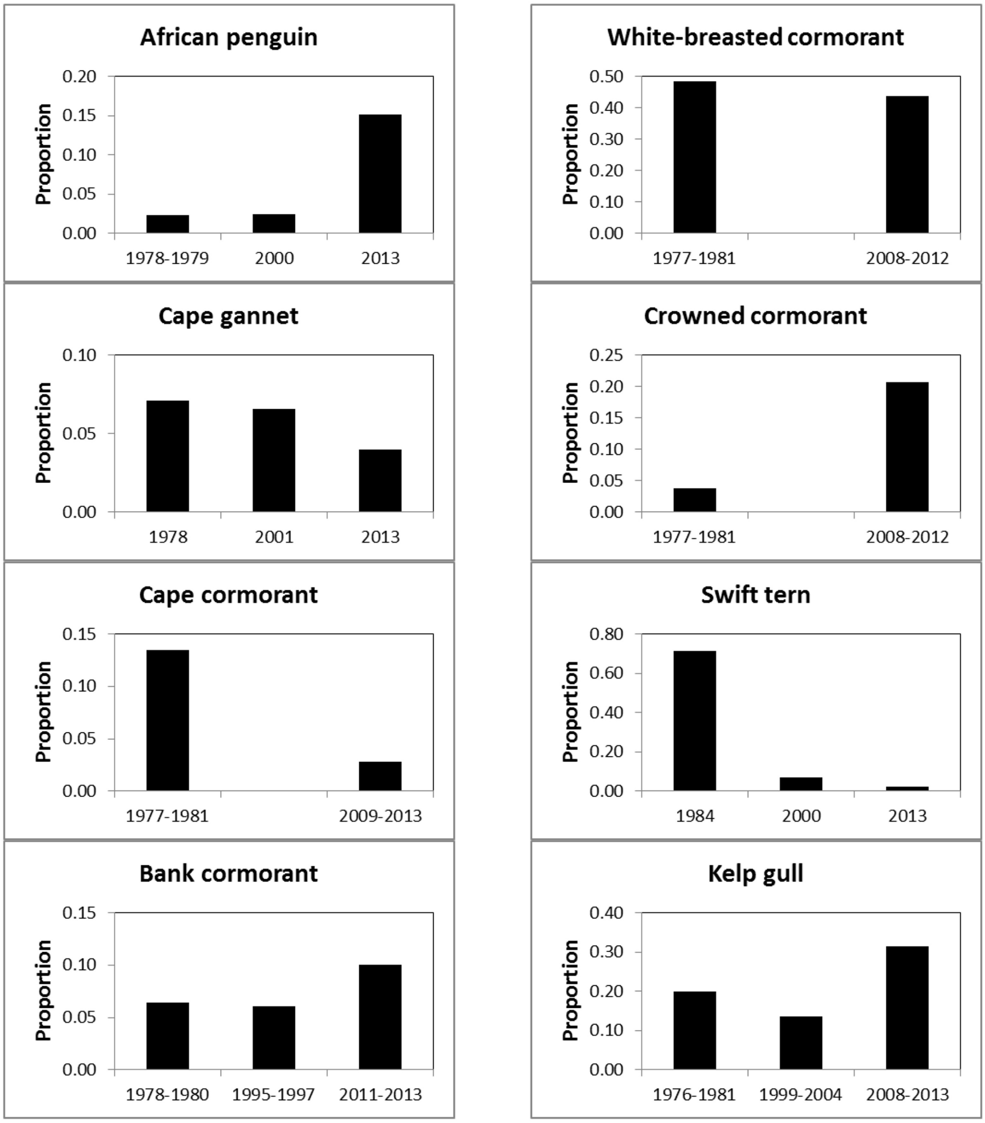

FIGURE 3 | Proportions of eight seabirds breeding on South Africa's mainland, as opposed to its maritime islands, during 1977–1984, 1995–2004, and 2008–2013.

2004; Crawford et al., 2008d), as do the anti-clockwise shifts to the south and east around the South African coast in the proportions of the three seabirds considered here that do not compete substantially with fisheries for prey (**Figure 2**; Crawford et al., 2013b; Whittington et al., in press). Kelp gulls may scavenge from fishing boats (Whittington et al., 2006), but the food of crowned cormorants, mainly small fish that occur inter-tidally or inshore sub-tidally (Crawford et al., 2012), and of white-breasted cormorants, mainly inshore and estuarine fish species (Crawford et al., 2013b), is unlikely to be influenced by commercial fishing activities. Although other factors, such as disturbance and predation, may have influenced decreases of white-breasted cormorants and kelp gulls off northwest South Africa (Crawford et al., 2013b; Whittington et al., in press), there was a concurrent extension in the range of the cool-water, kelp-bed forming seaweed *Ecklonia maxima* to the east of Cape Agulhas (Bolton et al., 2012) suggesting a cooling of the environment in the vicinity of Cape Agulhas. Prior to this extension, the breeding range of bank cormorants was broadly related to that of *E. maxima* (Cooper, 1981).

Amongst the seabirds that compete with South Africa's purse-seine fishery for anchovy and sardine there was a varied response to the altered distributions of these forage species. Populations of Cape gannets and swift terns showed marked increases, whereas those of African penguins and Cape cormorants decreased by more than 50% and ca. 40%, respectively (**Table 1**). The success of gannets is attributable to a large increase in its easternmost colony at Bird Island in Algoa Bay, which may have been aided by immigration of first-time breeders from decreasing western colonies (Crawford et al., 2007, 2014b). Swift terns are nomadic between breeding colonies, which gives them the ability to adapt to an altered distribution of their prey (Crawford et al., 2002), and they likely had good breeding success in the 2000s (Crawford, 2009). By contrast, marine top predators that exhibit behavioral inertia are at greater risk from environmental change (Pichegru et al., 2010b). Breeding African penguins show high fidelity to their partners and hence to breeding localities (Randall, 1989; Crawford et al., 1995). Although Cape cormorants may move between breeding localities (Crawford et al., 1994), they also show fidelity to natal and nest sites (Berry, 1977; Hockey et al., 2005). Both African penguins and Cape cormorants have a restricted foraging range when breeding (e.g., Heath and Randall, 1989; Pichegru et al., 2010a; Hamann et al., 2012) and they suffered high adult mortality in the 1990s and 2000s in periods of prey scarcity off western South Africa (Crawford et al., 1992, 2011; Waller and Underhill, 2007; Sherley et al., 2014). Cape gannets have a much greater foraging range during breeding (Lewis et al., 2006) and supplement their diet by feeding on offal discarded by fisheries when their natural prey is scarce, thereby buffering adult survival (e.g., Berruti et al., 1993; Pichegru et al., 2007; Grémillet et al., 2008; Distiller et al., 2012; Crawford et al., 2014b).

Bank cormorants, which compete with the rock lobster fishery, may move short distances between breeding localities (Crawford et al., 1999) but are relatively sedentary, the maximum recorded movement of birds older than 1 year being 168 km (Cooper, 1981). They are benthic feeders that in Namibia foraged up to 9 km from a breeding locality in waters less than 50 m deep (Ludynia et al., 2010). Although rock lobsters have not shifted their distribution to the same extent as anchovy and sardine, their reduced populations off northwest South Africa appear to have been insufficient to support formerly large colonies of bank cormorants in this region (Crawford et al., 2008a). Recent nest failures for bank cormorants at Robben Island were related to wave heights and air temperature, with chick survival being reduced in years when major storm events occurred during breeding and destroyed nests (Sherley et al., 2012b).

The considerably better recent performance off western South Africa of the two cormorants that do not compete with fisheries for prey than the two that do and the African penguin (**Figure 2**) highlights the possibility that fishing substantially reduced prey availability off northwest South Africa following displacement of the three forage resources to the south and east. Unfortunately for the affected seabirds, many fish processing plants were located off northwest South Africa and fishers continued to seek fish near to their factories. This may have exacerbated the local depletion of prey (e.g., Crawford et al., 2008c; Durant et al., 2010). The exploitation rate of sardine west of Cape Agulhas showed a substantial increase in the mid-2000s (Coetzee et al., 2008). Off Peru, local depletion of anchovy (*E. ringens*) by fishing had a negative impact on foraging parameters of Peruvian boobies (*Sula variegata*) that competed with the fishery for food (Bertrand et al., 2012).

Equally unfortunately for the affected seabirds, the displacement of forage resources to the south and east brought about a mismatch in the distributions of the breeding localities and prey of the seabirds (Crawford et al., 2008c). There are no large islands at which seabirds may breed between Robben and Dyer islands off southwest South Africa and then a distance of about 600 km to the seabird islands in Algoa Bay (**Figure 1**). Consequently, several seabirds, including African penguin and bank cormorant, appear to have attempted to offset the mismatch of colonies and food by breeding in increasing proportions on the mainland (**Figure 3**). The decreases in the number of Cape gannets, Cape cormorants and swift terns breeding on the mainland is mainly attributable to decreases in numbers at the two islands in the north Western Cape that were joined to the mainland and hence assumed to be part of the mainland—Cape gannets and Cape cormorants at Bird Island (Lambert's Bay) and swift terns at Marcus Island (**Table 1**; Crawford et al., 2007; Crawford, 2009). However, substantial numbers of Cape cormorants have joined African penguins and bank cormorants in breeding at the southern mainland locality of Stony Point and they formed a new colony at Knysna Heads (Supplementary Material; Crawford et al., 2011).

A better understanding of the mechanisms driving seabird populations in South Africa will result from development of integrated population models that account for movement between colonies (e.g., Sherley et al., 2014) and of models that account for multiple factors that may be influencing populations. The former are hampered to some extent by insufficient mark-recapture information properly to estimate survival and rates of migration between regions for some species and age classes of birds (e.g., Distiller et al., 2012). Progress has been made on developing a systems dynamics approach to modeling multiple drivers of African penguin populations that uses expert opinion in the absence of quantitative information (e.g., Ludynia et al., 2014; Weller et al., 2014). Developing new technology, e.g., remotely operated drones, may prove useful in obtaining more frequent information on numbers of seabirds breeding at localities that are difficult to access and hence reducing the uncertainty of population estimates.

Potential mechanisms to mitigate the adverse impacts of environmental change on seabirds off South Africa are implementation of spatial management for fisheries of shared forage resources, including both allocations of catch limits at a regional scale and localized closures to fishing around impacted seabird colonies (e.g., Durant et al., 2010; Pichegru et al., 2010a, 2012), and offsetting the present mismatch of breeding localities and food through establishing new seabird colonies nearer the present location of food (e.g., Department of Environmental Affairs, 2013). Penguins attempted to form a new colony on the southern mainland east of Cape Agulhas between 2003 and 2007 but were prevented from doing so by indigenous carnivores (Crawford et al., 2011), whereas at Knysna Heads Cape cormorants were more successful (Supplementary Material). Given the known frequency of formation of new colonies by different species and their use of man-made structures and habitats for breeding, establishment of new colonies may be easier for cormorants, gulls and terns (Supplementary Material; Crawford, 2009; Crawford et al., 2012, 2013b; Whittington et al., in press) than for penguins (Crawford et al., 2013a) and especially gannets (Crawford et al., 1983).

With regard to the Cape gannet, it is noteworthy that there has been a long-term redistribution to the south and east of its breeding population. Whereas 80% of Cape gannets bred in Namibia in the 1950s and 1960s, at present about 90% breed in South Africa (Crawford et al., 2007, 2014b). Within South Africa, the proportion breeding in the Eastern Cape, which now supports about 70% of the global population (Crawford et al., 2014b), has increased. As Algoa Bay is at the eastern extremity of the greater Benguela upwelling region, juxtaposed to the warm, south-west flowing Agulhas Current (Hutchings et al., 2009), which is likely to be unsuitable habitat for the gannets, there appears to be no further opportunity for the species to expand its range to the east. Similar difficulties in adjusting distributions to an altered environment can be expected, for example, for less mobile seabirds such as Crozet shags (*Phalacrocorax* [*atriceps*] *melanogenis*) and Gentoo penguins, and perhaps even more wide-ranging species such as rockhopper penguins, at the well-separated archipelagos of the sub-Antarctic (e.g., Crawford et al., 2008b, 2014a; Allan et al., 2013). In such instances, human interventions to mitigate adverse impacts of climate change will not prove easy and may best be directed at attempting to maintain the substantially reduced abundances of seabirds that have survived changes to date. Certainly conservation planning will be aided by a better understanding of the ultimate causes of the distributional changes.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fevo.2015.00010/abstract

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Are arrival date and body mass after spring migration influenced by large-scale environmental factors in a migratory seabird?

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Changes in the timing of migratory events have been observed recently in many migratory species, most likely in response to climatic change. In the common tern *Sterna hirundo* we examined such changes in spring arrival date and body mass based on an individual-based longitudinal data set from a transponder marked colony from 1994 to 2012. Although no long-term trend was observed in either trait, strong inter-annual and age-specific variation in arrival date and mass was evident. We investigated whether environmental factors such as (i) global climate phenomena, i.e., North Atlantic and Southern Oscillation Indices, NAOI and SOI, and/or (ii) local factors, i.e., food abundance in the wintering and breeding area represented by fish stock or marine primary productivity, could explain this variation. We found that 2-year-old birds on their first spring migration advanced arrival in relation to spring NAOI and delayed arrival in relation to sprat *Sprattus sprattus* abundance. The arrival date of 3-year-olds also advanced in relation to NAOI and delayed in relation to winter SOI. In contrast, adults delayed arrival with NAOI and advanced in relation to SOI. Within age groups, earlier annual arrival coincided with higher mass, indicating that a fast and/or early migration did not come at a cost to body condition. Changes in arrival mass relative to environmental covariates were found only in 2-year-olds on their first spring migration: in these birds arrival mass was positively related to herring *Clupea harengus* and sprat abundance in the breeding area as well as spring NAOI and negatively related to SOI. In conclusion, traits related to migration of common terns were linked with environmental conditions, but showed no long-term trends over the past two decades. Age-related differences were marked, suggesting that common terns might be subject to differing environmental constraints or respond differently to conditions during their annual cycle depending on their age.

Keywords: age-related changes, arrival date, body mass, environmental impact, long-distance migrant, timing of migration, NAOI, SOI

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Introduction

Physical condition and timing of arrival in the breeding area are important parameters for migratory species with a relatively short reproductive season. In migratory birds, for example, the probability of reproducing successfully increases with an earlier arrival and a greater body mass

(Chastel et al., 1995a,b; Kokko and Johnstone, 1999; Bêty et al., 2004; Verhulst and Nilsson, 2008; Descamps et al., 2011; Sergio et al., 2014), and early arrival and a greater mass at arrival have been associated with a reduced mortality risk and increased lifespan (Zhang et al., 2015b). Arrival date and mass are influenced by, among other factors, environmental conditions during migration and in the wintering area (e.g., Hüppop and Hüppop, 2003; Crick, 2004; Visser and Both, 2005; Parmesan, 2006; Newton, 2008). In many species, phenology has been observed to change in response to environmental conditions before and during the pre-breeding migration (e.g., Forchhammer et al., 1998; Frederiksen et al., 2004; Barbraud and Weimerskirch, 2006; Wanless et al., 2009).

Variation in temperature, wind and rainfall influences food availability and foraging success of migrants, which in turn can affect timing of migration and breeding propensity (Stenseth et al., 2002). Migratory seabirds are especially affected by offshore conditions (Schreiber, 2001). Stormy weather, strong winds and rain complicate foraging in piscivorous birds (Dunn, 1973; Finney et al., 1999; Daunt et al., 2006), while local weather also affects prey availability (Misund et al., 1998, 1997). Adverse weather can exhaust birds, causing migration to be prolonged (Newton, 2006). Conditions during winter can affect the physical state and molt of individuals, the length of migration, their ability to return to the colony site and their ability to breed (Schreiber, 2001; Sandvik et al., 2005). In consequence, environmental conditions can affect traits such as arrival date and mass after migration and cause inter-annual variation in reproductive performance and survival probability. Despite within-individual consistency in experienced breeders, substantial variation in arrival dates of birds was found (Bêty et al., 2004; Arnaud et al., 2013; Sergio et al., 2014), indicating plasticity and capacity of response in phenology toward short- and long-term environmental perturbations. Based on an understanding of inter-annual variation in the timing of arrival and of the birds' condition upon arrival at the breeding sites, these traits can be used as indicators of changing environments at wintering sites or on migration routes and as a tool for monitoring population health.

The common tern *Sterna hirundo* is a small-sized, long-distance migrant and visual hunter, relying on small pelagic fish caught by plunge-diving in the upper water layers (Becker and Ludwigs, 2004). Because of their low body reserves, common terns are sensitive to food shortage (e.g., Frank and Becker, 1992). Arrival date (Ludwigs and Becker, 2002; Dittmann and Becker, 2003; Ezard et al., 2007; Becker et al., 2008a; Arnaud et al., 2013; Zhang et al., 2015b) and arrival mass (Ezard et al., 2007; Limmer and Becker, 2007) in this species are strongly age-dependent and associated with fitness: earlier arrival and higher mass increase breeding success (Wendeln and Becker, 1999; Ezard et al., 2007) and are associated with reduced mortality and an increased lifespan (Zhang et al., 2015b). The common tern therefore represents a good species to examine the dependence of these migratory traits on environmental conditions in its year-round habitats.

Environmental conditions can be represented by global climate phenomena, such as the North Atlantic Oscillation Index NAOI (Hurrell et al., 2001, 2003) or the Southern Oscillation Index SOI (Trenberth and Caron, 2000; Stenseth et al., 2003). They affect local weather and fish abundance over large geographical areas and might therefore be good integrated indicators of overall conditions faced by migrant birds, with more predictive power than local weather variables (Stenseth et al., 2002; Hurrell and Deser, 2009). Food abundance for common terns breeding on western European coasts, such as the studied colony, can be measured in West African fish stock (wintering area, see **Figure 1**) and North Atlantic herring *Clupea harengus* and sprat *Sprattus sprattus* abundance (breeding area, see **Figure 1**). The preferred wintering area of European common terns (Becker and Ludwigs, 2004) is located in the northwest African upwelling zone with higher than average marine primary productivity, which directly influences fish stock (McGregor et al., 2007). In a preliminary study, some indications were found that NAOI and SOI might influence return rates and arrival dates, but not arrival mass of birds in the study colony (Favero and Becker, 2006), although a similar connection was not found in survival rates (Szostek and Becker, 2015). Instead, marine primary productivity in the wintering area was found to be positively related to common tern survival and recruitment probability (Szostek and Becker, 2015).

Measuring time of first arrival at the breeding grounds and body mass upon arrival for individual birds is challenging, especially obtaining large sample sizes and annually repeated measurements. In a long-term integrated population study of common terns on the German North Sea coast, we were able to record annual spring arrival date and body mass with high reliability for a considerable number of known-age individuals over nearly two decades, from 1994 to 2012. Because of the age-related change in these traits (see above), information on the age of individuals is vital to studies investigating changes in arrival date and mass (Ezard et al., 2007).

In this study we focussed on inter-annual variation in arrival date and body mass and disentangled the variation caused by age, sex and environmental factors such as food supply and global climate indices. The aim was to find which of the many environmental constraints faced by the terns year-round exerted most influence and which part of the common tern life-cycle was most limiting. We regarded potential differences between age groups with respect to their sensitivity to the environment and possible carry-over effects between the wintering and breeding seasons. Specifically we wanted to address the following questions: (1) Is there inter-annual variation in spring arrival date and body mass in relation to age and sex? (2) Is there a time trend in arrival date and body mass between 1994 and 2012, against the background of global climate change? (3) Do environmental covariates affect arrival date and body mass and do effects differ between age groups? (4) Are environmental conditions most influential during winter or during migration?

Methods

Study Species

Common terns are small, long-lived, piscivorous seabirds (Becker and Ludwigs, 2004). As common terns are highly visual plunge-divers, their foraging abilities can be severely

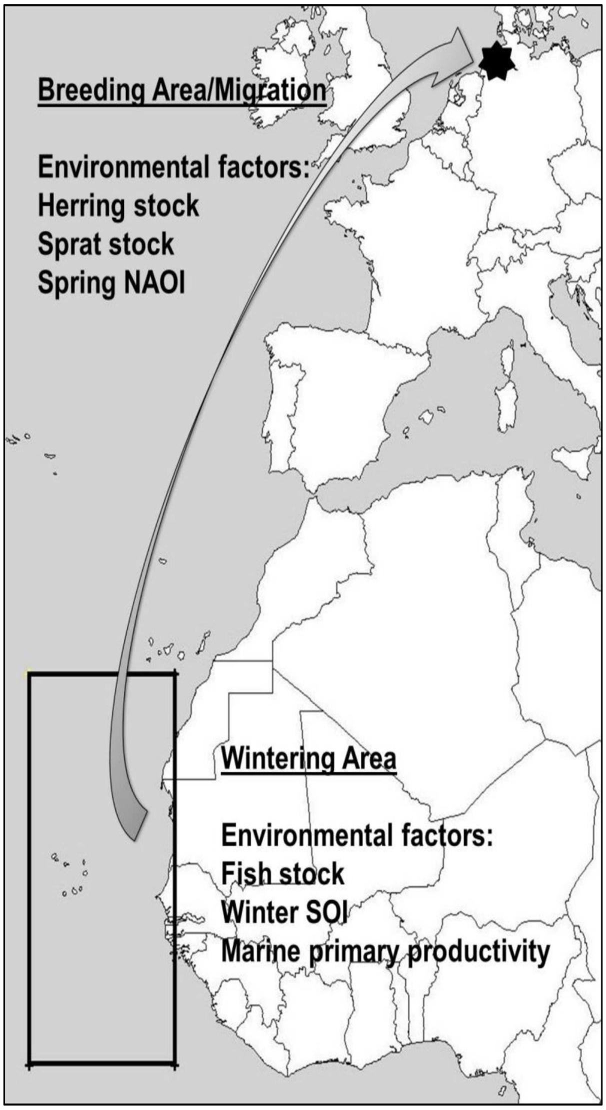

FIGURE 1 | Wintering and breeding area of the Banter See common terns, as well as approximate spring migration route. Environmental covariates are given, along with the geographical locations where they are expected to affect common terns from the study colony.

compromised by stormy or rainy conditions (Dunn, 1973; Becker et al., 1985; Becker and Specht, 1991; Frank and Becker, 1992). Juvenile common terns remain in the wintering area for their first summer, returning to the breeding grounds as 2-year-olds (Becker and Ludwigs, 2004). Most individuals spend a "prospecting" season at the colony as non-breeders before recruitment (Dittmann and Becker, 2003; Dittmann et al., 2007). Arrival mass increases with age until it reaches a plateau at around 6 years (Limmer and Becker, 2007). Arrival date at the colony also advances with age and experience (Dittmann and Becker, 2003; Becker et al., 2008a; Zhang et al., 2015a). First-time arrival date has been linked with age at first reproduction and can be regarded as a proxy for individual quality (Becker et al., 2008a; Zhang et al., 2015b).

Study Site

The Banter See common tern colony is located on the German North Sea coast (53°30′40″N, 08°06′20″E). Since 1984 all chicks at this site have been ringed and since 1992, all fledglings and 101 adult terns from this colony have additionally been injected with small passive transponders (TROVAN ID 100, 11 × 2 mm) that identify individuals remotely and automatically by antenna. In a long-term study, we collected individual life-histories of all native terns at this colony through remote sensing. Antennas were distributed on prominent platforms around the colony site and placed around each nest for 1–2 days to identify breeders. In addition, some platforms were equipped with electronic scales (Sartorius, TE6100; accuracy ± 1 g) which weighed birds automatically, while also recording their identity by antenna. In 1994 the system included 11 antennas and 7 scales and the devices were alternated between resting platforms throughout the colony. The number of registration devices was continuously increased as the colony grew until there were 44 permanent registration platforms (since 2002) of which 22 were also equipped with scales. The system recorded individual presence and mass throughout the breeding season with minimal disturbance to the colony (Becker and Wendeln, 1997; Becker et al., 2008b). For this study we used data between 1994 and 2012. Permissions were granted by the regional authorities "Bezirksregierung Weser-Ems, Stadt Wilhelmshaven" and "Nds. Landesamt für Verbraucherschutz und Lebensmittelsicherheit Oldenburg."

Arrival Date and Arrival Mass

Common terns are generally registered immediately upon arrival, as they like to sit on the elevated platforms. Arrival dates were defined as the first automatic registration of a bird at the colony (cf. Ludwigs and Becker, 2002; Dittmann and Becker, 2003; Becker et al., 2008a). Dates were disregarded, if the first registration was less than 10 days before the recorded laying date for breeders (9.2% of cases per year), thereby excluding birds first recorded on the nest. Arrival body mass was calculated as the mean of masses measured independently during the first 3 days after arrival at the colony. Measurements that were falsified by wind or rain influencing the reading of the scale were disregarded (for details see: Wendeln and Becker, 1996; Limmer and Becker, 2007). In total the data set comprised 7576 arrival dates and 3664 arrival masses from 1607 individuals. The arrival mass data for each individual included on average 5.05 ± 7.97 (range 1–110) independent measurements.

Environmental Covariates

We focussed on six environmental covariates, concerning food abundance and global weather patterns both in the wintering and breeding area (for details see **Table 1**). We chose global climate indices (NAOI and SOI) rather than local weather variables for two reasons: firstly we did not want to include too many covariates (Frederiksen et al., 2014) and a compound parameter makes that possible; secondly, exact enough data on where the terns spend their winter months and by which route they migrate are currently not available. The data that are available from geolocation (Becker et al., unpublished) show that adult birds spread widely across the West African coast and do not always use the

TABLE 1 | Covariates used in statistical analyses: abbreviation, definition, source and available timeframe.

Variable	Definition	Unit	Range (min–max)	Source	Available data
wSOI	Southern Oscillation Index during the winter period (October–March): standardized mean monthly values		−1.80–2.23	International Research Institute for Climate and Society (IRI) Data Library (http://iridl.ldeo.columbia.edu/docfind/databrief/?sem=iridl%3AClimate-Indices)	1994–2012
sNAOI	North Atlantic Oscillation during the spring migration (April–June): monthly principle component values		−1.52–2.33	Climate Data Guide at the National Centre for Atmospheric Research (https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based)	1994–2012
Prim	Primary productivity in the wintering area	mg C/m^2/day	1088–1293	College of Science, Oregon State University, USA (http://www.science.oregonstate.edu/ocean.productivity/standard.product.php)	2002–2012
Herring	Abundance of herring (recruitment, size class 0) in the North Sea (area roughly Southern North Sea and Eastern Channel)	Estimated number of individuals	21423521–86616423	International Council for the Exploration of the Sea (ICES), 2013, Report of the Herring Assessment Working Group for the Area South of 62 N (HAWG), page 111	1994–2012
Sprat	Abundance of sprat (all size classes—larvae to ca. 15 cm) in the North Sea (area roughly Southern North Sea and Eastern Channel)	Abundance index: landings per unit effort (lpue)	736–4921	International Council for the Exploration of the Sea (ICES), 2013, Report of the Herring Assessment Working Group for the Area South of 62 N (HAWG)	1994–2012
wFood = Fish stock in the wintering area	Abundance of small pelagic fish off the Northwest African coast (between the southern border of Senegal and the northern Atlantic border of Morocco)—size between ca. 4 and 20 cm.	Weight in tons	1138524–1450632	Food and Agriculture Organization of the United Nations (FAO), 2011, Fisheries and Aquaculture Report No. 975, page 120	1994–2009

same migration route. This makes global climate indices more likely to show a broad effect than local weather data. NAOI is likely to affect individuals on migration, although its effects are strongest in the winter and therefore might not be relevant to very late migrating individuals, such as young birds. SOI has global influence, but is most likely to affect birds in the wintering area and we therefore restricted this variable to the winter months.

Food abundance in the breeding area and on the final part of migration in the English Channel and North Sea was represented by the most common prey species herring and sprat. These estimates were based on fishery data corrected for fishing effort (ICES, 2013). Fish stock in the wintering habitat was represented by small pelagic fish of various species in consumable size for common terns, including the the most common prey of common terns, sardines *Sardina pilchardus*; *Sardinella* sp. and anchovies *Engraulis encrasicolus* (cf. Dunn and Mead, 1982; Becker and Ludwigs, 2004), but also horse mackerel *Trachurus trachurus, t. trecae, Caranx rhonchus* and chub mackerel *Scomber japonicus*. In this case, fishery data were not corrected for fishing effort (FAO, 2011) and therefore this variable must be used with caution. As another indicator of food abundance in the wintering area we included marine primary productivity. Although the relationship between primary productivity and the presence of top-predators is not always straightforward (Grémillet et al., 2008) we used very wide ranging temporal and spatial constraints. So even if a spatial or temporal mismatch were to occur, the average values used in this study are an indication of a year of high or low food abundance.

TABLE 2 | Arrival date and body mass, including mean, standard deviation, range per age group (2-year-olds, 3-year-olds and adults) and sample size.

	Age group	Mean	*SD*	Min	Max	*N*
Arrival body mass (g)	2 year	125	2.92	119	129	644
	3 year	129	3.52	120	137	698
	Adults	132	2.42	128	138	2424
Spring arrival date (day-of-year)	2 year	181	6.45	175	197	1433
	3 year	148	6.02	131	158	1139
	Adults	120	2.82	113	124	5279

Statistics

All arrival date and mass variables per age group (**Table 2**), as well as all covariates were normally distributed (Kolmogorov-Smirnov test: $p > 0.05$, $N = 11–19$ years). We tested the environmental covariates for inter-correlation using Pearson's correlation, based on which we eliminated the variable NAOI during autumn migration, as it correlated with winter SOI. None of the other environmental covariates were correlated ($p > 0.05$, $R^2 < 0.353$).

To test for a relationship between arrival date and mass, we performed an additive cross-classified random effects model with normally distributed errors and a Markov chain Monte Carlo estimation algorithm with 100,000 iterations (Browne et al., 2007). Arrival mass ($N = 3663$ cases from 1138 individuals) was the dependent variable, with age group (ages 2 years, 3 years and adults of 4 years and older; age-group 2 years was the

TABLE 3 | Minimal adequate additive cross-classified random effect model describing significant effects of age, sex and environmental covariates on arrival date of common terns (1994–2012).

	Parameter	Estimate	*SE*	Chi-square	*P*
Factor	Sex	−1.748	0.351	24.782	< 0.001
	Age (2)	Ref			
	Age (3)	−28.438	1.973	1687.816	< 0.001
	Age (4+)	−56.022	1.379		
Covariates	sNAOI	−2.945	0.737	15.967	< 0.001
	wSOI	0.583	0.847	0.474	0.491
	Sprat	0.153	0.077	3.911	0.048
	Age*sNAOI	0.539	1.094	28.007	< 0.001
		4.211	0.854		
	Age*wSOI	1.429	0.745	44.745	< 0.001
		−2.007	0.572		
	Age*sprat	−0.157	0.074	7.478	0.024
		−0.110	0.045		
Cross-classified random factor	Year	7.829	3.758		
	Id	231.645	3.781		

Non-significant terms were excluded in a stepwise progression, until only significant terms remained. N = 7576 cases from 1607 individuals.

TABLE 4 | Minimal adequate additive cross-classified random effect model describing significant effects of age, sex and environmental covariates on arrival mass of common terns between 1994 and 2012.

	Parameter	Estimate	*SE*	Chi-square	*P*
Factors	Sex	−1.420	0.277	26.227	< 0.001
	Age (2)	Ref			
	Age (3)	8.929	1.901	67.915	< 0.001
	Age (4+)	12.411	1.510		
Covariates	sNAOI	1.258	0.649	3.758	0.053
	wSOI	−1.432	0.673	4.526	0.033
	Herring	0.095	0.032	8.596	0.003
	Sprat	0.077	0.052	2.212	0.137
	Age*sNAOI	−1.473	0.879	8.501	0.014
		−2.205	0.756		
	Age*wSOI	1.104	0.646	12.274	0.002
		1.797	0.537		
	Age*herring	−0.092	0.032	18.312	< 0.001
		−0.093	0.022		
	Age*sprat	−0.048	0.056	8.172	0.017
		−0.105	0.037		
Cross-classified random factor	Year	3.001	1.572		
	Id	68.529	1.610		

Non-significant terms were excluded in a stepwise progression, until only significant terms remained. N = 3663 from 1138 individuals.

reference group) and sex as fixed factors, as well as arrival date as covariate. Cross-classified random effects were year and bird-ID, which accounted for inter-annual and within-individual variation. These random effects remained in the model irrespective of their significance.

In order to test for year-, age- and sex-effects in arrival date and mass, we used additive cross-classified random effects models in which arrival date ($N = 7576$ cases from 1607 individuals) and arrival mass ($N = 3663$ cases from 1138 individuals) were dependent variables with age group and sex as fixed factors as well as year as covariate to test for a trend in time. As above, the cross-classified random effects year and bird-ID accounted for inter-annual and within-individual variation, respectively, and remained in the model irrespective of their significance.

We calculated the effects of environmental covariates, as well as age group and sex on arrival date/arrival mass using additive cross-classified random effect models, as described above. Since birds of different age migrate at different times and might therefore be influenced by different environmental influences, we also included an interaction of each environmental covariate with age group. Full models were simplified by backward stepwise removal of non-significant covariates and interactions. Significance ($p < 0.05$, two-tailed) was assessed using the Wald statistic, which approximates a χ^2 distribution. Statistics were done using MLwiN 2.26 (Rasbah et al., 2012). Please note that a negative relationship between arrival date and an environmental covariate indicates an advanced arrival, while a positive relationship indicates a delayed arrival. Any relationships between arrival date, arrival mass and environmental factors found in this study are not necessarily causal and since we considered only a subsection of possible environmental covariates, there might be other relevant factors not included here. However, reliable data on potentially relevant environmental covariates are scarce and not always readily available.

In fact, not all covariates regarded here were available for the full study period, 1994–2012. The entire set of covariates was available between 2002 and 2009. In order to make best use of the extensive longitudinal data-set available, we ran the analyses for four subsets of data: firstly including those covariates that were available for the entire time period (1994–2012: herring, sprat, NAOI, SOI—**Tables 3**, **4**), then three reduced time periods (2002–2009: all covariates; 1994–2009: herring, sprat, NAOI, SOI, fish stock in the wintering area; 2002–2012: herring, sprat, NAOI, SOI, primary productivity—Supplementary Tables 1–6). Out of the covariates, only fish stock in the wintering area showed a trend over time ($R = 0.914$, $p > 0.001$, $N = 16$ years), possibly due to continuously increasing fishing effort.

Results

Arrival Date

There was no apparent long-term trend for arrival date in any age group (2 year: $R^2 = 0.008$, 3 year: $R^2 = 0.009$, adults: $R^2 = 0.003$; $p > 0.05$; **Figure 2**). Mean arrival date (**Table 2**) per year was not correlated between age groups (adults vs. 3-year-olds: Pearson's $R = 0.155$, $p = 0.526$, $N = 19$ years; adults vs. 2-year-olds: $R = -0.111$, $p = 0.652$, $N = 19$; 2-year-olds vs. 3-year-olds: $R = -0.063$, $p = 0.797$, $N = 19$). Also, incidents of very early or very late arrival were not coordinated between age groups (Supplementary Table 7).

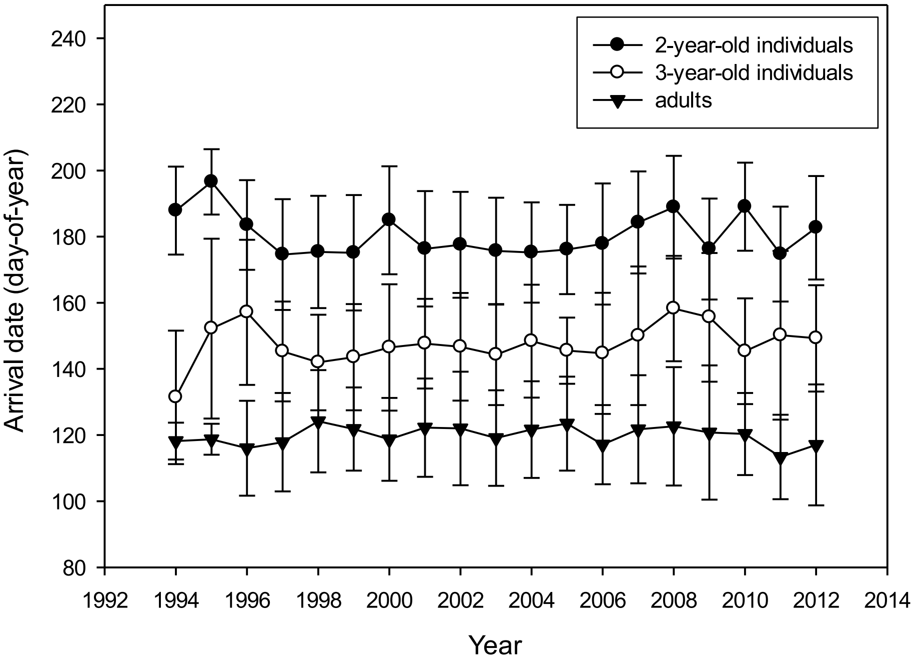

FIGURE 2 | Arrival date (day-of-year: mean ± SD; raw data) at the colony for 2-year-olds, 3-year-olds and adults between 1994 and 2012 ($N_{2y} = 1433$, $N_{3y} = 1139$, $N_{ad} = 5279$).

Accounting for the cross-classified random effects of year and bird-ID (year: estimate = 6.648; *SE* = 2.877; ID: estimate = 234.452; *SE* = 3.808), when testing for year-, age- and sex-effects on arrival date there was a significant difference between age groups (2 year: reference; 3 year: estimate = −31.581; *SE* = 0.658; adults: estimate = −60.201; *SE* = 0.495; $\chi^2 = 15782.214$; $p < 0.001$) and between sexes (females compared to males: estimate = −1.740; *SE* = 0.353; $\chi^2 = 24.289$; $p < 0.001$), but the model confirmed the absence of a time trend (covariate year: estimate = 0.106; *SE* = 0.106; $\chi^2 = 1.000$; $p = 0.317$).

Arrival Mass

There was no apparent long-term trend for mean arrival mass in any age group ($R^2 < 0.001$; $p > 0.05$; **Figure 3**). Mean arrival mass per year was not correlated between age groups (adults vs. 3-year-olds: Pearson's R = 0.201, $p = 0.409$, $N = 19$ years; adults vs. 2-year-olds: $R = -0.123$, $p = 0.626$, $N = 19$; 2-year-olds vs. 3-year-olds: $R = 0.128$, $p = 0.611$, $N = 19$). Very high or very low arrival mass did not occur in the same years for different age groups (Supplementary Table 7).

Accounting for the cross-classified random effects of year and bird-ID (year: estimate = 2.136; *SE* = 1.047; ID: estimate = 69.077; *SE* = 1.618), when testing for year-, age- and sex-effects on arrival mass there was a significant difference between age groups (2 year: reference; 3 year: estimate = 4.277; *SE* = 0.502; adults: estimate = 6.416; *SE* = 0.406; $\chi^2 = 255.848$; $p < 0.001$) and between sexes (females compared to males: estimate = −1.387; *SE* = 0.277; $\chi^2 = 25.056$; $p < 0.001$), but there was no time trend (covariate year: estimate = −0.087; *SE* = 0.071; $\chi^2 = 1.508$; $p = 0.219$).

Relationship between Arrival Date and Mass

We found a significant negative correlation between arrival date and mass on arrival (covariate arrival date: estimate = −0.107; *SE* = 0.006; $\chi^2 = 360.947$; $p < 0.001$). When accounting for arrival date, the significant but small age group differences in arrival mass between the sexes remained (estimate = −1.666; *SE* = 0.274; $\chi^2 = 37.064$; $p < 0.001$), while age effects disappeared (2 year: ref; 3 year: estimate = 0.831; *SE* = 0.604; adult: estimate = 0.262; *SE* = 0.734; $\chi^2 = 3.138$; $p = 0.208$). Cross-classified random factors were year and bird ID (year: estimate = 1.809; *SE* = 0.915; ID: estimate = 67.321; *SE* = 1.582). Incidents of very early (or late) arrival date were in some cases coordinated with very high (or low) arrival mass between age groups (Supplementary Table 7).

Environmental Covariates: Effects on Arrival Date

A model with arrival date as dependent variable, age group and sex as factors, year and bird ID as additive cross-classified random factors as well as all environmental factors as covariates (time period 2002–2009) revealed that there were significant differences between sexes, as well as significant interactions of age group with winter SOI and sprat. These interactions showed a positive relationship between arrival date and SOI in 2- and 3-year-olds (i.e., they delayed arrival with higher SOI), while there was no relationship in older birds. In relation to sprat, 2-year-olds advanced arrival with higher sprat abundance, while 3-year-olds and adults delayed arrival. Females consistently arrived between 1 and 2 days earlier than males.

The equivalent model over the period 1994–2012 (including herring, sprat, sNAOI, wSOI; **Table 3**) revealed similar

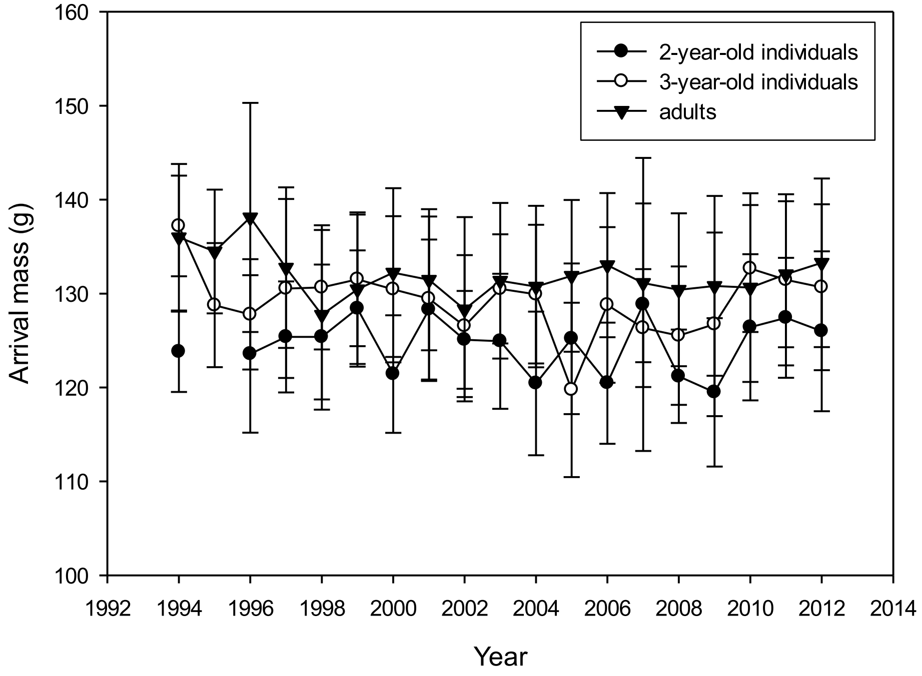

FIGURE 3 | Mass on arrival (mean over first 3 days of colony attendance ± SD; raw data) for 2-year-olds, 3-year-olds and adults between 1994 and 2012 ($N_{2y} = 644$, $N_{3y} = 698$, $N_{ad} = 2424$).

interactions of age groups with winter SOI and sprat, but also an additional interaction of age with spring NAOI (**Table 3**, **Figure 4A**). Here, interactions indicated a negative relationship between arrival date and spring NAOI in 2- and 3-year-olds (they arrived 11 and 9 days earlier over the entire measured range of spring NAOI), while in adults arrival was delayed by 5 days in relation to NAOI. In response to winter SOI, 2- and 3-year-olds delayed arrival (by 2 and 8 days, respectively), as in the short model, while adults now exhibited advanced arrival date with SOI (by 6 days). The relationship with sprat was now positive in 2-year-olds (corresponding to a 6 day delay), while adults still showed a slight positive relationship (2 day delay) and 3-year-olds showed no response. Females consistently arrived between 1 and 2 days earlier than males.

Environmental Covariates: Effects on Arrival Mass

Analysis of arrival mass in the same framework (time period 2002–2009) again revealed significant age and sex effects. Out of the environmental covariates, only winter SOI was negatively correlated with arrival mass and in interaction with age group (Supplementary Table 4). The interaction indicated an increase in arrival mass with higher SOI in 2- and 3-year-olds, while adults showed no relationship. Males consistently arrived 2–3 g heavier than females.

The equivalent model over the period 1994–2012 also included the age-SOI interaction, but additionally showed significant age-interactions with spring NAOI, herring and sprat (**Table 4**, **Figure 4B**). In the interaction with SOI the response in arrival mass was contrary to the model comprising the short time-span: in 2-year-olds there was a negative relationship (corresponding to a mass decrease of 6 g over the entire measured range of winter SOI), while in 3-year-olds and adults there was a very small increase (1 g). A positive relationship was found between NAOI and arrival mass in 2-year-olds (corresponding to a 5 g increase in arrival mass), while there was a weak negative relationship in 3-year-olds (1 g decrease) and adults (3 g decrease). The interaction with herring was strong in 2-year-olds, who showed an increase in arrival mass with higher herring abundance by 6 g over the entire observed range of herring abundance; 3-year-olds and adults exhibited no response. Sprat showed a weaker positive relationship with arrival mass in 2-year-olds (corresponding to a 3 g increase), with 3-year-olds and adults responding very little (a 1 g in- and decrease, respectively). Between 1994 and 2012, males consistently arrived 1–2 g heavier than females.

Discussion

Our analyses revealed strong variation in both arrival date and body mass upon arrival in a small and long-lived piscivorous bird species, the common tern. Surprisingly and in contrast to findings in other species (see refs below), however, there was no long-term trend in either trait. Instead, arrival date was linked with various environmental covariates, with the strength and direction of relationships depending on age. Carry-over effects from the wintering area seemed particularly relevant to arrival date: SOI significantly predicted arrival in all age groups. Conditions during migration and in the breeding habitat, as represented by NAOI and sprat abundance, also appeared influential.

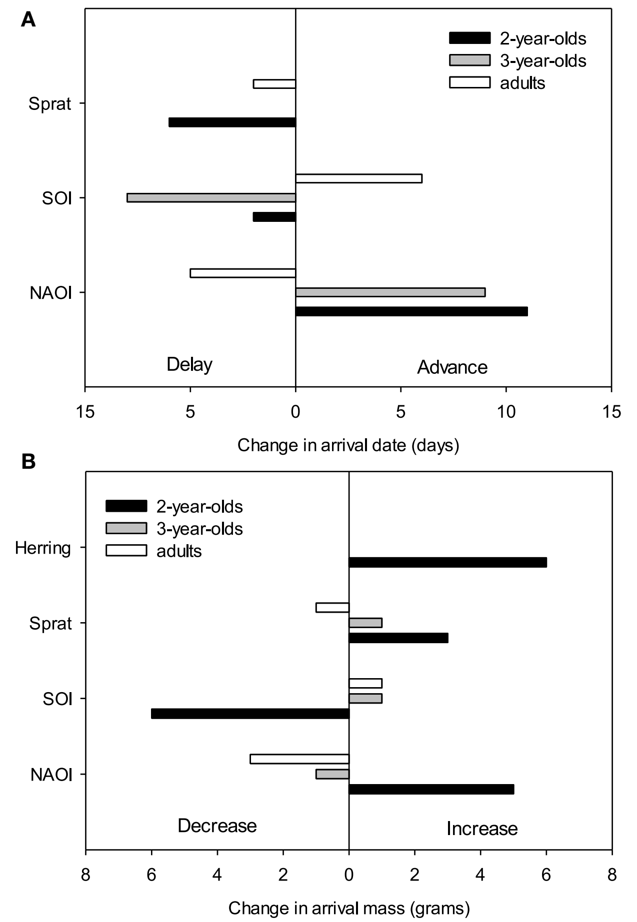

FIGURE 4 | Predicted effects of environmental factors on the change in (A) arrival date (in days, Table 3) and (B) arrival mass (in grams, Table 4) in three age groups (2-year-olds, 3-year-olds and adults) over the observed range of the respective covariates between 1994 and 2012.

The fact that there was no correlated annual fluctuation between age groups and often contrary responses to the same environmental covariates indicates that different age groups experience differing environmental constraints during their annual cycle, which might have a compensatory effect against environmental stochasticity and thereby help maintain population stability. Arrival body mass at the colony was affected by environmental covariates only in the youngest age group on their first spring migration. These 2-year-olds' arrival mass showed a correlation with winter SOI and spring NAOI and was also related to sprat and herring abundance, indicating effects during the latter part of migration.

Arrival Date and Body Mass

Arrival date advances strongly with age (Dittmann and Becker, 2003; Becker et al., 2008a; Zhang et al., 2015a) and experience (Ludwigs and Becker, 2002), as does arrival mass, to a certain extent (Limmer and Becker, 2007). On average, 2-year-olds arrive between 40 and 60 days after adult birds (Becker et al., 2008a; Arnaud et al., 2013). They either need far more time for their first spring migration than adults and 3-year-olds, or they depart from the wintering area later, or both (Sergio et al., 2014). Since 2-year-old individuals are mostly prospectors and very rarely breed they might not be under great pressure to arrive early in the season (Ludwigs and Becker, 2002; Szostek and Becker, 2012). Similarly, 3-year-old terns arrive on average between 20 and 40 days later than adults. Although they gained some experience from their first migration they still either depart later or need more time to migrate than experienced adults, or both (cf. Sergio et al., 2014). Contrary to some earlier studies (Dittmann and Becker, 2003; Becker et al., 2008a) we found that females arrived marginally earlier than males (1–2 days). Males arrived marginally heavier (1–3 g) than females, which is consistent with findings that males are generally slightly larger than females (e.g., Nisbet et al., 2007). Although differences were small, they appeared consistently and were significant in all models.

With regard to inter-annual variation and long-term trends, results for arrival date and body mass were very coherent. Although a distinct age-distribution was apparent in arrival date and to a lesser extent in arrival mass, and variation was strong both within and between years, there was no long-term trend in either variable (**Figures 2**, **3**, also cf. Ezard et al., 2007). In other bird species in the northern hemisphere, however, an advancement in arrival or laying date due to climate change was apparent (e.g., Hüppop and Hüppop, 2003; Crick, 2004; Visser and Both, 2005; Parmesan, 2006), including an advancement of breeding date in relation to spring temperature and NAOI in the Arctic tern *Sterna paradisaea* (Møller et al., 2006). In British terns (Arctic, common, and sandwich *Sterna sandvicensis*) an advancement in arrival and laying date was found (Wanless et al., 2009), while in the common terns of the study colony, laying date was unexpectedly found to become delayed over time (Ezard et al., 2007). It is possible that arrival and laying date are influenced by different environmental factors or that cues affecting departure from the wintering area are not linked with those in the breeding area (Both and Visser, 2001; Végvári et al., 2010). This is consistent with the lack of correlations we found between environmental covariates in the wintering and breeding area. Prey fish become increasingly available in the breeding area around early April when water temperatures start to increase, triggering the migration of juvenile herring and sprat into the coastal waters of the Wadden Sea (Dänhardt and Becker, 2014). If an increase in temperatures resulted in earlier herring and sprat availability, it would be an advantage for adult terns to advance their arrival and thereby extend their breeding season.

Arrival date and mass were not correlated between age groups, so there were no "bad" or "good" years over the entire age spectrum, only for the distinct age groups. This indicates that different intrinsic or extrinsic factors might be affecting each age group or that the same factor might change over time within the year and thus might affect the age groups differently as they migrate at different times. Stronger temporal variation in arrival date of 2- and 3-year-olds indicates stronger susceptibility to environmental factors in these younger age groups (**Table 2**; Favero and Becker, 2006; also for survival: Szostek and Becker, 2012). These age-related differences can be attributed to experience to some extent, but since arrival date is in part a heritable trait and early arrival improves reproductive success, this variation might also represent a target for selection and the lower variability in adults could be due to canalization (Arnaud et al., 2013). Furthermore, variation in plasticity of traits such as arrival date could also be heritable and selected for in interaction with environmental influences (Brommer et al., 2008).

Arrival date and mass were negatively correlated. Generally, the later arriving individuals tend to be the younger ones that find it harder to maintain their body mass in stressful circumstances, such as migration (cf. Dittmann and Becker, 2003; Ezard et al., 2007; Limmer and Becker, 2007). However, arrival mass still decreased with later arrival date when corrected for age group, individual and annual variation. This indicates that an early arrival date is not achieved at a cost to body condition, but is rather an indicator for individual quality (cf. Becker et al., 2008a; Zhang et al., 2015a). In this context, age was not a significant predictor of arrival mass any longer, as this general rule seems to be true for all age groups: Earlier birds are "better" individuals that can maintain a higher body mass.

Environmental Covariates: Effects on Arrival Date

There were strong age-related differences in the relationships between environmental covariates and arrival date. Generally, 2-year-olds and adults often reacted in opposite ways to the same environmental covariate, whereas 3-year-olds responded alternately with their older or younger counterparts or showed no response (**Figure 4A**). Considering the different time periods that the age groups migrate in and the differing pressures they are under, this is not unexpected.

In the breeding area, sprat, but not herring, was associated with a delay of 2-year-old arrival date by 6 days over the entire measured range of sprat abundance. Sprat in the North Sea (= breeding area) was available to terns on the latter part of their migratory journey, so high abundance and availability of their main prey items might cause them to spend more time foraging during and after migration before visiting the breeding colony, resulting in a later arrival. As 2-year-olds might not be under strong pressure to breed, such a behavioral strategy might give them the chance to improve their body condition after their first spring migration. Furthermore, an effect of NAOI on the advancement of arrival date by 11 days over the total observed range of NAOI was also apparent in 2-year-olds (see **Figure 4A**, **Table 3**). During low NAOI years strong wind systems can be suppressed (Hurrell et al., 2003), which may help inexperienced birds migrate faster. Additionally, the NAOI influences food abundance (Attrill and Power, 2002), although the negative relationship indicates an earlier arrival under "worse" feeding conditions. This is consistent with the finding that 2-year-old common terns delay arrival in response to higher sprat abundance. In combination, these findings suggest that young birds engage in a trade-off: when feeding conditions are favorable, they accept a later arrival in exchange for an improved body condition, while they might speed up their migration when food availability is poor. Spring arrival date has been linked to the NAOI in several passerine and non-passerine migrants (e.g., Hüppop and Hüppop, 2003; Žalakevičius et al., 2009), as has timing of breeding in black-legged kittiwake (*Rissa tridactyla*) and common guillemot (*Uria aalge*: Frederiksen et al., 2004). The relationship with SOI was very slight in 2-year-olds: it resulted in a 2 day delay with increasing SOI.

The relationship of 3-year-old birds' arrival date with environmental covariates was similar to that of 2-year-olds in direction, but the relative impact was mostly different. Three-year-olds showed an advancement of arrival with rising NAOI of 9 days, which was similar to their younger conspecifics and might well be due to similar underlying mechanisms. Their response to winter SOI, however, was much stronger, resulting in an 8 day delay over the total measured range of this global climate index. The strong delay of arrival date with winter SOI indicates that environmental conditions in the wintering area were an important driver of a fast and/or early migration in terms of weather conditions and possibly food abundance. This would have a lasting carry-over effect on the breeding career of a 3-year-old pre-breeder, as an early arrival improves the chances for a first-time breeding attempt (Ludwigs and Becker, 2002; Becker et al., 2008a). Contrary to younger birds, there was no relationship with sprat abundance, which could be explained by the older birds' improved foraging efficiency, or by the different time of arrival, when other food sources might be more relevant.

In adult birds, relationships between arrival date and environmental covariates were mostly contrary to those in the younger age groups. Generally, we would expect the older and more experienced birds to be less dependent on environmental conditions than their younger and less experienced conspecifics, as they showed far less inter-annual variability in arrival date and body mass, as well as in their vital rates (Ezard et al., 2006; Szostek and Becker, 2012). However, since the sample size was very high for this group it is likely that even correlations with small effect size became significant in these analyses. In any case, the covariates with the strongest effect were related to the global climate indices: Adult birds advanced their arrival date by up to 6 days over the entire measured range of winter SOI in accordance with the tendencies found by Favero and Becker (2006). Similarly, relationships between arrival date and SOI have been reported from the southern hemisphere, although there they appeared in conjunction with a delay in arrival and laying date (Barbraud and Weimerskirch, 2006), or in concurrence with El Niño events (Kalmbach et al., 2001). A tropical roseate tern *Sterna dougallii* population showed delayed breeding in years of high multivariate ENSO, a climate index related to the SOI, but the effects were also related to local sea surface temperature (Ramos et al., 2002). A significant correlation was also found in adult birds with spring NAOI, which resulted in a delay of up to 5 days, indicating an earlier arrival when weather conditions (Hurrell et al., 2003) and food abundance (Attrill and Power, 2002) are favorable. A very slight delay of 2 days could be attributed to sprat abundance in the breeding area, although such a small delay may not have strong implications for reproductive success or survival. Although arrival date was shown to be delayed in 2-year-old and adult terns in response to prey fish abundance, it is possible that despite a slightly later arrival date, the increase in body condition resulting from increased foraging success might advance laying, as shown in common terns by Wendeln (1997) and Dänhardt and Becker (2014). Diamond and Devlin (2003) found an impact of herring stock in the breeding area on laying dates of puffins *Fratercula arctica*, yet not on Arctic terns *Sterna paradisaea* or common terns in the same habitat.

That birds of different age groups migrate at different times of the year and are under varying amounts of pressure to arrive in the breeding area early is not a new idea, but we have shown here that the three age groups are affected differently by environmental constraints in their year-round habitats. While 2-year-olds, as inexperienced hunters (Dunn, 1972 for sandwich terns), are more strongly dependent on food abundance and weather conditions during migration, 3-year-olds show carry-over effects from the wintering habitat and adults seem less strongly affected overall. There is no clear season where environmental conditions appear most limiting to arrival date, this trait seems to be sensitive to conditions during migration as well as being subject to carry-over effects from the wintering area.

Environmental Covariates: Effects on Arrival Mass

The findings concerning arrival mass were mostly consistent with those relating to arrival date. However, differences between age groups were even more strongly pronounced. While 2-year-olds were strongly affected by multiple factors, the older age groups of 3-year-old and adult birds showed no strong response in arrival mass to any environmental covariate (**Figure 4B**). There was a slight decrease in adult arrival mass in relation to NAOI, but it resulted in only a 3 g change over the entire NAOI range, which birds would be able to recover from quickly during the precourtship period (Frank and Becker, 1992; Wendeln and Becker, 1996).

As 2-year-olds are likely to be less proficient foragers (Dunn, 1972) and are also inexperienced as migrants, it is not unexpected that they would show the greatest response in their body condition on arrival. We found a strong increase in response to higher herring abundance in the breeding area of 6 g and a weak increase of 3 g in response to higher sprat abundance. Since clupeoids and especially herring are among the most common and nutritious food sources for common terns in the breeding area (Massias and Becker, 1990; Frank, 1992; Wendeln, 1997), it makes sense that body mass would vary according to the abundance of herring (Wendeln and Becker, 1996). Since herring is available on the last leg of the migratory journey, these results indicate that terns probably feed continuously during migration or that their body condition quickly adapts to the wealth or dearth of food in the breeding area upon arrival (for daily mass changes see Frank and Becker, 1992). In addition, there was an equally strong relationship with the climate indices, which resulted in an increase of 5 g in relation to spring NAOI. This is most likely due to the NAOI affecting prey, other than herring and sprat, causing better feeding conditions during periods of low NAOI (Attrill and Power, 2002). Furthermore, we found a 6 g decrease in arrival mass in response to winter SOI. The most limiting conditions for arrival mass seem to appear during the migration period and the early breeding season, and yet arrival mass is also subject to strong carry-over effects from the wintering area in the youngest age group of common terns.

Concluding Remarks

Our findings underline the importance of age in the study of phenological traits including those related to migration (cf. Ezard et al., 2007). The strong advancement of arrival with age combined with an improvement of body condition reflects the process of canalization in the timing of arrival along with a reduction in variance with age (Arnaud et al., 2013). Yet, even when accounting for age, no long-term trends across the 19 years of the study were evident in either trait. For arrival date in spring this result is in contrast with many other, mainly passerine, bird species, which advanced their arrival over the past decades (refs see above).

Instead, we found effects of environmental factors on arrival date and mass, operating both during the wintering season and spring migration. Most interesting here was our finding that age groups responded very differently to variation in environmental conditions. Still, the relationship between arrival date and environmental factors remains a complicated one. As a long-distance migrant, the common tern is dependent on conditions in two distinct habitats connected by the migration route (**Figure 1**). Relevant environmental factors are not necessarily synchronous (we found them not to be correlated) and might affect the terns in opposing ways in their wintering area and on migration, or their effects might cancel each other out.

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Supplementary Material

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fevo.2015.00042/abstract

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Climate and changing winter distribution of alcids in the Northwest Atlantic

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Population level impacts upon seabirds from changing climate are increasingly evident, and include effects on phenology, migration, dispersal, annual survivorship, and reproduction. Most population data on seabirds derive from nesting colonies; documented climate impacts on winter ecology are scarce. We studied interannual variability in winter abundance of six species of alcids (Charadriiformes, Alcidae) from a 58-year time series of data collected in Massachusetts 1954–2011. We used counts of birds taken during fall and winter from coastal vantage points. Counts were made by amateur birders, but coverage was consistent in timing and location. We found significant association between winter abundance of all six species of alcids and climate, indexed by North Atlantic Oscillation (NAO), at two temporal scales: (1) significant linear trends at the 58-year scale of the time series; and (2) shorter term fluctuations corresponding to the 5–8 year periodicity of NAO. Thus, variation in winter abundance of all six species of alcids was significantly related to the combined short-term and longer-term components of variation in NAO. Two low-Arctic species (Atlantic Puffin and Black Guillemot) peaked during NAO positive years, while two high Arctic species (Dovekie and Thick-billed Murre) peaked during NAO negative years. For Common Murres and Razorbills, southward shifts in winter distribution have been accompanied by southward expansion of breeding range, and increase within the core of the range. The proximate mechanism governing these changes is unclear, but, as for most other species of seabirds whose distributions have changed with climate, seems likely to be through their prey.

Keywords: alcid, climate change, NAO, multiscale, Northwest Atlantic, Massachusetts

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Introduction

Fluctuating oceanic climate impacts population size (Montevecchi and Myers, 1997; Thompson and Ollason, 2001), survivorship (Sandvik et al., 2005), fecundity (Guinet et al., 1998; Durant et al., 2003, 2005; Wanless et al., 2007), phenology (Aebischer et al., 1990; Gjerdrum et al., 2003; Frederiksen et al., 2004), and both summer and winter distribution (Veit et al., 1997; Manne, 2013) of seabirds. Impacts of climate shifts on seabirds occur at multiple temporal scales, that can be loosely grouped into "short-term" (<1 year: Hunt et al., 1992; Veit et al., 1996), "medium term" (5–10 years) corresponding to fluctuations indexed by El Niño-Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO), and long-term trends (>10 years) that may also reflect longer term fluctuations that our 50 year time series is less likely to resolve (Veit and Montevecchi, 2006).

Since seabirds in general have long lifespans and produce relatively few young per year, they are adapted to tolerate short-term environmental disturbances (Veit and Montevecchi, 2006) and populations have recovered from such short-term catastrophes as El Niño events (Schreiber, 2002). Population responses to persistent, long-term changes are less well-documented but climate change on the scale of decades has caused substantial changes in the range and distribution of seabirds (Montevecchi and Myers, 1997; Veit and Montevecchi, 2006; Gaston and Woo, 2008; Nisbet et al., 2013).

Unambiguous, if complex, changes have occurred in the physical and biological characteristics of the North Atlantic Ocean during this century (Stenseth and Mysterud, 2002; Hurrell and Dickson, 2004; Stenseth et al., 2004), and these changes have had substantial biological impacts, even though ascribing such impacts unambiguously to climate is daunting (Hemery et al., 2008; Overholtz and Link, 2009). Difficult to disentangle from climate-induced impacts on seabirds are those resulting from changes in fish stocks due to commercial fisheries. For example, the spectacular collapse of northwestern Atlantic Cod stocks in the early 1990s, and the decline of the herring fishery in the late 1960s and early 1970s were almost certainly primarily the result of overfishing (Fogarty and Murawski, 1998). The collapse of these stocks has had broad-reaching impacts on other components of the ecosystem, including seabirds (Fogarty and Murawski, 1998; Montevecchi and Stenhouse, 2002). Other changes are not so easily attributed to any one particular cause. For example, the enormous increase of sand lance (*Ammodytes* spp.) during the 1970s in the Northwest Atlantic (Sherman et al., 1981) may have resulted from the disappearance of herring and other predators due to overfishing, but other factors may have been important as well. Many seabirds benefitted from the sand lance increase (Veit and Petersen, 1993; Nisbet et al., 2013), but whether any of these changes has a link to climate forcing is unknown, and it is therefore difficult to disentangle whether impacts on seabirds derive from climate, fisheries, a combination of the two, or some other factor.

Much of the previous work on this subject has focused on the northeast Atlantic, where changing climate is having a measurable effect upon seabirds, and it is thus highly likely that such effects have occurred in the Northwest Atlantic as well. There are, however, interesting differences in the direction of climate-related effects between the two sides of the Atlantic. For example abundance of the widespread copepod *Calanus finmarchicus* is negatively correlated with NAO in the eastern, but positively correlated with NAO in the western Atlantic (Conversi et al., 2001; Drinkwater et al., 2003), as is also SST and population changes in guillemots (Irons et al., 2008). There is no question that climate-related changes to the pelagic system are occurring, but how these may have impacted seabird abundance off the North American east coast is unknown.

NAO is a multivariate physical index used to characterize the overall climatological state of the North Atlantic (Hurrell and Dickson, 2004). The NAO is designed to reflect the distribution of sea level atmospheric pressure, but its values correlate strongly with predominant flows of winds and surface currents. The NAO has changed from a pattern of negative values during ~1930–1975 to one of predominantly positive values from 1975 to 2000 (Hurrell and Dickson, 2004; Irons et al., 2008). The more recent period of positive values reflects colder conditions in the Northwest Atlantic; conversely, negative NAO years are associated with warmer waters. Documented and statistically significant shifts in intensity and direction of NAO have occurred in recent years and, as shown below, these shifts have clearly impacted the biology of the North Atlantic (Hurrell and Dickson, 2004).

At a decadal scale, southward shifts in alcid abundance seem to match shifts in NAO (**Figure 1**). Veit and Guris (2008) found statistical links between Razorbill (*Alca torda*) and Dovekie (*Alle alle*) abundance and NAO in New England waters. Razorbills have been increasing steadily since the 1980s, with peak abundance occurring in NAO positive years, while Dovekies have increased dramatically since about 2005, after a general absence since about 1975. Abundance of Dovekies in New England has been more erratic, but also statistically related to NAO, with maximum numbers occurring in NAO-negative years (a pattern strongly supported by maximum abundance in 2010–2011) and thus opposite to the pattern shown by Razorbills. The proximate mechanism for the link between seabirds and NAO remains unclear, but the majority of seabird-climate links has proven to be indirect, and based on changes in seabird prey (Frederiksen et al., 2004; Durant et al., 2005).

Alcid Winter Range

Alcids are notoriously erratic in their dispersal southwards during winter (Nettleship and Birkhead, 1985; Gaston and Jones, 1998) and some species, especially Dovekies, are prone to southward irruptions, very likely in response to abrupt changes in prey availability (Gaston and Jones, 1998). Despite such variability during winter, long-term changes in abundance off the U.S. East Coast are apparent (Veit and Guris, 2008; Nisbet et al., 2013). As recent major shifts in oceanographic climate have also been described for the North Atlantic (Hurrell and Dickson, 2004; Regular et al., 2010), it behooves us to ask whether shifts in winter alcid distribution are related to changes in oceanographic climate. Innovations of this study include an extensive uninterrupted, 58 year time series on seabird abundance from Massachusetts and the fact that it documents the winter, non-breeding distribution of these birds. We therefore hypothesize that fluctuations in oceanic climate impact the variability of winter abundance and distribution of seabirds.

Methods

Massachusetts Time Series

In Massachusetts there are a number of coastal vantage points from which seabirds have been counted annually since the 1930s. The level of effort has been reasonably constant over the period 1954-present; while the number of observers in the field has increased, the number of sites has not, so that the number of hours devoted to counting is unlikely to have changed. Furthermore, both increases and decreases in abundance have occurred during the period we have analyzed, so changes in abundance cannot be simply the consequence of increased effort. Thus, we

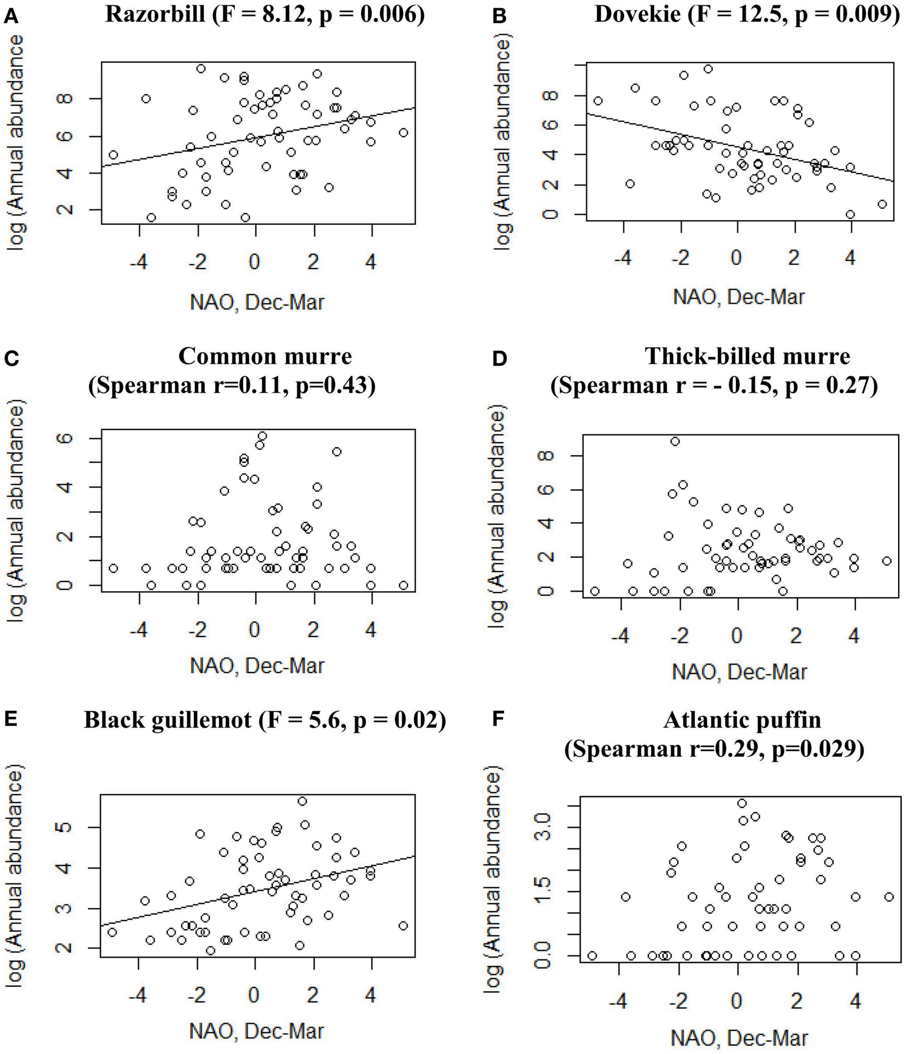

FIGURE 1 | Winter abundance vs. NAO for six alcid species in Massachusetts.

used this 58 year time series of bird abundance to ask whether changes over that time period in alcid abundance are at least in part related to changes in oceanic climate.

We extracted data on alcids from the publications Records of New England Birds (1954–1968), Bird Observer of Eastern Massachusetts (1972–1986), Bird Observer (1987-present), and North American Birds and its predecessors (1954-present). Gaps for the period 1969–1971 were filled by records maintained at the Massachusetts Audubon Society by Ruth P. Emery (unpublished database). Data in these publications were published as monthly or bimonthly summaries.

The data used in the analyses were estimates of maximum number present in any given winter. We considered that all counts on outer Cape Cod (~50 km long, mostly censused from Provincetown, **Figure 2**) could possibly involve the same birds, so we conservatively used the maximum number reported during a winter anywhere on outer Cape Cod as the maximum for that year. On the other hand, we assumed that birds counted at Cape Ann or Nantucket were separate from birds counted on outer Cape Cod, and tallied separately, for each winter, maxima from Cape Ann, Cape Cod, and Nantucket. Although the bird abundance data is limited in spatial scope, because of the enormous spatial scope of seabird foraging ranges, samples from a limited area are representative of the ocean basin as a whole (Veit et al., 1997). The species in this analysis collectively cover 35° of latitude, from Northern Greenland to Maine during the nesting season and an even larger area during winter. Thus, this dataset from Massachusetts is not only important for its length; it also samples a substantial portion of the North Atlantic avifauna.

We used NAO index values averaged over December-March for the years in which we extracted data on birds. So birds recorded in November 2000–March 2001 were related to the NAO index for December 2000–March 2001 (Hurrell and Dickson, 2004, http://www.cgd.ucar.edu/cas/jhurrell/indices.html).

FIGURE 2 | Map of the study area showing the three main census locations: Cape Ann, Provincetown (outer Cape Cod), and Nantucket.

We log transformed all bird abundance data. For four species [Razorbill, Dovekie, Thick-billed Murre (*Uria lomvia*), and Black Guillemot (*Cepphus grylle*)] the transformed data did not differ significantly from normal (Kolmogorov–Smirnoff test, $p > 0.1$), and we used cross-correlation to identify the temporal scale for which correlation between bird abundance and NAO was highest. Maximum correlation was found at a lag of 0 years for all species except Razorbill for which NAO in the previous year (lagged NAO) gave a better fit (Razorbill numbers following NAO). For these four species we used linear regression to relate abundance in Massachusetts to NAO index in the same winter. For the other two species [Atlantic Puffin (*Fratercula arctica*), and Common Murre (*Uria aalge*)] the log-transformed data differed significantly ($p < 0.05$) from the normal distribution so we used Spearman rank correlation coefficients to test for a correlation between abundance and NAO.

To disentangle the possible population temporal autocorrelation from direct effects of NAO on winter abundance, we compared eight regression models for each species: a model with only a year term (assuming a Poisson distribution vs. a negative binomial distribution), models having a single NAO term (Poisson vs. negative binomial), models having both year and NAO (Poisson vs. negative binomial), and models with year, NAO and a lag term for the population size the previous year (Poisson vs. negative binomial). Among those eight models, the model with the lower Akaike Information Criterion (AIC), but only where the lower AIC differed from the next-higher AIC by more than two units (Burnham and Anderson, 2002), was a better fit to the data for that species. If the lower AIC occurred for a model incorporating NAO, then we concluded that even after time series and lagged population effects had been accounted for, NAO acted as a structuring effect for that species' abundance. For ease of visualization, we show graphs of the log-transformed responses (species abundances). All analyses were conducted using R (R Core Development Team, 2012).

Results

Five species (Razorbill, Common Murre, Thick-billed Murre, Black Guillemot, and Atlantic Puffin) increased significantly over the 58-year period ($p < 0.05$), and Dovekies decreased significantly over the same period ($p = 0.019$, **Figure 3**). A significant increasing linear trend is evident for NAO (**Figure 3G**). Thus, all six species of alcids were significantly related to a 58-year trend in NAO (**Figure 3**). At shorter timescales, five species were significantly correlated with NAO as revealed by the modeling (**Table 1**). For four of six species analyzed, the best model was one that included effects of year, NAO and lagged intraspecific abundance (**Table 1**); a fifth species' best model included only NAO, and the sixth species (Atlantic Puffin) was best modeled by year alone. Thus, the importance of both a long-term (58 year) trend and shorter term (5–8 year) oscillations in NAO significantly impacted winter abundance of five out of six alcid species in New England. For Razorbills, the best model was that which included year, lagged NAO and lagged abundance of Razorbills. In all cases, the chosen model was that assuming the negative binomial distribution; the AIC-values for the negative binomial models were all much lower than those for the Poisson models.

Table 1 also shows the maximum likelihood pseudo-R^2-values to give an idea of how much variation in alcid abundance is explained by the best models. Atlantic Puffin was the least well-modeled, with a pseudo-R^2-value of 0.15, while Razorbill showed the highest pseudo-R^2, of 0.88.

Residual analyses showed no clear pattern in the residuals for any of the best models. Since the NAO index itself has a positive trend over the timespan we studied (1954–2012, Hurrell and Dickson, 2004), our interpretation is that there are at least two temporal scales over which variation in ocean climate impact winter abundance of alcids off Massachusetts. Put another way, our model shows that variation in winter abundance of alcids off Massachusetts was significantly related to the combined shorter-term and longer-term components of variation in NAO.

Black Guillemots and Razorbills occurred in high abundance with *positive* NAO index values, whereas Dovekies and Thick-billed Murres occurred in high abundance with *negative* NAO. Thus, peak numbers of high-arctic Dovekies and Thick-billed Murres tended to move south to Massachusetts in strongly negative-NAO winters. Common Murre and Atlantic Puffin show small but only borderline significant relationships to NAO on an annual scale. Therefore, response by these birds to NAO varied with the temporal scale at which they were analyzed. The differing response to NAO shown by the different species is reflected in the correlation of abundance among species: The abundances of all species other than Dovekie were positively

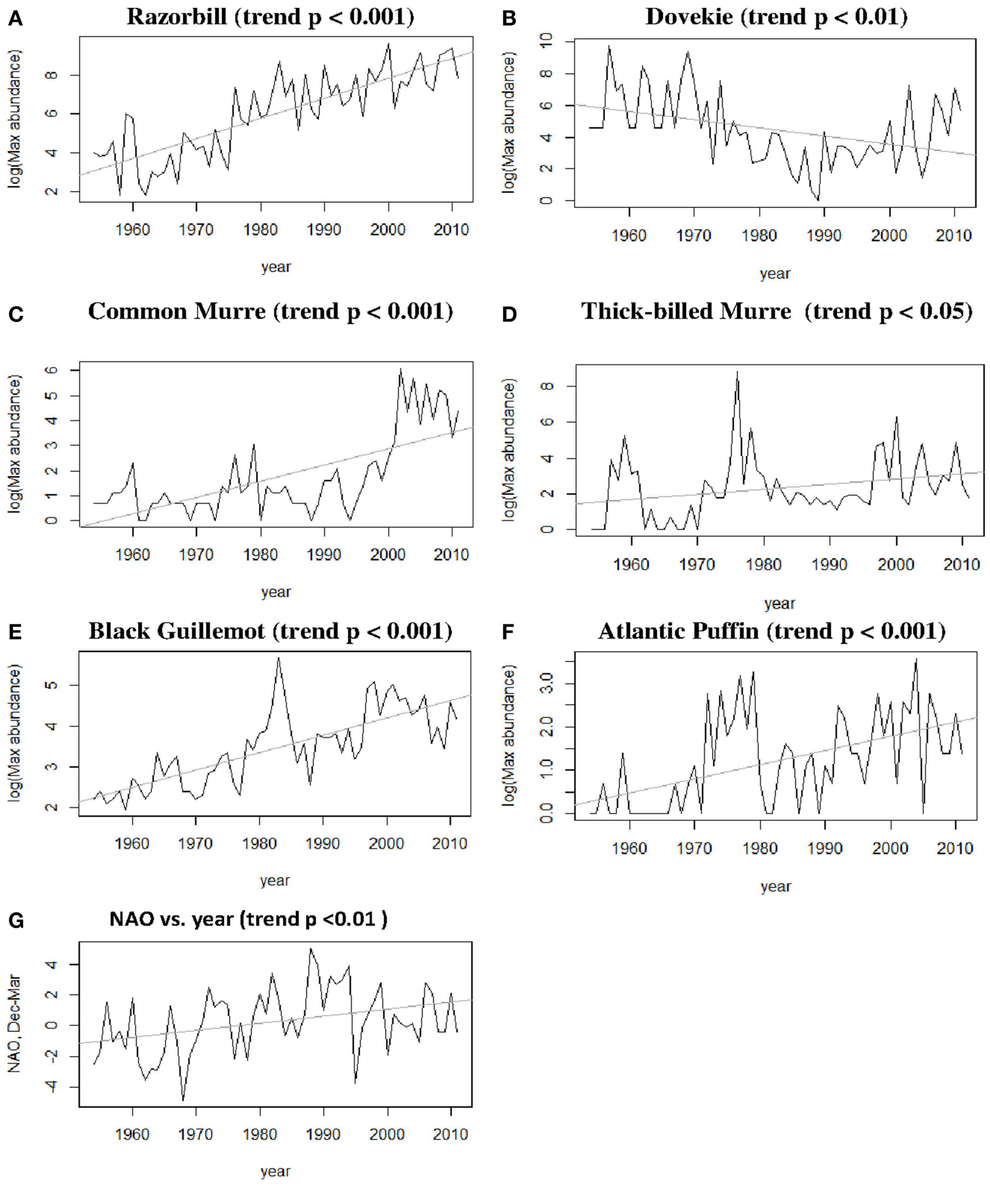

FIGURE 3 | (A–F) Winter abundance (raw time series) of alcids in Massachusetts over the period 1955–2012; **(G)** NAO over time, showing both trend and periodic fluctuation.

correlated with one another, and that of Dovekie was negatively correlated with those of the other five species (**Table 2**).

Discussion

Winter alcid abundance depends significantly on NAO, which in turn shows both a long-term (~50 year) trend and shorter term periodicity (**Figure 3**). Thus, our analysis supports previous suggestions that climate acts upon seabirds at more than one temporal scale (Schreiber, 2002; Jenouvrier et al., 2005; Veit and Montevecchi, 2006; Irons et al., 2008). Here, we found that four species vary with shorter term NAO fluctuations (**Table 1**), and all six species vary with the longer-term NAO trend (**Figure 3**).

The data we have analyzed are on winter abundance. Changes in abundance could reflect either distributional shifts, changes in population size, or a combination of the two. Razorbills, Common Murres, Atlantic Puffins, and perhaps Black Guillemots, are clearly increasing in abundance within their breeding ranges and expanding southward into our study area (Chapdelaine et al., 2001; Bond and Diamond, 2006; Regular et al., 2010). The increase of Atlantic Puffins in our study area has been hastened by reintroduction of birds from Canada to breeding islands in the Gulf of Maine (Kress and Nettleship, 1988). Whatever the proximate cause of increased abundance off Massachusetts in winter, the ultimate cause in most cases seems linked to variation in oceanographic climate.

TABLE 1 | Results of model selection for six alcid species wintering population numbers; sign of relationship with predictors given in best model.

Response (Abundance of….)	**Distribution**	**Predictor 1 (significance)**	**Predictor 2 (significance)**	**Predictor 3 (significance)**	**AIC**	**Maximum likelihood pseudo-R^2 (best model only)**
Black Guillemot	Poisson	Year ($p < 0.001$)			1805	
		Year ($p < 0.001$)	NAO ($p < 0.001$)		1777	
		NAO ($p < 0.001$)			2538	
		+Year ($p < 0.001$)	+NAO ($p < 0.001$)	+BG$_{t-1}$ ($p < 0.001$)	1476	
	Negative binomial	Year ($p < 0.001$)			527	
		Year ($p > 0.001$)	NAO		527	
		NAO ($p < 0.01$)			563	
		+Year ($p < 0.001$)	**+NAO ($p < 0.05$)**	**+BG$_{t-1}$ ($p < 0.001$)**	**508**	**0.68**
Common Murre	Poisson	Year ($p < 0.001$)			2589	
		Year ($p < 0.001$)	NAO ($p < 0.001$)		2560	
		NAO ($p < 0.001$)			5929	
		+Year ($p < 0.001$)	−NAO ($p < 0.001$)	−COMU$_{t-1}$ ($p < 0.001$)	2514	
	Negative bionomial	Year ($p < 0.001$)			380	
		Year ($p < 0.001$)	NAO (ns)		381	
		NAO (ns)			433	
		+Year ($p < 0.001$)	**−NAO (ns)**	**+COMU$_{t-1}$ (ns)**	**379**	**0.64**
Dovekie	Poisson	Year ($p < 0.001$)			139,081	
		Year ($p < 0.001$)	NAO ($p < 0.001$)		133,047	
		NAO ($p < 0.001$)			163,429	
		−Year ($p < 0.001$)	−NAO ($p < 0.001$)	−DOVE$_{t-1}$ ($p < 0.001$)	124,174	
	Negative binomial	Year ($p < 0.001$)			787	
		Year ($p < 0.05$)	NAO ($p < 0.01$)		784	
		NAO ($p < 0.001$)			787	
		−Year ($p < 0.05$)	**−NAO ($p < 0.01$)**	**+DOVE$_{t-1}$ (ns)**	**772**	**0.48**
Atlantic Puffin	Poisson	Year ($p < 0.001$)			535	
		+Year ($p < 0.001$)	+NAO ($p < 0.05$)		532	
		NAO ($p < 0.001$)			585	
		Year ($p < 0.001$)	NAO ($p < 0.05$)	PUFF$_{t-1}$ (ns)	531	
	Negative binomial	**+Year ($p < 0.001$)**			**298**	**0.15**
		Year ($p < 0.01$)	NAO (ns)		298	
		NAO ($p < 0.05$)			304	
		Year ($p < 0.01$)	NAO (ns)	PUFF$_{t-1}$ (ns)	298	
Razorbill	Poisson	Year ($p < 0.001$)			91,866	
		Year ($p < 0.001$)	NAO ($p < 0.001$)		84,712	
		NAO$_{t-1}$ ($p < 0.001$)			191,950	
		+Year ($p < 0.001$)	−NAO ($p < 0.001$)	−RAZO$_{t-1}$ ($p < 0.001$)	71,114	
		+Year ($p < 0.001$)	+NAO$_{t-1}$ ($p < 0.001$)	+RAZO$_{t-1}$ ($p < 0.001$)	75,389	
	Negative binomial	Year ($p < 0.001$)			898	
		Year ($p < 0.001$)	NAO (ns)		900	
		NAO$_{t-1}$ ($p < 0.001$)			936	
		Year ($p < 0.001$)	NAO (ns)	RAZO$_{t-1}$ (ns)	850	
		+Year ($p < 0.001$)	**+NAO$_{t-1}$ ($p < 0.05$)**	-**RAZO$_{t-1}$ (ns)**	**845**	**0.88**
Thick-billed Murre	Poisson	Year ($p < 0.001$)			52,700	
		Year ($p < 0.001$)	NAO ($p < 0.001$)		44,152	
		NAO ($p < 0.001$)			44,451	
		+Year ($p < 0.001$)	−NAO ($p < 0.001$)	−TBMU$_{t-1}$ ($p < 0.001$)	43,526	
	Negative binomial	Year ($p < 0.1$)			536	
		Year (ns)	NAO ($p < 0.001$)		513	
		−NAO ($p < 0.001$)			**512**	**0.36**
		+Year (ns)	−NAO ($p < 0.001$)	−TBMU$_{t-1}$ (ns)	511	

Boldface indicates the best model as judged by either lowest AIC value (in cases where AIC was lower than next-lowest by more than 2 units) or by least complex model (in cases where models have low and tied or near-tied AIC values, e.g., Atlantic Puffin).

TABLE 2 | Spearman rank correlation coefficients of abundance among species.

	Razorbill	Dovekie	Common Murre	Thick-billed Murre	Black Guillemot	Atlantic Puffin
Razorbill	1.0	**−0.42**	**0.56**	**0.41**	**0.7**	**0.47**
Dovekie	**−0.42**	1.0	−0.09	−0.01	**−0.45**	−0.11
Common Murre	**0.56**	−0.09	1.0	**0.34**	**0.53**	**0.51**
Thick-billed Murre	**0.41**	−0.01	**0.34**	1.0	0.23	**0.47**
Black Guillemot	**0.7**	**−0.45**	**0.53**	0.23	1.0	**0.37**
Atlantic Puffin	**0.47**	−0.11	**0.51**	**0.47**	**0.37**	1.0

Boldface values are significant at $p < 0.05$.

Shifts in at-sea distribution of seabirds have previously been linked to changing oceanic climate (Veit et al., 1996, 1997; Hyrenbach and Veit, 2003; Péron et al., 2010). The presumption in these studies is that ocean temperature is an index of productivity and advection; consequently, warmer temperatures lead to lowered primary productivity, and thus less secondary productivity and food for seabirds. We postulate that the mechanism underlying the changes in abundance we have described is change in abundance or distribution of seabird prey, which in turn responds to changing oceanic climate, as has been concluded in a number of other recent studies (Frederiksen et al., 2004; Irons et al., 2008; Sydeman et al., 2013) including changes in seabird distribution (Veit et al., 1996, 1997; Gaston and Woo, 2008; Péron et al., 2010).

Razorbills feed on a variety of schooling fishes such as herring and sand lance (Nettleship and Birkhead, 1985). There have been negatively correlated fluctuations in the populations of Atlantic Herring (*Clupea harengus*) and American Sand Lance (*Ammodytes americanus*) over the period 1970-present (Sherman et al., 1981; Overholtz and Link, 2007, 2009), one suggestion being these two plankton-feeding fishes replace one another as one gets fished out. A major increase in sand lance in the late 1970s was accompanied by very large numbers of seabirds, including Razorbills, feeding upon them at the time (Veit and Petersen, 1993). Increased abundance of Razorbills, Common Murres, Thick-billed Murres, Black Guillemots, and Atlantic Puffins in Massachusetts occurred during the 1970s (**Figure 3**) at a time when a dramatic increase in sand lance was documented in the area (Sherman et al., 1981; Veit and Petersen, 1993). Gaston and Woo (2008) show how Razorbills have expanded their breeding range into NW Canada following northward expansion of Capelin (*Mallotus vallosus*) and sand lance (*Ammodytes,* spp.).

Both species of Murres and Atlantic Puffins, similarly to Razorbills, eat schooling pelagic fishes including sand lance (Gaston and Hipfner, 2000; Ainley et al., 2002; Lowther et al., 2002; Bond and Diamond, 2006), and, though we lack dietary data from these species in our study area, it seems reasonable that part of their recent increases reflects increasing sandlance abundance. Black Guillemots also eat fish, including sand lance, but they feed in much more inshore waters than any of the other five species and therefore also take a variety of benthic species (Butler and Buckley, 2002). Dovekies are planktivorous (Montevecchi, 2002) and in this study region often focus their foraging over mid shelf fronts where they aggregate over patches of copepods and amphipods (Veit and Guris, 2008).

Another possible explanation for changes in population numbers is as a result of changes in fishery operations. Large numbers of alcids, especially Common Murres, are killed as by-catch in gill nets (Montevecchi, 2002). A gill net fishery for Atlantic Cod (*Gadus morhua*) and other groundfish in and around Newfoundland collapsed in 1992 due to the disappearance of cod, and a corresponding increase in the Common Murre population of Newfoundland has been at least partly attributed to this factor (Regular et al., 2010). In the Massachusetts data, there is a strong increase in Common Murre abundance at about this same time (**Figure 3**), but there is also a parallel increase in Dovekie abundance that seems unlikely to be related to reduced mortality in gill nets. From the Massachusetts data considered here, the increase in Razorbills seems to be longer term than the increase in Common Murres, and there is little if any apparent acceleration in the early 1990s. Thus, although the closing of the Newfoundland cod fishery almost certainly helped alcid numbers, there are other processes at work to explain changes in numbers of both Dovekies and Razorbills. Finally, chronic oil pollution and hunting, especially of Thick-billed Murres, are likely to impact population growth of alcids (Wiese et al., 2004).

Dovekies are planktivorous (Nettleship and Birkhead, 1985; Gaston and Jones, 1998) while the other five species we studied feed mainly on fish (Gaston and Jones, 1998). This suggests response to climatic oscillations at multiple trophic levels; it should be noted that most alcid diet studies are on diet in the breeding season, and little is known of their winter diets. We know that seabird numbers respond both directly to climate (Schreiber, 2002; Nisbet et al., 2013), and directly to prey base numbers, which may reflect an indirect response to climate via the prey base (Durant et al., 2003; Frederiksen et al., 2004). We have found here a strong response of alcids to climate (as measured by NAO) at multiple timescales, and we can speculate knowledgably that this strong response is comprised of a direct and indirect component. This is the first documentation of alcid response to NAO, and gives greater weight to the importance of managing marine bird populations for their continued persistence in the face of continued climate change.

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Supplementary Material

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fevo.2015.00038/abstract

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There is more to climate than the North Atlantic Oscillation: a new perspective from climate dynamics to explain the variability in population growth rates of a long-lived seabird

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Predicting the impact of global climate change on the biosphere has become one of the most important efforts in ecology. Ecosystems worldwide are changing rapidly as a consequence of global warming, yet our understanding of the consequences of these changes on populations is limited. The North Atlantic Oscillation (NAO) has been used as a proxy for "climate" in several ecological studies, but this index may not always explain the patterns of variation in populations examined. Other techniques to study the relationship between ecological time series and climate are therefore needed. A standard method used in climatology is to work with point maps, where point correlation, point regression or other techniques are used to identify hotspots of regions that can explain the variability observed in the time series. These hotspots may be part of a teleconnection, which is an atmospheric mode of variability that affects remote regions around the globe. The NAO is one type of teleconnection, but not all climate variability can be explained through it. In the present study we have used climate-related techniques and analyzed the yearly variation in the population growth of a Common Guillemot *Uria aalge* colony in the Barents Sea area spanning 30 years. We show that the NAO does not explain this variation, but that point analysis can help identify indices that can explain a significant part of it. These indices are related to changes of mean sea level pressure in the Barents Sea via the Pacific—forming a teleconnection-type pattern. The dynamics are as follows: in years when the population growth rate is higher, the patterns observed are that of an anomalous low-pressure system in the Barents Sea. These low-pressure systems are a source of heat transport into the region and they force upwelling mixing in the ocean, thus creating favorable conditions for a more successful survival and breeding of the Common Guillemot.

Keywords: climate, Common Guillemot, North Atlantic Oscillation, statistical methods, population growth rate

Introduction

The past two decades have produced a plethora of ecological studies that hinge on the North Atlantic Oscillation (NAO) as a proxy for "climate" (Sætre et al., 1999; Ottersen et al., 2001; Forchhammer et al., 2002; Stenseth et al., 2003; Durant et al., 2004; Sandvik et al., 2005, 2012; Dippner et al., 2014). This ubiquitous proxy usage may have led to the spread of a misconception of what NAO actually represents in an ecological context. Finding a statistical relationship without fully comprehending the underlying physics hinders the understanding of the climate-ecology interaction (Hallett et al., 2004; Stenseth and Mysterud, 2005). The point sometimes overlooked is that the NAO is just one of a number of modes of climate variability in the Northern Hemisphere (Barry and Carleton, 2001; Stenseth et al., 2003), as highlighted in **Table 1**. Thus, a better understanding of climate dynamics is critical before hinging on a proxy.

The NAO is defined as one of the leading modes of variability in the North Atlantic sector. It is characterized by an anomalous dipole of atmospheric pressure with centers over Iceland and Azores: a positive phase corresponds to a higher than normal subtropical high-pressure system and a deeper than normal low-pressure system called the Icelandic low (Hurrell, 1995; Barry and Carleton, 2001; Hurrell et al., 2003; Bader et al., 2011). The NAO could be considered as a manifestation of changes in the storm distribution: the cumulative effect of the storms and the associated changes in the storm track lead to the NAO signal (Mesquita et al., 2008, 2011). Nevertheless, the NAO is also influenced by other climatic processes, such as sea-ice changes in the Arctic and the Sea of Okhotsk in the North Pacific, and may shift its sign within a season (Bader et al., 2011; Mesquita et al., 2011). Even a single storm may have enough momentum to shift the NAO sign (Rivière and Orlanski, 2007) and the NAO is known to have a variable center of action (Zhang et al., 2008).

Indeed, with so many climatic features, it is no wonder the NAO "has recently become increasingly common to use" (Durant et al., 2004, p. 338). The use of the NAO as a "proxy," without looking for other climatic clues, is implicitly based on the simplifying assumption that NAO is "climate variability." This may, in the worst case scenario, lead to the erroneous conclusion that a certain ecological process is unrelated to climate, only because no relationship with NAO has been found. Furthermore, Sandvik et al. (2012) have shown that the relationship between the NAO and population growth rate of seabirds is highly variable, both within and across species. This alone does not mean that populations that do not co-vary with the NAO are unaffected by climate, however.

Furthermore, when studies use NAO without providing a clear climate dynamics framework behind its effect on ecology, they become pointless (Mysterud et al., 2000). Statistical results need to be supported by physical mechanisms. Finding that there is a relationship with a proxy without providing a physical mechanism for it may even make the validity of the relationship dubious. Correspondingly, Ottersen et al. (2001, p. 9), in an early review of the ecological effects of the NAO, warn against an overuse of a proxy without understanding its full implications: "Unless a mechanistically based explanation is provided, the veracity of any statistical NAO-ecology relationship will thus remain uncertain." Moreover, relying on a specific proxy also makes it harder for ecologists to explain how atmospheric dynamics influence ecology (*cf.* Sydeman et al., 2014).

Thus, the objective of the present study is to illustrate standard statistical methods used in climatology to understand the connection between climate and ecological dynamics. Here, these methods will be applied to the population dynamics of the Common Guillemot *Uria aalge*, a long-lived seabird that breeds on Hornøya, a small island in northern Norway. Instead of starting with a proxy, this study will look one step before that, viz. finding what is affecting the species and where these climatic influences come from. Only afterwards, an appropriate climatic measure (or proxy) will be chosen. Our findings clearly demonstrate that there is more to climate than the NAO that impacts seabird populations.

Materials and Methods

Study Species, Study Area, and Data Collection

The Common Guillemot is a medium-sized (about 1000 g) seabird belonging to the auks (Alcidae). It is a colonial cliff-breeder with a circumpolar distribution in the boreo-low Arctic region. The Common Guillemot lays a single egg, which is incubated for 33 days on average. The chick is fed by both parents for 3 weeks, before it leaves the colony, still flightless, with its father. Birds start to breed when they are 5–7 years old, and annual adult survival is high (87–95%; Gaston and Jones, 1998). The Norwegian population amounts to approximately 15 000 breeding pairs, which represents a 90% reduction compared to the population size of the 1960s. The species is therefore listed as critically endangered in Norway (Kålås et al., 2010).

The fieldwork was carried out from 1980 to 2011 on Hornøya (70° 23′ N, 31° 9′ E), a 0.5 km^2 island in northeastern Norway. Annual counts of individual Common Guillemots on predefined monitoring plots were made by one of us (R.T.B.) late in the incubation period or during hatching. To minimize the day-to-day variation, five to ten counts were made on different days, and the mean number was used as an index of population size. The monitoring followed internationally standardized methods (Walsh et al., 1995). Successive annual estimates of the total population on Hornøya were based on a single, total count of 1900 individuals made in 1987 and the annual rates of change documented in the monitoring plots. See Barrett (1983, 2001) and Erikstad et al. (2013) for more details.

As can be seen from the population trajectory in **Figure 1**, there was a pronounced crash in population size from 1986 to 1987 (*cf.* Vader et al., 1990; Erikstad et al., 2013). To estimate the yearly variation in population growth rate r, we used the variation in estimate of the total population size N in each census from 1 year to the next [$r_t = \ln(N_t/N_{t-1})$].

Climate Datasets

Mean Sea Level Pressure Data

Mean sea level pressure (hereafter "MSLP") from the European Centre for Medium-Range Weather Forecasts (ECMWF) Re-Analysis Interim Project (hereafter "ERA-Interim") was used throughout this study (Berrisford et al., 2009; Dee et al., 2011).

TABLE 1 | Major teleconnection patterns in the Northern Hemisphere.

Extratropical teleconnection patterns	Seasonal occurrence
North Atlantic Oscillation (NAO) (Barnston and Livezey, 1987)	All months
East Atlantic (EA) pattern (Wallace and Gutzler, 1981)	September to April
East Atlantic Jet (EA-Jet) pattern (Washington et al., 2000)	April to August
West Pacific (WP) pattern (Wallace and Gutzler, 1981)	All months
East Pacific (EP) pattern (Bell and Janowiak, 1995)	All months except August to September
Pacific/North American (PNA) pattern (Wallace and Gutzler, 1981)	All months except June to July
North Pacific (NP) pattern (Barnston and Livezey, 1987)	March to July
Pacific Transition pattern (Barnston and Livezey, 1987)	May to August
East Atlantic-Western Russia (Eurasia, EU) pattern (Wallace and Gutzler, 1981)	September to May
Scandinavia (SCAND) pattern (Barnston and Livezey, 1987)	All months except June to July
Polar/Eurasian pattern (Barnston and Livezey, 1987)	December to February
Tropical/Northern Hemisphere (TNH) pattern (Barnston and Livezey, 1987)	November to January
Asian Summer pattern (Barnston and Livezey, 1987)	June to August
Arctic Oscillation (Thompson and Wallace, 1998)	All months
Aleutian Low-Icelandic Low seesaw pattern (AL-IL) (Honda et al., 2005)	Late winter

Table adapted from Barry and Carleton (2001, pp. 396–397) showing the names, and acronyms when available, of the major modes of variability in the Northern Hemisphere together with their seasonal occurrence.

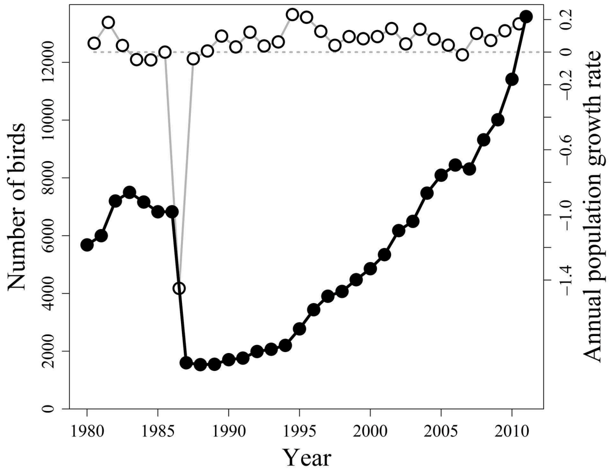

FIGURE 1 | Dynamics of the Common Guillemot population on Hornøya, Northern Norway, from 1980 to 2011. Counts and estimates of numbers of breeding birds (filled circles, left-hand *y*-axis) and annual population growth rates *r* (open circles, right-hand *y*-axis). Figure adapted from Erikstad et al. (2013).

Re-analysis data "provide a multivariate, spatially complete, and coherent record of the global atmospheric circulation," and the ERA-Interim reanalysis, particularly, is one of the most sophisticated gridded datasets at high-resolution at present (Dee et al., 2011, p. 554).

ERA-Interim data were created using the ECMWF Integrated Forecast System (IFS) model with fully coupled atmosphere, land surface, and ocean waves (Dee et al., 2011) together with the 4-dimensional variational assimilation (4D-Var) system (Courtier et al., 1994; Veerse and Thepaut, 1998; Dee et al., 2011). So, available observations from different sources (e.g.: satellite, station data) were assimilated into the model simulation, which allows for a product that is realistic (and in accordance with observational) data, with the advantage that it is on a three-dimensional lattice. In fact, rigorous quality control and experience from previous projects, such as ERA-40 (the precursor of ERA-Interim), have turned ERA-Interim into a state-of-the-art dataset for climate studies. ERA-Interim horizontal resolution is at T255 (nominally 0.703125°, or around 79 km) and it contains 60 vertical model levels, with the highest being at 0.1 hPa. The horizontal resolution in ERA-Interim (79 km) is higher than that for another reanalysis product (with resolution on the order of 250 km) used in recent ecological studies (Dippner et al., 2014).

Thus, in the present study, 6-hourly ERA-Interim MSLP data from 1980 to 2011 were used. The winter season, referred to here as DJF (December, January, and February) was retained, starting from December 1979. These seasonal data were then aggregated into yearly averages per grid point. So, from here on, we will refer to the MSLP as starting from 1980 (i.e.: December 1979, January and February 1980). This means, for instance, that when we discuss the year "1987" (outlier in the population growth rate data), we mean the winter 1986/87 (December 1986, January and February 1987) for the MSLP variable. This provides the equivalent of 32 years of data, which conforms to a 30-year period considered by the World Meteorological Organizations to be the minimum requirement for climate studies (Parry et al., 2007; Baddour, 2011).

Wind Data for Polar Low Tracking

High-resolution data are needed to identify and track polar lows due to their small-scale compared with synoptic-scale low-pressure systems. For this end, another high-resolution data product is needed. Here, wind data at the 850-hPa atmospheric level from the NCEP Climate Forecast System Reanalysis (NCEP-CFSR) data were used (Saha et al., 2010, 2013). The

NCEP-CFSR is a state-of-the-art reanalysis fully coupled product at the spectral T574 horizontal resolution (~27 km) and 64 vertical levels, which is arguably one of the most advanced products at high-resolution to date. The importance of reanalysis data to climatologists was also expressed in Saha et al. (2010 p. 1015), "The general purpose of conducting reanalysis is to produce multiyear global state-of-the-art gridded representations of atmospheric states." Thus, the combination of an advanced storm-tracking algorithm (described below) with high-resolution advanced reanalysis dataset makes the result of this study unique.

Differently from ERA-Interim, the NCEP-CFSR was based on a fully coupled model system, the Climate Forecast System version 2 model (CFSv2), combined with an advanced data assimilation system (Saha et al., 2013); but like the ERA-Interim, NCEP-CFRS made use of the same observations from a number of sources in its assimilation system. These sources come from satellite data, aircraft and upper air balloon observations, as well as surface datasets.

Statistical Methods

Point Correlation Maps

Point correlation maps allow for the organization of large-data information and make it possible to identify climatic modes of variability (Wilks, 2011, pp. 67–70). This technique has been used in climate science for several decades. In fact, Wilks' (2011, p. 69) figure 3.28 shows the reproduction of a figure taken from the Norwegian climatologist Bjerknes (1969, p. 169). This figure illustrates that by using the method of point correlation for annual surface pressures around the globe with those in Djakarta, Indonesia, Bjerknes was able to identify a strong negative correlation with Easter Island, which reflects the atmospheric component of the El Niño-Southern Oscillation (ENSO). This is an example of a teleconnection pattern, that is, a remote phenomenon can affect other regions around the world (Glanz et al., 2009). It is interesting to note that Bjerknes' figure was also a reproduction of the earlier work of Berlage (1957), which exemplifies that this technique has been around for a long time as a means of understanding climate dynamics.

In this study, point correlation maps were created using the sample cross correlation at lag 0. Other lags could have been shown, but Sandvik et al. (2005 p. 823) find that the NAO has the highest correlation with the survival of Common Guillemot at lag 0 and here we test this effect. So, let $\boldsymbol{X_{i,j}}$ be the vector of MSLP for latitude-longitude coordinate points *i* and *j* in the ERA-Interim grid, and $\boldsymbol{Y}$ be the vector of population growth rates for Common Guillemot. Thus, the sample correlation is determined as:

$$\boldsymbol{\rho_{i,j}} = \frac{\boldsymbol{Cov(X_{i,j}, Y)}}{\sqrt{\boldsymbol{Var(X_{i,j})Var(Y)}}}$$

where $\rho_{i,j}$ is the correlation coefficient at location *i* and *j*. *Cov* and *Var* represent the covariance and variance, respectively. The statistical significance of the correlation coefficient can be determined using Student's *t*-test (von Storch and Zwiers, 2002, pp. 77–78).

Point Regression Maps

Similarly, point regression maps can be created to aid the identification of hotspots where the predictor variable (e.g.: MSLP in this case) and the response variable (e.g.: population growth rate) are linearly related. These maps can be created through the least squares method, which is used to obtain meaningful information about the dependency relationships between variables (Draper and Smith, 1998). Also, the creation of such maps is often used in climatology and can provide further insights on how remote processes can affect other regions around a hemisphere or the globe (Bader et al., 2011; Mesquita et al., 2011).

Regression maps are created by plotting the regression coefficient, that is, the slope (β_1) of the linear regression equation:

$$Y_{k;i,j} = \beta_0 + \beta_1 X_{k;i,j} + \varepsilon_{k;i,j}$$

where $Y_{k;i,j}$, represents the *k*-th element of the response variable at location *i* and *j*, β_0, and β_1 are the intercept and the slope parameters, respectively; and ε is the error variable. The slope is estimated β_1 as follows (Draper and Smith, 1998):

$$\beta_1 = \frac{\sum (X_{k;i,j} - \overline{X}_{i,j})(Y_{k;i,j} - \overline{Y}_{i,j})}{\sum (X_{k;i,j} - \overline{X}_{i,j})^2}$$

where the overbar represents the mean values of *X* and *Y* at location *i, j* on the lattice. A *t*-test was used for significance for each grid point, which can then be overlayed on the map. A significance level of 0.1 was used to identify potential regions that can later be combined to construct an index.

Composite Analysis

Composite analysis is a well-known technique in climatology, which is used to construct climatic states that are typical (von Storch and Zwiers, 2002, p. 378). In order to illustrate the definition of composite analyses, we adapt the definition given in von Storch and Zwiers (2002, p. 378) as follows. Let $\boldsymbol{z}$ be a univariate index and $\boldsymbol{M}$ be the vector of the mean sea level pressure variable at a certain grid point. The composite is defined as:

$$\boldsymbol{M_\Theta} = \varepsilon(\boldsymbol{M}_t | \boldsymbol{z}_t \epsilon \Theta)$$

where $\boldsymbol{\Theta}$ represents sets of the index $\boldsymbol{z}$ and *t* represents time. The expectation of the composite is generally estimated as:

$$\boldsymbol{M_\Theta} = \frac{1}{k}\sum_{s=1}^{k} \boldsymbol{M}_{t_s}$$

for the observing times $t_1, \ldots, t_k$ for which $z_t \in \Theta$. In this study, composites were made for two sets: MSLP for the 5 years with the highest population growth rates (Θ_h) and MSLP for the 5 years with the lowest population growth rates (Θ_l). We estimate the difference between $M_{\Theta_h} - M_{\Theta_l}$ applied to each grid point on the globe. In more general terms, composite analysis is the difference between selected states. For example, the difference between the mean of MSLP maps corresponding to years when the population growth rate of Common Guillemot is above/below a certain threshold with the mean of MSLP maps for years when the population growth rate is above/below a certain threshold average. This technique provides insights into atmospheric patterns that are more common for specific states of the population growth rate.

Storm Tracking Algorithm

In order to understand the 1987 crash, the storm-tracking algorithm TRACK, developed by Hodges (1995, 1999), was used. TRACK is a computer algorithm, which has been applied in several storm-related studies (Mesquita et al., 2008, 2011; Bader et al., 2011; Zappa et al., 2014). Storms were identified in relative vorticity maps at the 850-hPa atmospheric level and were tracked temporally through a cost function. Relative vorticity represents the curl of the wind and how much it spins. It is determined from the $\boldsymbol{u}$ (west-east direction) and $\boldsymbol{v}$ (north-south direction) components of the wind, and is defined as (Holton, 2004, p.92):

$$\zeta = \frac{\partial \boldsymbol{v}}{\partial x} - \frac{\partial \boldsymbol{u}}{\partial y}$$

For the present study, polar lows, which are short-lived storms with a radius on the order of 100–500 km and surface wind speeds above 15 m s^{-1}, were tracked using the criteria detailed in Zappa et al. (2014, p. 2603) with NCEP-CFSR (described above) as the input data.

Population Modeling

As a test of the utility of the different climatic indices in explaining Common Guillemot population dynamics, these indices were used as covariates in stochastic population models. Different models were compared using their $\mathrm{AIC_C}$ (Akaike Information Criterion corrected for small sample size). All estimates are provided as means alongside their 95% confidence intervals.

Population dynamics of the Common Guillemot population on Hornøya were density-independent, as evidenced by the absence of a negative correlation between annual growth rates r_t and population sizes N_t (correlation coefficient $R = +0.0005 \pm 0.3664$, $p = 0.998$), and the fact that the $\mathrm{AIC_C}$ of the density-dependent (logistic) population model exceeded that of the density-independent (Brownian) model by 2.48 units. The model used thus had the form:

$$\ln N_{t+1} = \ln N_t + \bar{r} - \frac{1}{2}\sigma_{\mathrm{d}}^2 N_t^{-1} + \sum \beta_i X_{i,t} + \varepsilon_t$$

where β_i represents the slope of the ith environmental covariate X_i; ε, environmental noise, i.e., an independent variable with zero mean and variance σ_{e}^2; N_t, population size in year t; $\bar{r}$, long-term intrinsic population growth rate; σ_{d}^2, demographic variance; $X_{i,t}$, environmental covariate i in year t. The parameters β_i, $\bar{r}$, and σ_{e}^2 were estimated using maximum likelihood (for details, see Sæther et al., 2009; Sandvik et al., 2014), while σ_{d}^2 was assumed to be 0.1, which is a realistic value for long-lived birds (Lande et al., 2003). To ensure that the latter assumption did not critically affect the results, different values of σ_{d}^2 were tested; varying σ_{d}^2 tenfold (0.01–1) changed the estimate of β by less than 2%. As the crash from 1986 to 1987 represented an influential outlier, population dynamics were analyzed with and without the population count for the year of 1986 included.

Computations were carried out through: (a) the R environment (R Development Core Team, 2013); (b) NCL (The NCAR Command Language, 2014[1]); (c) CDO, the Climate Data Operators (Schulzweida, 2013), and (d) the coupled general circulation model MPI-ESM1 (Giorgetta et al., 2013).

Results

Correlation Maps

The point correlation between winter MSLP and the population growth rate variable are shown in **Figure 2**. Colors in red represent areas where the correlation is positive, meaning that high values of pressure in winter are associated with high values of the population growth rate that year (i.e., from the previous to next breeding season). An increase in pressure is related to a high-pressure system, which can promote cold air activity in winter, and a decrease in storm activity. Colors in blue are related to negative correlation between the variables. So in this case, a decrease in the values of winter pressure is associated with high values of the population growth rate. A decrease in pressure is related to low-pressure systems, which bring moisture and heat from lower to higher latitudes that create milder conditions in winter.

Figure 2A shows the correlation with the raw population data (includes the trend). It shows a clear dipole structure in the Arctic, as well as a wave-like propagation of positive-negative centers of correlation in mid-latitudes. The figure shows little or no resemblance to the NAO pattern in the Atlantic, but shows some resemblance, although shifted in center of action, to the Arctic Oscillation (Thompson and Wallace, 1998). It is, however, more similar to the Aleutian Low and Icelandic Low (AL-IL) seesaw pattern observed in later winter, another atmospheric mode of variability, which results in a dipole in the Arctic. The AL-IL is also the dominant pattern in late winter and it has consequences for climate in the surrounding regions (Honda et al., 2005).

The correlation with the detrended population data (**Figure 2C**) is quite similar in structure to that in **Figure 2A**. In fact, this pattern suggests that the trend in the population growth rate does not account for the seesaw-like pattern; it is a feature of another aspect of the population data. In order to investigate this, **Figure 2B** shows the data with trend, but removing the outlier in 1987 (i.e.: winter 1986/87 for MSLP; 1987 for r). Here, the features look very different indeed. The low pressure over where the colony is located is still there, but the seesaw pattern is much weaker. Also, for mid-latitudes, there is an increase in negative correlation.

Finally, the data with no trend together with the removal of the year 1987 is shown in **Figure 2D**. The pattern is similar to

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[1] The NCAR Command Language. (2014). Boulder, Colorado: UCAR/NCAR/CISL/VETS. Available online at: http://dx.doi.org/10.5065/D6WD3XH5

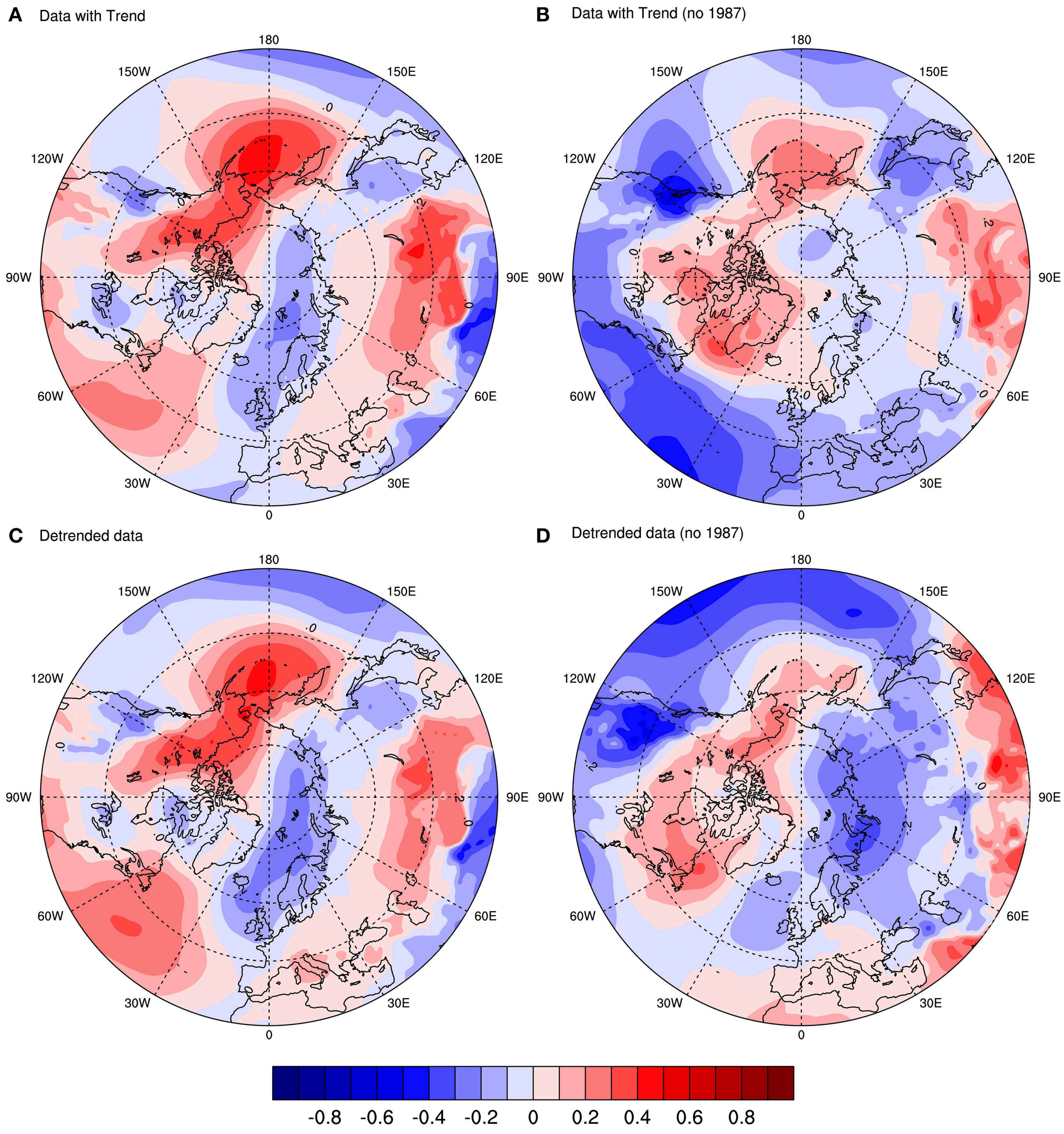

FIGURE 2 | Point correlation between mean sea level pressure (MSLP) and guillemot population growth rate (*r*) based on the period from 1980 to 2011. The four plots display the correlation coefficient calculated as: **(A)** MSLP and raw *r*; **(B)** MSLP and *r* with 1987 removed from both series; **(C)** MSLP and detrended *r*; **(D)** MSLP and detrended *r* with 1987 removed from both series.

that in **Figure 2B**, but it has much stronger correlation features, especially over the Barents Sea, where the colony is located. The features in the mid-latitude Pacific and Atlantic are also different compared with **Figure 2B**, with almost an opposite effect. The pattern in the Atlantic sector resembles another mode of variability called the Barents Oscillation (Chen et al., 2013), an anomalous atmospheric oscillation associated with flow over the Nordic Seas, although with a shifted center of action.

Thus, 1987 is indeed an outlier, which seems to be related to a strong seesaw pattern in the Arctic. The main feature of the four figures is the low-pressure system over the Barents Sea and Pacific sector, as well as the high pressure over the Bering Sea. Both the outlier and the low-pressure system over the Barents Sea are investigated further in subsequent sections. But first, we investigate the aforementioned features through the use of point regression.

Regression Maps

Regression maps are given in **Figure 3**. Similar to correlation maps, the colors indicate regions of high (red) or low pressure (blue) associated with the population growth rate. Looking at the significant regions across **Figures 3A–D**, one can see some

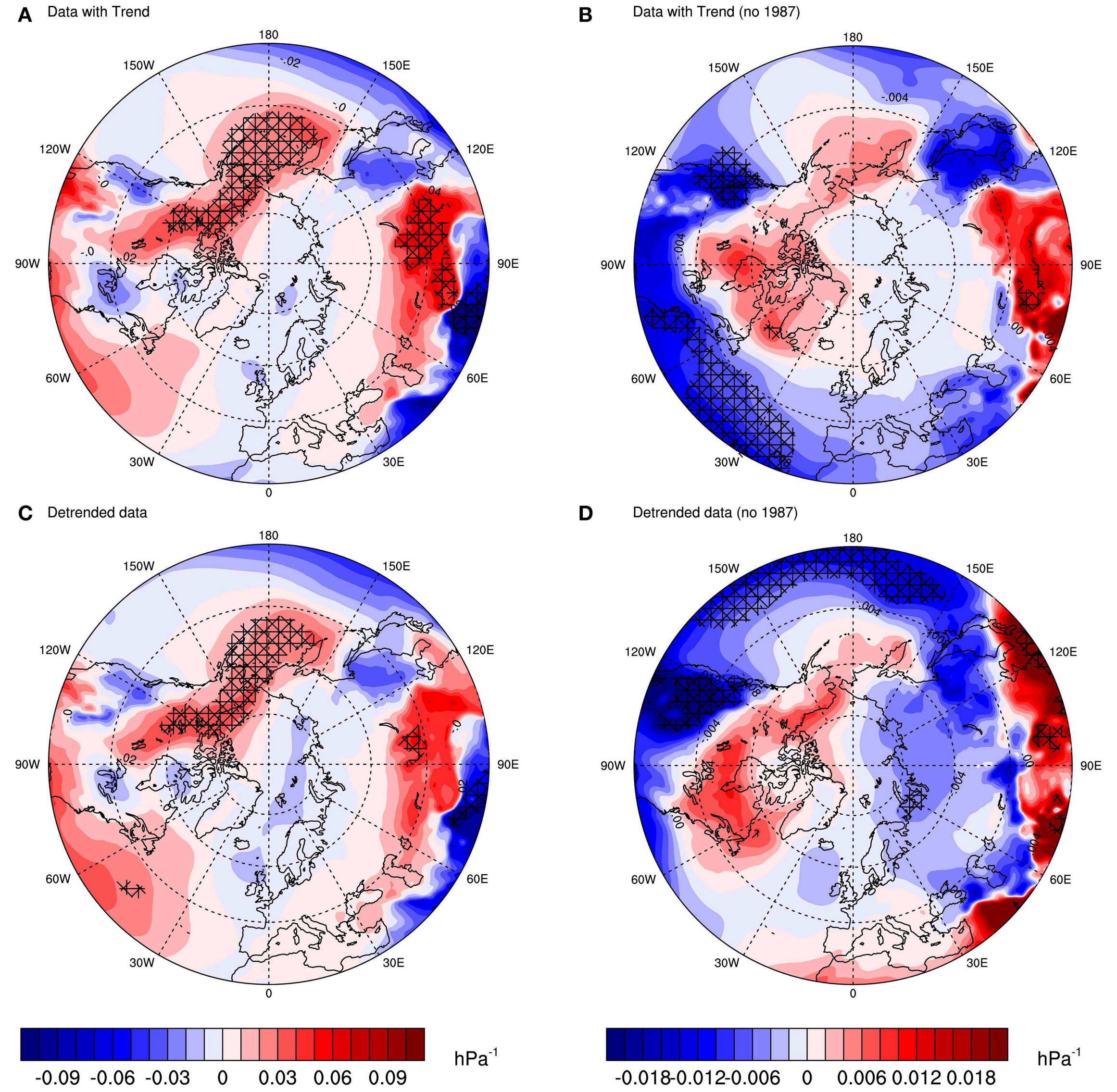

FIGURE 3 | Point linear regression coefficients between MSLP and guillemot population growth rate (*r*) based on the period 1980–2011. Each plot shows the regression coefficient between: **(A)** MSLP and raw *r*; **(B)** MSLP and *r* with 1987 removed from both series; **(C)** MSLP and detrended *r*; **(D)** MSLP and detrended *r* with 1987 removed from both series. Crosses represent regions where the *p*-value of a *t*-test statistic is less than 0.10. Units: population growth rate/hPa.

consistent patterns, such as the Bering Sea, Pacific Ocean and northwestern parts of North America, as well as the Barents Sea. If we focus on the latter, that is, the region where the colony is located, we observe that the regression with the detrended data without 1987 is significant. Thus, the trend and the outlier seem to mask the significance, showing that the pattern over the Barents Sea is the true underlying process (or signal) associated between pressure and population growth rate.

Regression maps are very useful in identifying "hotspots" of regions that have potential in explaining the association between the dependent and explanatory variables. Here they show, as pointed out before, that the pattern of the NAO does not emerge in **Figures 2**, **3**. For instance, if a consistent dipole pattern between a region around Iceland and the Azores emerged, one would then relate it to the NAO. But this is not the case here.

Composite Maps

In **Figure 4**, composite plots of MSLP are displayed for the 5 years with the highest (i.e.: 1995, 1996, 1982, 2011, 2002) and the lowest (i.e.: 1987, 1985, 1984, 1988, 2007) detrended population growth rates. These plots provide further support to the robustness of the findings in **Figures 2**, **3**, and are commonly used in climate studies. **Figures 4A,B**, show that the general patterns seem similar, however, the absolute values of the contour lines in the Pacific and Atlantic basin, as well as the distance between contours are different. The latter refers to the strength

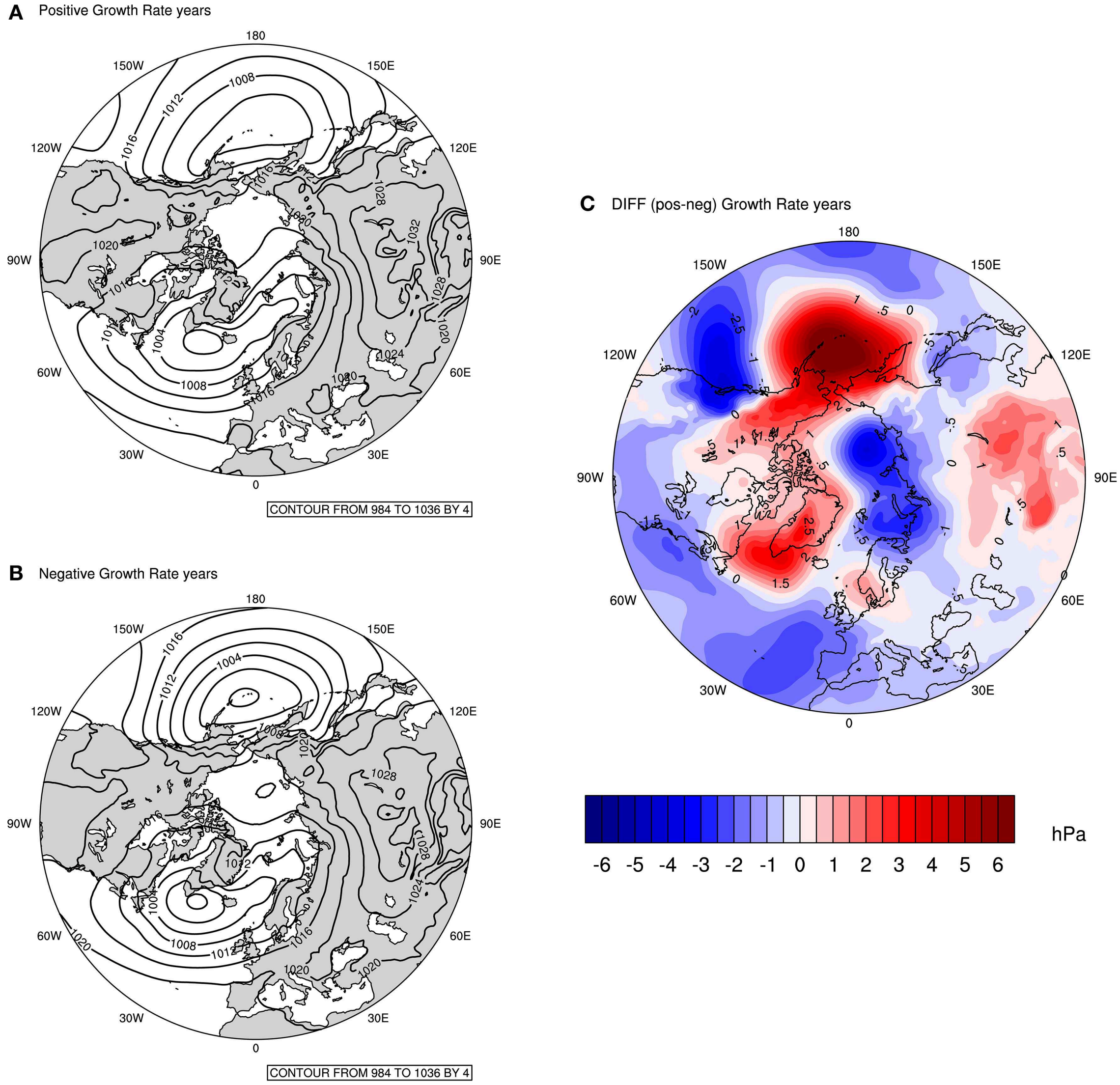

FIGURE 4 | MSLP Composite for: (A) Five years with the highest positive guillemot population growth rates (top left); **(B)** Five years with the highest negative population growth rates (bottom left); **(C)** Difference between 5 years with highest positive and 5 years with highest negative population growth rates. Units: hPa.

of the pressure gradient and provides an indication of the relative strength of the wind. So, in years with negative population growth rates, there is an intensification of the pressure gradient in both ocean basins compared to years with positive population growth rates.

The difference plot (**Figure 4C**) shows the difference between the MSLP for years with positive and negative population growth rates (i.e.: Figure A minus Figure B). Here, there is a striking similarity with the features observed in **Figures 2**, **3**; more importantly, the dipole pattern in the Arctic between the Barents and Bering seas are evident. Thus, the fact that the feature observed in the Barents Sea is clearly seen in this composite confirms that the population growth rate is associated with the low-pressure system over the Barents region during winter. The dynamics behind this system will be explained further on.

Analysis of the Outlier

Composite Analysis

Composite analysis has also been used to understand what the atmospheric features of 1987 were and how anomalous it was with respect to different climate baselines. **Figure 5** displays these composite maps. **Figure 5A** shows the MSLP configuration for the winter 1986/1987. Compared with **Figure 4**, the isobars (lines of same pressure level) seem to be much tighter both in the Pacific and the Atlantic basins. In fact, if one would rank **Figures 4A,B**, **5A** based on the spacing of the isobars, **Figure 5A** would feature as the one with the least spacing between then. This is a first indication that the 1986/87 winter had an atmospheric feature that was stronger than that of the MSLP for the years with the lowest negative population growth rates.

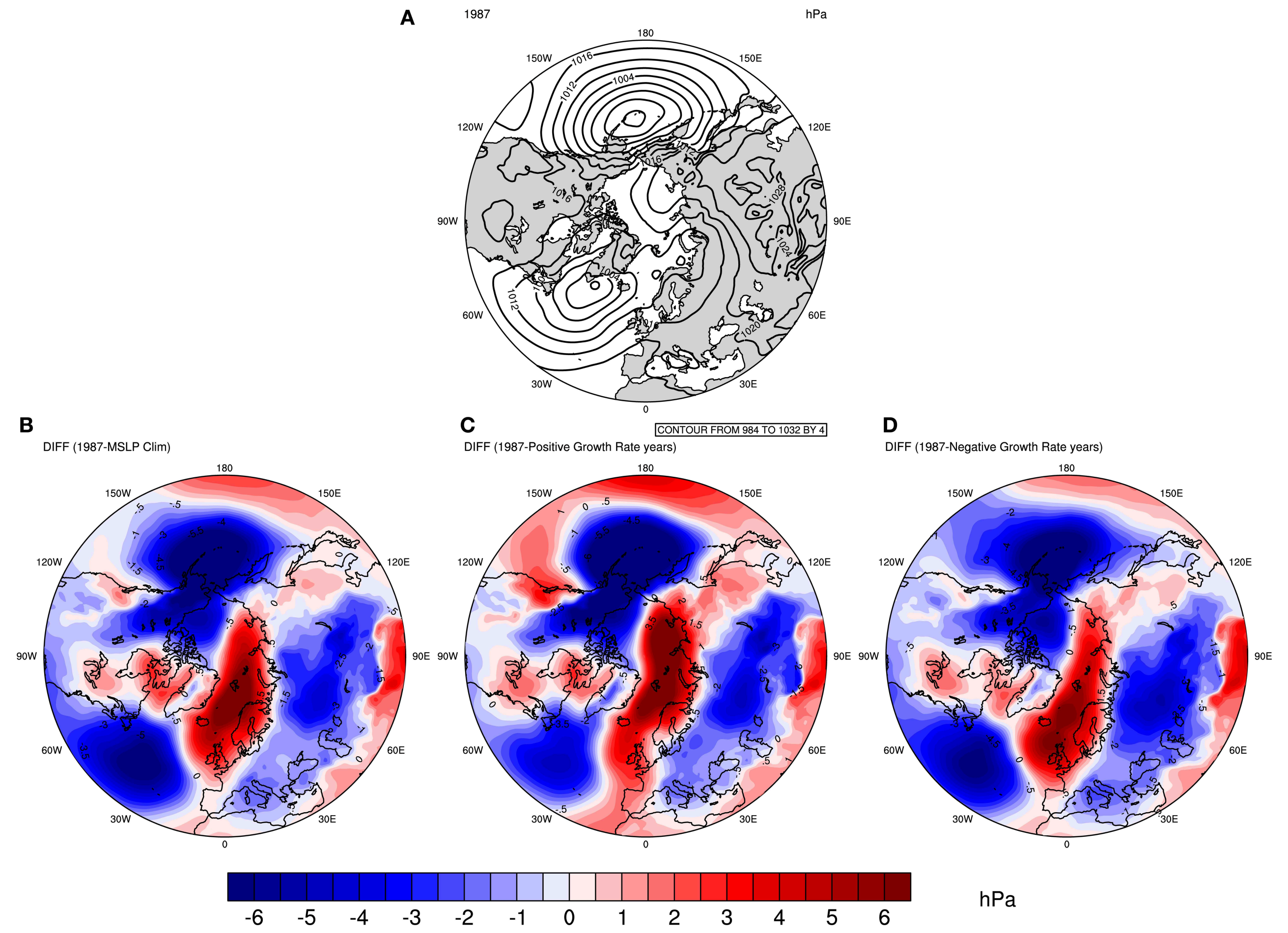

FIGURE 5 | Comparison between MSLP in 1987 with different baselines. (A) The MSLP in 1987. The bottom figures represent the MSLP in 1987 minus the MSLP in the following periods: **(B)** mean of 1980–2011; **(B,C)** Five years with the highest guillemot positive population growth rates of the detrended dataset; **(C,D)** Five years with the lowest negative population growth rates of the detrended dataset excluding year 1987.

The bottom panel in **Figure 5** shows anomaly plots, defined as the difference between MSLP for winter 1986/87 minus different winter baselines (from left to right): the mean of 1980 to 2011; the 5 years with the highest positive population growth rates in the detrended dataset (i.e.: 1985, 1984, 1988, 1998, 2007); and the 5 years with the lowest negative population growth rates in the detrended dataset excluding year 1987 (i.e.: 1982, 1992, 1995, 1996, 2011). These figures show a major correspondence with those in **Figures 2–4**, but with the colors shifted. This correspondence is especially seen for the Barents–Bering dipole pattern. The red color observed over the Barents Sea means that 1987 had an anomalous high-pressure system over the region, and as considered in the previous figures, a high-pressure system during winter in the Barents Sea is associated with a low population growth rate for that year.

Thus, the winter of 1986/1987 features as having an anomalous atmospheric configuration compared with different baselines. It had a major zone of high-pressure system, the so-called atmospheric blocking, over the Barents Sea. The latter feature was anomalous throughout the climatology of the region for the period considered here (1980–2011).

Effect of Local Weather

The results in the previous subsection indicate that the winter 1986/87 was indeed an outlier when it comes to the climatological conditions in the Barents Sea. It is therefore useful to look at the weather conditions that winter. Polar lows are a common feature in that region, which bring anomalously cold air from the pole, can have relative strength of a violent tropical storm (Nordeng and Rasmussen, 1992) and have damaging effects at the surface, such as icing (Icing implies the deposition and formation of ice on surfaces). **Figure 6** shows mesocyclones, which are medium-sized storms, and polar lows in the North Atlantic and Barents Sea. The figure shows at least four polar lows crossing the central Barents Sea, which is the area where Common Guillemots from Hornøya spend the entire winter, according to ring recoveries (Barrett and Golovkin, 2000) and 3 years of geolocator data (Erikstad et al., unpubl. data). These polar lows were quite strong

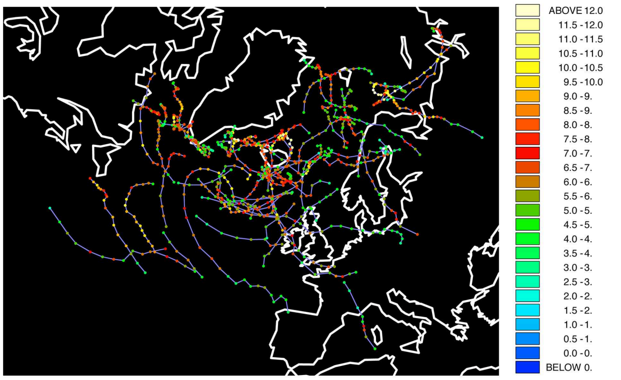

FIGURE 6 | Mesocyclones and polar lows in winter 1986/1987 from NCEP-CFSR data and tracked through Hodges' TRACK algorithm. Colors represent strength as based on vorticity. Units: 10^{-5} s^{-1}.

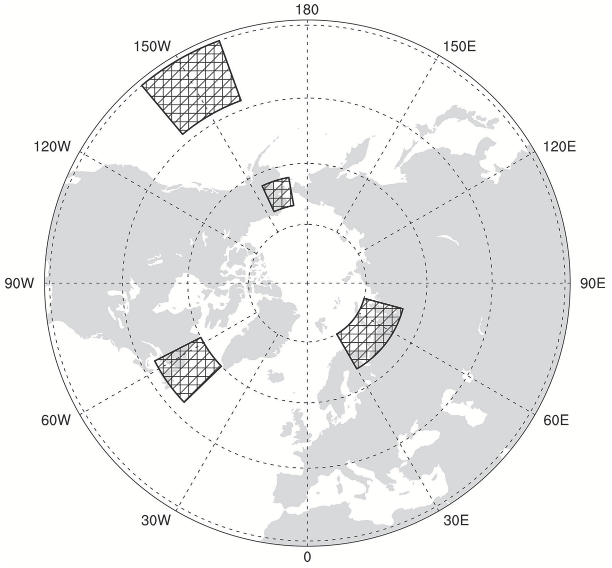

FIGURE 7 | Regions selected for the MSLP-based index.

systems, as indicated by the vorticity, which represents how much the wind spins, with values higher than about $9 \times 10^{-5}s^{-1}$. This suggests that through elevated thermoregulatory costs (due to low temperatures) and periodic difficulties in finding food (through high winds) the polar lows that winter could have increased the mortality of Common Guillemot. Indeed, many corpses of emaciated Common Guillemots were found washed ashore in Finnmark that winter (Vader et al., 1990).

Building Proxies

Four regions were selected for the construction of climatic indices, or proxies (**Figure 7**). These were selected based on the correlation and regression patterns discussed previously. Note that other regions could have been chosen, but here we illustrate how a useful climate "proxy" could be created and used in ecology. The regions are as follows: Barents, "BAR" (65-75N, 30-75E), north-eastern North America, "NEA" (48-60N, 46-63W), Alaska, "AKA" (63-70N, 155-170W), and Pacific, "PCF" (30-43N, 140-160W). The indices were constructed by first calculating the DJF MSLP average of each region and then making different combinations of similar polarity (i.e.: combining regions with positive correlation against negative correlation regions). These indices were then normalized. They are: IDX1 (BAR−NEA), IDX2 (PCF−AKA), and IDX3 [(PCF+BAR)−(NEA+AKA)].

Testing the Proxies

As a test of the utility of the indices described above, these indices, as well as the NAO index, were used as covariates in stochastic population models. When detrended, the two indices IDX2 and IDX3 improve the null population model (without covariates) by more than two AIC_C units (**Table 2**). Both models are thus equally well supported, and considerably better so than the null model. Each of these two covariates explains 15% of the population dynamics. IDX2 and IDX3 with trends retained, as well as a pure trend model, are much poorer, in that they are roughly equally well supported as the null model (**Table 2**). NAO and IDX1 do not improve the null model, and explain less than 5% of the population dynamics. The finding that the NAO cannot physically explain the population dynamics of the Common Guillemot, is in accordance with the observation that NAO does not appear to be a mode of variability identified in **Figures 2–5**, either.

Models with two or more covariates did not improve upon the best models with one covariate (results not shown). Lagged covariates performed more poorly than their unlagged counterparts and/or the null model in all cases (time lags of 1–3 years were considered; results not shown).

The above results are based on population dynamics with the crash year removed. Even when 1986 is retained in the population time series, however, a detrended IDX3 is able to significantly improve upon the null population model (AIC_C 2.5 units lower than null model, $p = 0.026$, $R^2 = 0.148$). The remaining indices (IDX1, IDX2, NAO) do not differ from the null model in this case (results not shown).

Discussion

Although the analysis of the population growth rate of Common Guillemot under classical climatological methods focused mainly on the mean sea level pressure variable, it addressed the main objective of this paper, that is, to highlight the need to understand the climate dynamics behind an ecological variable before constructing a so-called "proxy." In what follows, we present a discussion of the main results and propose a model to explain the atmospheric dynamical effect on the population growth rate variable.

The Hornøya population of the Common Guillemot, a species that is classified as "critically endangered" according to the Norwegian Red List (Kålås et al., 2010), declined by 80% in winter 1986/87 (Vader et al., 1990; Erikstad et al., 2013). The year 1987 was indeed an extreme event, as could be confirmed

TABLE 2 | Stochastic population models of the Common Guillemot population on Hornøya.

Model	Estimate [LCI; UCI]	ΔAIC_C	p	R^2
IDX2, detrended	**−0.031 [−0.057; −0.005]**	**0.00**	**0.028**	**0.154**
IDX3, detrended	**−0.031 [−0.058; −0.004]**	**0.12**	**0.030**	**0.149**
Trend	+0.024 [−0.003; +0.053]	2.02	0.094	0.092
IDX2	−0.022 [−0.048; +0.004]	2.28	0.111	0.084
Null model	–	2.34		
IDX3	−0.016 [−0.042; +0.010]	3.36	0.228	0.049
NAO	−0.021 [−0.058; +0.014]	3.47	0.246	0.045
IDX1, detrended	−0.014 [−0.042; +0.014]	3.87	0.329	0.032
NAO, detrended	−0.017 [−0.055; +0.021]	4.05	0.381	0.026
IDX1	−0.005 [−0.030; +0.021]	4.68	0.711	0.005

The models differ in the covariates included. Models are sorted in order of increasing ΔAIC_C (i.e., decreasing model fit). Models that are better supported than the null model (i.e., the model without any covariate) are highlighted using boldface. Estimates are provided with lower (LCI) and upper (UCI) 95% confidence intervals. The estimates of the trend model were multiplied by 10.

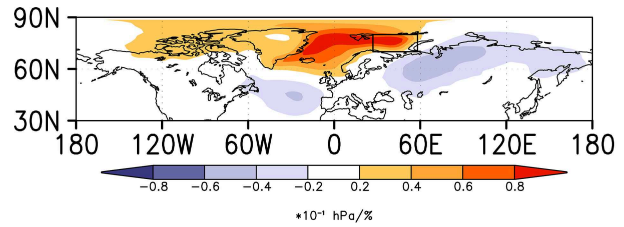

FIGURE 8 | Surface pressure regressed on sea-ice concentration in the Barents Sea. Sea-ice time series selected from the region indicated by the box. The data are based on the Coupled Model Intercomparison Project through the Max Planck Institute Earth System Model, CMIP5 MPI-ESM, control integration. Units: Coloring shows the change in hPa per one percent sea-ice concentration change multiplied by 10.

by the anomalous high-pressure system over the Barents Sea, where the colony is located. It has been previously shown that the crash of Common Guillemot was related to low fish stocks (Vader et al., 1990; Erikstad et al., 2013), but it is possible that this situation was aggravated by (or even causally related to) the overlaying atmospheric condition in the winter 1986/87. From the clear and robust pressure system over the Barents region, as a response from the Pacific Ocean teleconnectivity, we could hypothesize that biotic responses (fish and/or birds) might have been forced by the atmospheric conditions over the Barents Sea. Note also that, the response in the Barents Sea is also forced through changes in sea ice, as shown in **Figure 8**. This highlights the importance of considering the climate system as a whole in the understanding of changes in ecological variables (*cf.* Sydeman et al., 2006).

There is mixed evidence for the relevance of NAO in ecology. NAO can explain variation in some different ecological variables in some species, but not in others (e.g.: Sætre et al., 1999; Forchhammer et al., 2002; Durant et al., 2004; Sandvik et al., 2005; Sæther et al., 2009; Dippner et al., 2014; Sandvik et al., 2014). These studies and others illustrate the fact that NAO can be highly relevant for some variables and species; but an association may not mean causation. More is needed to assess NAO's usefulness, in this case, by finding a climate dynamics link to explain the association. The latter is clearly expressed in Forchhammer et al. (2002, p. 1002) when discussing the impact of climate perturbations on arrival on breeding grounds and later survival and reproduction: "the timing of migration must be adapted ultimately to large-scale atmospheric systems." This large-scale referred to by the authors is the idea of looking at the bigger picture, before making a choice of an index to explain the variability. Therefore, looking for the dynamics first, before selecting an index, is here suggested as a more promising approach.

Sandvik et al. (2005, p. 826) also recognize that: "causal pathways of these interactions are not easily identified. The NAO is defined as a temporal fluctuation of sea level pressure anomalies... and can as such hardly be said to be the cause of any of these responses. Rather it is convenient to treat the NAO as a "proxy" for different climatic processes... A full understanding of any climate-related response requires that one identifies the factors that cause it." The latter points to the need to look at the spatial contribution first to identify what affects the variability. In the present study, the variability explained by the NAO is not robust and does not appear in the spatial analysis of the relationship between MSLP and population growth rate, as concluded from the analysis of a long time series of the population growth rate of Common Guillemots. The local effects in the Barents Sea, which include the atmospheric forcing, mediated via teleconnectivity as found in this study, and the SST effects on the food web may act to affect the food web. This is also in line with the fact that there are positive correlations between SST and herring recruitment and stock biomass, which are relevant for Common Guillemot (Erikstad et al., 2013).

In the light of the results found in the present paper, and the discussions of previous scientific work, we propose the following mechanism to explain the variability in the population growth rate of Common Guillemot:

- An anomalous low-pressure over the Barents Sea during winter, forced via teleconnectivity through the Pacific and local sea-ice changes, leads to the increase of moisture and heat brought by storm tracks into the region. This forces the SST locally and leads to warmer conditions—favorable conditions for Common Guillemot.

- An anomalous high-pressure over the Barents Sea during winter, forced via teleconnectivity through the Pacific and local sea-ice changes, leads to blocking of storm tracks and loss of long-wave radiation from the surface to space. This leads to cold conditions both in the atmosphere and ocean—unfavorable conditions for Common Guillemot.

Based on this model, the anomalous year of 1987 can also be explained. During the 1986/87 winter, the high-pressure was more anomalous than any other years in the study period. This led to extremely unfavorable conditions to Common Guillemot. With lack of food and increased energetic costs, these seabirds were at a great disadvantage. Any other external factor might be enough to cause a crash, such as the polar lows that brought even colder air from the pole and high winds into the region.

We conclude that the role played by the Pacific as well as the Barents Sea is significant. It might indicate that the changes observed in the Barents Sea, where the colony is located, is triggered by a teleconnection from the Pacific via Alaska or via the north-east North America regions; these changes are also influenced by local changes in sea-ice.

Conclusion

The ubiquitous use of the NAO as a "proxy" in ecology and the search for alternative means of explaining variability have been analyzed in this research work. Although the NAO can explain the climate variability in the Atlantic sector, it is not the only teleconnection index available, and there needs to be a physical basis for the use of the NAO. So, the NAO as a "proxy" on its own should be used with caution. Also, before a decision is made on any proxies, one needs to see the bigger picture of what the possible climatic mechanisms are and how they can influence an ecological process.

Here, in search of such mechanisms, classical methods used in climatology to study climatic interactions were illustrated to study population growth rate of Common Guillemot: spatial maps of correlation and regression, compositing and a tracking algorithm to search for polar lows. We have used one climate covariate at the surface level for the analysis (i.e.: MSLP), and it has revealed an important climate mechanism at the Barents Sea. MSLP is just one of many other variables that could have been explored, such as: surface temperature, sea ice, temperature at different altitudes, geopotential height, precipitation, relative humidity, among others, to create a larger picture of the climate system and the interaction with the species studied here. Also, these variables could have been combined into a multivariate study and other advanced methods could have been used to explore their relationship. Thus, the present study illustrates the richness of information one gains through looking at ecology using the perspective that there is more to climate than the NAO.

Also, a possible physical mechanism was then proposed from the analysis, which linked teleconnectivity interaction via the Pacific into the Barents Sea, as well as interaction with sea ice changes in the Barents Sea region. An anomalous winter low-pressure system over the Barents Sea is associated with higher population growth rates, compared with years when an anomalous high pressure system is present: it creates warmer conditions brought by synoptic-scale storm track into the region. The opposite is true in anomalous winters with high-pressure system over the Barents Sea. The crash in 1987 could be explained by the extreme conditions of the severe anomalous high-pressure system over the region and the presence of polar lows.

One might ask if the techniques presented here apply to other species or variables. The answer is yes, but each species or variables would need to be analyzed on a case-to-case basis or through the use of multiple regression techniques. The latter is the subject of the next phase of this research work, where the idea of synchronization with different species and teleconnectivity will be explored. In doing so, other climate variables will also be addressed, such as sea surface temperature and geopotential height—in order to provide more insights into the dynamics of climate interactions and seabirds.

Overall, this research work has pointed to the importance of looking at what the data are telling in connection with climate-related variables, instead of starting from on a specific "proxy." Only after the larger picture is obtained, can one narrow down existing modes of variability and/or create indices based on the response from the data. Thus, instead of looking at the data given the "proxy" (or mode of variability), [Data|Mode], one should explore the idea of looking at the climatic forcing given the data, [Forcing|Data], in search of modes of variability. Future work should address what is happening in the Pacific that triggers a wave-like pattern of teleconnectivity, as well as an integrated approach to understanding how climate affects seabirds, by looking at the role of climate forcing (ocean and atmosphere) on predator and prey in a multivariate fashion.

Author Contributions

M.d.S.M wrote the manuscript, devised the climate analyses, concept and design of the research work; K.E.E. provided data, figure and participated in the conception and design of the work; H.S. conducted the population modeling, wrote part of the manuscript and critically evaluated the work; R.T.B. provided ecological expertise, data information and critically evaluated the work; T.K.R. contributed with ecological expertise, discussions on the climate mechanism and critically evaluated the work; T.A.-N. provided ecological expertise, helped draft the work and critically evaluated it; K.I.H. conducted the polar low analysis, provided figure, critically evaluated the work and helped with climatological methods; J.B. helped draft the work, critically evaluated it, provided a figure and helped with climatological methods.

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Skipped breeding in common guillemots in a changing climate: restraint or constraint?

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Climate change may have demographic consequences for marine top predators if it leads to altered rates of skipped breeding. Here we examine variation in skipping propensity at both the population and individual levels in common guillemots *Uria aalge* in relation to climate and oceanographic variables and explore the extent to which skipping may be adaptive or an unavoidable consequence of ecological or social constraints. We assumed a detection probability for birds present in the colony of 1.00 and skipping events were defined to include both resightings of non-breeders and failures to resight individuals known to be alive (not present at the colony but resighted in future years). Skipping frequency was higher in years where sea surface temperatures (SST) were higher in winter (both in the current and previous year), when guillemots from our study colony disperse widely across the southern North Sea. Individuals differed consistently in their average skipping propensity and their responses to SST. Males and females were equally likely to skip on average and the frequency of skipping increased in the oldest age classes. Birds that skipped in year t had lower breeding success in year $t + 1$ if they laid an egg, compared to birds that did not skip in year t. Lifetime reproductive output was negatively related to individual skipping frequency. These results imply that skipping is driven by individual-specific constraints, although we cannot rule out the possibility that birds benefit from skipping when environmental (or internal) signals indicate that breeding in poor years could be detrimental to their residual reproductive value. While future climate change might lead to guillemots skipping more often due to carry-over effects from wintering to breeding periods, the net demographic impacts may be subtle as the absolute frequency of skipping may remain low and individuals will not be equally affected.

Keywords: phenotypic plasticity, intermittent breeding, non-breeding, non-breeders, life history buffering, environmental cue

INTRODUCTION

A central premise of life history theory is that reproduction is costly (Stearns, 1989). At a proximate level, animals may only be able to breed if exogenous food and nutrient intake, or endogenous reserves, surpass a critical threshold (Erikstad et al., 1998; Meijer and Drent, 1999), while investment in breeding entails potential physiological costs such as reduced immune function or increased susceptibility to oxidative stress (Harshman and Zera, 2007; Monaghan et al., 2009). At an ultimate level, parents face a fitness trade-off between current and future reproduction: increased allocation of resources to current offspring production may come at the expense of reduced parental survival chances and hence reduced residual reproductive value (Williams, 1966; Charlesworth, 1994).

Annual reproductive investment in iteroparous species involves a series of sequential "decisions," chief among which is the decision of whether to breed or not (Clutton-Brock, 1988; Newton, 1989). For some vertebrate species living in seasonal environments, the norm is for mature individuals to breed in alternate years or less often (e.g., obligate biennial breeding in albatrosses, Jouventin and Dobson, 2002; and in many fish, amphibians and reptiles: Bull and Shine, 1979). However, more typically annual breeding is the norm but in such situations a variable (often substantial) fraction of individuals that have already bred before may skip in some years, i.e., facultative annual breeding (Aebischer and Wanless, 1992; Chastel, 1995; Harris and Wanless, 1995; Cam et al., 1998; Nur and Sydeman, 1999; Reed et al., 2004; Johnston and Post, 2009; Rideout and Tomkiewicz, 2011). Given its pervasive direct and indirect ecological effects, climate likely plays an overarching role in determining both how often individuals skip (proximate influence of climate via cues or constraints) and when skipping would be profitable from a fitness-maximization perspective (ultimate influence of climate).

Hypotheses to explain intermittent breeding can be grouped into adaptive and non-adaptive explanations. In temporally varying environments, skipping may be adaptive when the costs of reproduction are higher during unfavorable seasons (Schaffer, 1974; Bull and Shine, 1979; Erikstad et al., 1998; McNamara and Houston, 2008). Long-lived species, in particular, are expected to exhibit restrained reproductive investment under poor conditions because even small reductions in adult survival will reduce the number of subsequent breeding seasons and hence depress lifetime reproductive success substantially (Curio, 1988; Linden and Møller, 1989). For example, Coulson (1984) reasoned that common eider (*Somateria mollissima*) refrain from breeding in years of low adult survival in order not to incur further survival costs or reductions in future reproductive success, while Aebischer and Wanless (1992) made similar adaptive arguments for skipped breeding in European shags *(Phalacrocorax aristotelis*). The capacity to regulate breeding effort by skipping in certain years (i.e., adaptive phenotypic plasticity in breeding propensity) would presumably only evolve if cues are available to individuals prior to the breeding season that reliably correlate with environmental conditions later in the year (including potentially the following winter) that actually determine the fitness costs of reproduction (Erikstad et al., 1998; Bårdsen et al., 2011).

Non-adaptive explanations suggest that skipping breeding in some years is itself not advantageous, but rather an unavoidable outcome of other events. For example, Danchin and Cam (2002) found that black-legged kittiwakes (*Rissa tridactyla*) that changed breeding areas between years were 1.7 times more likely to skip breeding than those that remained in the same area. They argued that adult non-breeding may thus be a cost of breeding dispersal, given that dispersers often struggle to find a new breeding site or mate (Danchin and Cam, 2002). Similarly, experienced adults may have no option but to skip breeding following forced eviction from their previous breeding site or divorce from their previous mate (Harris and Wanless, 1995; Kokko et al., 2004; Jeschke et al., 2007). Skipping may therefore be non-adaptive in the sense that breeding propensity itself is not the direct target of selection, although it may be affected by other behaviors and traits (e.g., breeding dispersal, mate fidelity, resource gathering abilities) which *are* potential targets of selection. In reality, adaptive and non-adaptive explanations may both apply and skipping may be linked to future survival or reproductive success through both causal and non-causal mechanisms (Cam et al., 1998; Danchin and Cam, 2002). Moreover, individuals may vary in resource acquisition abilities or other traits that influence their physiological state, which in turn affects their ability to breed (Mills, 1989; Harris and Wanless, 1995; Cam et al., 1998; Cubaynes et al., 2011). While such individual heterogeneity may obscure trade-offs between current breeding and survival/future reproduction, it does not mean they do not exist: the fitness consequences of skipping may simply be different for different classes of individuals (Cam et al., 1998) and some may be better able to bear the costs of reproduction than others (Robert et al., 2012).

Among marine top predators, which tend to be long-lived, intermittent breeding is relatively common and variation in breeding propensity has been shown to have a strong influence on population numbers (Aebischer and Wanless, 1992; Jenouvrier et al., 2005a; Forcada et al., 2008). Climate may influence breeding propensity of marine top predators directly, for example if climate variables are used as cues to regulate breeding effort or if the survival benefits of non-breeding depend on weather conditions (Erikstad et al., 1998; Robert et al., 2012), or indirectly via bottom-up or top-down effects on marine ecosystems (Frederiksen et al., 2006). Few studies, however, have tested for associations between climate variables and breeding propensity and most have done so only at the population level (e.g., Jenouvrier et al., 2005a; Mills et al., 2008; Cubaynes et al., 2011). Given the global trend in climate warming (Solomon, 2007) coupled with increased climate variability (Rahmstorf and Coumou, 2011; Seager et al., 2012) there is a need to better characterize and understand such associations in wild populations and the conservation implications. Moreover, very little is known about individual-level patterns or fitness consequences of skipped breeding in marine top predators (Cam et al., 1998; Danchin and Cam, 2002), information that is important to predicting the evolutionary and demographic consequences of climate change (Forcada et al., 2008).

The aim of the current analysis was to shed light on these issues using long-term, individual-based data on common guillemots (*Uria aalge*) from a well-studied colony in Scotland. Common guillemots are long-lived and lay a single-egg clutch. Species with such a life history are good candidates for investigating potentially adaptive adult non-breeding because they (a) are expected to be prudent parents, given the importance of longevity to their lifetime reproductive success (Moreno, 2003; Reed et al., 2008), and (b) have fewer options than species that lay multiple eggs when it comes to adjusting reproductive effort (Cubaynes et al., 2011). While they could adjust investment in the single egg or chick in response to changes in the environment (e.g., Erikstad et al., 1997), not breeding in the first place may be less costly in terms of future fitness. Common guillemots from our study colony spend the winter months in the shallow southern North Sea (Reynolds et al., 2011), an area that has experienced extreme local warming rates over the past 30 years (Rayner et al., 2003). Previous studies of common guillemots have established links between demographic rates or phenology and marine climate experienced both locally around the breeding colony and further afield in the wintering area (e.g., Frederiksen et al., 2004a; Sandvik et al., 2005; Votier et al., 2008; Reed et al., 2009). We therefore (1) tested for population-level associations between breeding propensity and climate-related variables measured at different temporal and spatial scales, (2) investigated whether individuals varied in their climate responses, (3) tested for effects of age and sex on breeding propensity, and (4) explored the individual-level fitness consequences of skipping.

MATERIALS AND METHODS

STUDY SPECIES, SITE, AND DATA COLLECTION METHODS

Common guillemots (hereafter guillemots) are medium-sized seabirds with a circumpolar distribution in temperate and subarctic waters of the North Atlantic and North Pacific. They breed on cliffs from the age of 5 or 6 years and can live for 30 or more years (for general information, see Harris and Birkhead, 1985; Gaston et al., 1998). The data used here were collected as part of a long-term study on the Isle of May, Firth of Forth, Scotland (56°11′ N, 2°33′ W). Since 1982, breeding guillemots of unknown age in five study areas of varying cliff topography and bird density have been caught and fitted with unique metal and color leg-rings under license from the British Trust for Ornithology. Every year additional breeding adults are ringed to replace those disappearing from the study population to maintain sample size.

Average age of birds ringed in the earliest cohorts was assumed to be older than that of later cohorts, as new birds caught after the first few years of the study were likely to be (although could not be confirmed as) first-time breeders (Harris and Wanless, 1995; Crespin et al., 2006). The study areas were viewed from permanent hides 10–20 m away. All breeding sites were numbered on large photographs and the identities of both adults at all sites were ascertained several times every season. Intense searches were carried out at least daily throughout the breeding season to determine whether ringed birds (1) were present in the colony, (2) held a breeding site, (3) laid an egg, and (4) successfully fledged a chick, i.e., left the colony when aged at least 14 days old (Harris and Wanless, 1988). Particular attention was paid to adjacent areas to ensure that birds resident outside the main study plots were not overlooked. At this colony guillemot pairs typically persist across multiple years (Jeschke et al., 2007) and birds were sexed by observations of copulations. The dataset comprised 9741 records (bird-year combinations) over 33 years from 891 ringed individuals (412 females, 442 males, 37 sex unknown). For further details on the study population see Harris and Wanless (1988).

DEFINING AND MEASURING SKIPPED BREEDING

High-quality breeding sites are limited in this colony and fiercely contested (Kokko et al., 2004). Across all breeding seasons (1982–2014), an annual average of 7.1% (696/9741) of individuals that had bred at least once did not hold a site. The majority (86.1%, 599/696) of these siteless birds were recorded non-breeders in the colony, while the remainder (97/696) were not seen in that year (**Figure 1**). Observer effort remained very high over the study period and resighting probabilities (i.e., the probability that an alive bird was seen in a given breeding season on the island) of birds ringed as adults, as estimated from an integrated Bayesian analysis of mark–recapture–recovery data (Reynolds et al., 2009), were also very high and consistent across years (always >93%). Non-breeding guillemots spend much time in the colony near their last breeding site. Although it is not possible to say with 100% certainty that an unrecorded bird was not present somewhere in the colony, this seems very unlikely and we assume a detection probability for birds present in the colony (as breeders or non-breeders) of 1.00. Thus, we are confident that any ringed birds not seen in a given year did not actually return to the colony, but rather spent the summer somewhere away from the island (e.g., offshore). We defined skipped breeding as where an individual which bred previously was either seen somewhere in the colony during the breeding season without a breeding site, or was not seen in that breeding season but was seen in a subsequent season. This measure of skipping excluded cases where a bird was not seen that year and then never seen again (and therefore presumed to be dead), but it includes consecutive skipping events so long as the bird was seen again. The proportion of birds skipping could not be calculated for the 2014 breeding season, as birds not seen in this year may still be alive (confirming this requires resighting them in future years). The estimate for 2013 might also be an underestimate for the same reason. Birds observed without a site in their last year of being seen were defined as having skipped.

By this definition, "breeders" or "non-skippers" were adults that held a site during the breeding season, and an annual average of 92.9% (9045/9741) of known individuals fell into this category (**Figure 1**). The majority (99.1%, 8962/9045) that held a site bred i.e., an egg was recorded. Birds holding a site where no egg was recorded were included in the non-skippers category as we considered that they had made a substantially larger commitment than had those without a site. However, the results and conclusions were unchanged when they were included in the skippers category (results not presented).

STATISTICAL ANALYSES

For the population-level analysis, the annual incidence of skipping was quantified by summing the number of birds that skipped each year and dividing by the total number of birds (i.e., skippers + non-skippers). Similarly, for the individual-level analyses the incidence of skipping was a binary variable with a value of one assigned to birds that skipped, and a value of zero assigned to birds that did not skip. The data were then analyzed via logistic regression using either generalized linear models (GLMs, population-level analyses) or generalized linear mixed models

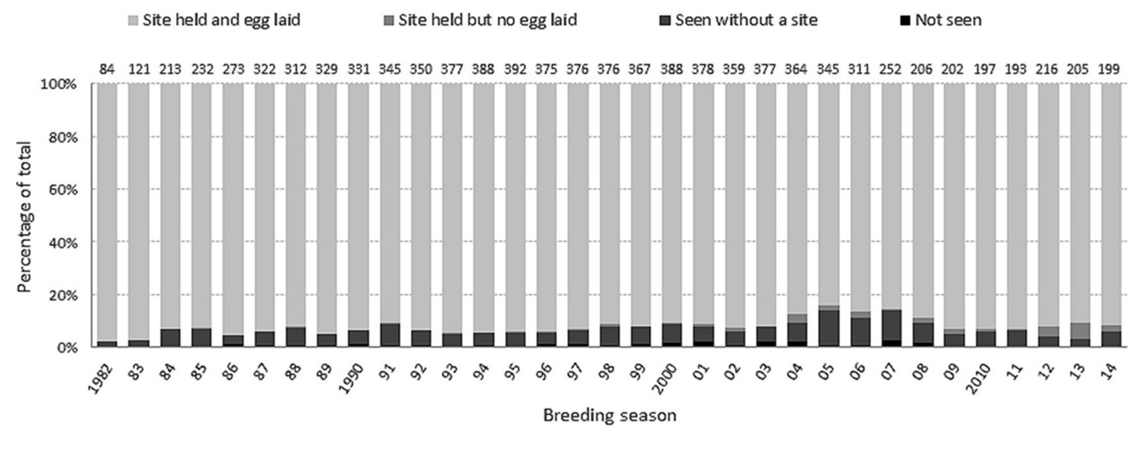

FIGURE 1 | Breakdown by breeding season of the percentage of birds in each category. Non-skipping encompasses the first two categories (site holders) and skipping encompasses the last two (seen without a site or not seen but known to be alive).

(GLMMs, individual-level analyses). Some previous studies (e.g., Cam et al., 1998; Forcada et al., 2008; Cubaynes et al., 2011; Sanz-Aguilar et al., 2011) used multi-state capture–recapture (or multi-event) models to estimate rates of adult non-breeding when non-breeders are unobservable (e.g., because they remain at sea during the breeding season). In our study, however, average resighting probability was extremely high (∼96%; Reynolds et al., 2009) so our estimates of breeding propensity were not unduly biased by recapture probabilities less than one (see also Danchin and Cam, 2002 for a similar justification for using logistic regression, rather than a multi-state mark recapture approach, to analyze factors influencing breeding status).

Population-level analyses

The population-level analyses tested for significant relationships between annual breeding propensity and candidate annual covariates linked directly or indirectly to climate. Guillemots disperse widely outside of the breeding season and ringing recoveries and data from geolocators indicate that in December and January adult guillemots from the Isle of May are concentrated in the southern North Sea (Reynolds et al., 2011; Harris et al., in press), although birds are also known to attend the breeding colony intermittently throughout the non-breeding season (Harris and Wanless, 1989, 1990). Weather or oceanographic conditions experienced in the winter range may therefore have a direct or indirect effect on annual breeding propensity via cues or constraints. Sea surface temperature (SST) is a good candidate variable in this regard, given that (a) birds may be able to directly sense SST or other closely correlated atmospheric/oceanographic variables and use this as a predictive cue for breeding decisions, and (b) SST correlates with various demographic rates in seabirds in the North Sea/Northeast Atlantic region (e.g., Frederiksen et al., 2004b; Sandvik et al., 2005). Weekly SST data were obtained from NOAA (Optimum Interpolation SST V2 obtained from http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html) for two regions of the North Sea. The first corresponded to the winter range (51–56°N, 1–5°E) and values were averaged for the months November, December and January (hereafter "winter range SST" or wSST). The second was an area in the immediate vicinity of the breeding colony (55–57°N, 3–0°W) and values were averaged for February and March (hereafter "local spring SST," locSST). The latter was included to capture environmental conditions that might affect breeding propensity prior to the breeding season, when birds are likely to forage closer to the breeding colony. We tested for lagged effects (1 year lag) of both SST variables, given that SST may affect seabird vital rates indirectly through the food chain (Frederiksen et al., 2006; Lahoz-Monfort et al., 2013). We also considered the winter North Atlantic Oscillation Index (wNAO, Hurrell, 2014), a broad-scale proxy measure that correlates well with life history traits and population dynamics of North Atlantic seabirds (Reid et al., 1999; Durant et al., 2004; Grosbois and Thompson, 2005; Reed et al., 2006; Sandvik et al., 2008, 2012). The wNAO index is the mean December–March value for year *t*, where December is in year *t*-1. Lagged effects of NAO have been documented for seabirds (Lewis et al., 2009; Sandvik et al., 2012) so we also considered a lag of 1 year. Finally, we considered an effect of population size (the annual count of breeding guillemots on the Isle of May) to test for density dependence.

As a preliminary step, we first tested for time trends in the annual frequency of skipping and each of the explanatory variables. The plot of annual skipping frequency vs. year (**Figure 2A**) suggested a non-linear trend, while exploratory analyses indicated temporal autocorrelation in the raw values at a lag of 1 year. A generalized additive model was therefore fitted to the time series, allowing for an auto-regressive serial correlation structure, using the gamm function in the R package mgcv (Wood, 2006). This uses cross-validation to estimate the optimal amount of smoothing for the continuous variable "year" and a normal error distribution was assumed. Three different models were compared: one with no residual correlation structure (i.e., residuals assumed to be independent) and models with serial correlation structures of orders one and two (i.e., lagged residual correlations of one and two years), respectively. The model with the lowest AIC was chosen as the best descriptor of the time series (Zuur et al., 2009). The same process was repeated for each of the candidate explanatory variables to test for temporal trends in each (**Figures 2B–E**). Pair-wise Pearson correlations among all explanatory variables were also tested for.

Next, a series of nested GLMs with logit link functions and binomial errors were fitted where the response variable was a concatenated vector of the number of birds that skipped breeding each year and the number of birds that did not skip. The full model consisted of additive effects of each annual covariate. and this was simplified using backwards selection, where each explanatory variable was dropped, in turn, and each time an analysis of deviance test applied (with the difference in deviance between nested models assumed to follow a chi-squared distribution with one degree of freedom). The variable with the highest *P*-value was removed, and then the process was repeated until all remaining variables were significant at the 5% level (Zuur et al., 2009). Interactions were not tested for as there were too few data points.

Individual-level analyses: explaining variation in skipping

A population-level relationship between breeding propensity and the environment could occur without necessarily existing within individuals (**Figure 3**). To characterize individual-level patterns, a GLMM was fitted where the binary response variable indicated whether the individual skipped or not that year. The population-level analysis revealed significant effects of wSST and lagged wSST (see Results). For the individual-level analysis, we focussed on the unlagged effect of wSST, as GLMMs including wSST, lagged wSST and their interactions with age and sex did not converge. To separate within- and between-individual effects of wSST, a technique known as "within-subject centering" (van de Pol and Wright, 2009) was used, which involved first calculating the mean value of wSST (wSST_mean) for each individual and then expressing annual values as deviations from this mean (wSST_dev). Both wSST_mean and wSST_dev were then included as fixed effects in the GLMM, with the former corresponding to the between-individual effect and the latter to the within-individual effect (see **Figure 3**). Fixed effects of sex (two-level factor: males and females; unknowns excluded) and years since ringing (as a proxy

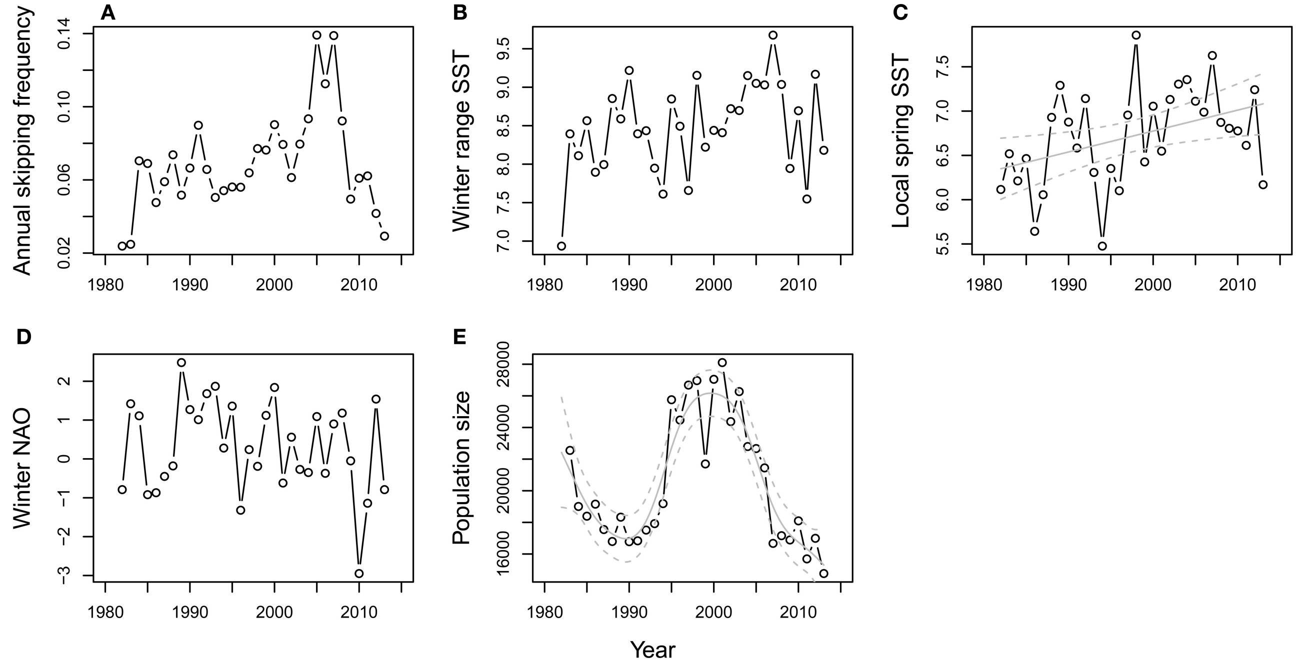

FIGURE 2 | Temporal trends in annual skipping frequency and the covariates considered in the population-level analyses. Trend in **(A)** annual skipping frequency, **(B)** winter range SST, **(C)** local spring SST, **(D)** winter NAO, and **(E)** population size. Significant GAM fits (± confidence bands) are included in gray for local spring SST and population size.

for age, see Crespin et al., 2006) and years since ringing squared were included. Models including two-way interactions did not converge so we only considered main effects. A random effect of year was included to account for interannual variation in skipping not captured by the fixed effects. A random effect of individual was included to account for non-independence of multiple measures of skipping on the same individual (and to quantify the magnitude of between-individual differences in average skipping propensity). Three random effects structures were compared: (1) random intercepts, (2) random intercepts and random slopes for the wSST deviation effect, correlation between intercept and slope constrained to zero; and (3) random intercepts and random slopes with the correlation estimated. The best random effects structure was chosen on the basis of likelihood ratio tests, including all fixed effects in each case regardless of the their statistical significance (Zuur et al., 2009, p. 121). Once the best random effects structure was found, non-significant fixed effects were then dropped sequentially from the model (using analysis of deviance tests) until all remaining terms were significant at the 5% level.

Individual-level analyses: fitness consequences of skipping

A GLMM was used to test the effect of skipping in year t on breeding success in year $t + 1$. The response variable was binary $1 =$ chick raised successfully in year $t + 1$, $0 =$ failure. This analysis was restricted to cases where an egg was laid in year $t + 1$. "Previous status" was defined as a factor with three levels: $1 =$ skipped breeding in year t; $2 =$ bred unsuccessfully in year t; $3 =$ bred successfully in year t. The fixed effects were previous status, sex, years since ringing and years since ringing squared. Random effects of individual and year were included. A similar GLMM was fitted with probability of skipping in year $t + 1$ as the response.

Finally, we calculated a proxy for lifetime reproductive success (LRS) for individuals that had disappeared (presumed dead) before 2013. Although it is rare for individuals not to be seen for two consecutive years, individuals not seen in 2013 or 2014 were excluded from this analysis since they could still have been alive. The first 3 years of the dataset were also excluded as individuals first caught at the start of the study were likely to have bred before. This gave relatively complete breeding life histories of 660 individuals (6841 bird-year combinations). For each individual, LRS was calculated by summing the number of chicks produced over their breeding lifespan. A generalized additive model (GAM) with LRS as the Poisson response variable (log link function) was then fitted, with smoothers for the effects of breeding lifespan (number of years from first capture to disappearance) and mean skipping propensity (proportion of years skipped) using cross validation (Wood, 2006), as exploratory analyses indicated non-linear effects. A GAM was also used to test for a relationship between breeding lifespan (response variable, Poisson error and log link function) and skipping frequency. To avoid over-fitting, these GAMs were constrained to have fixed degrees of freedom and three knots (Wood, 2006). All models were fitted in R version 3.1.1 (R Core Team, 2014). GLMMs were fit using the glmer function from the lme4 package (Bates et al., 2012).

RESULTS

TEMPORAL TRENDS

The annual covariates included as candidate explanatory variables in the population-level analysis were correlated to some degree; for example, wSST and locSST were correlated with $r = 0.69$ (Supplementary information, Table A1). The time series for annual skipping propensity and each explanatory variable are shown in **Figure 2**. The best GAM for annual skipping propensity indicated there was temporal autocorrelation with a lag of 1 year (i.e., years of high skipping propensity were followed by years of high skipping propensity). When this residual autocorrelation was taken into account, the smoother for the year effect was effectively linear and not significantly different from zero (estimated $df = 1$, residual $df = 1$, $F = 0.43$, $P = 0.52$), i.e., there was no evidence for a directional trend over time. The best model for wSST indicated no temporal autocorrelation in the residuals and a marginally non-significant positive effect of year (GAM smoother: estimated $df = 1$, residual $df = 1$, $F = 4.00$, $P = 0.054$). Similarly, the best model for locSST indicated no temporal autocorrelation in the residuals and a positive effect of year (GAM smoother: estimated $df = 1$, residual $df = 1$, $F = 6.06$, $P = 0.02$). No trend (GAM smoother: estimated $df = 1$, residual $df = 1$, $F = 1.20$, $P = 0.28$) or temporal autocorrelation in the residuals was apparent for wNAO. A significant non-linear trend in population size was present over the study period (GAM smoother: estimated $df = 6.33$, residual $df = 6.33$, $F = 23.38$, $P < 0.001$) with no temporal autocorrelation in the residuals after accounting for this trend.

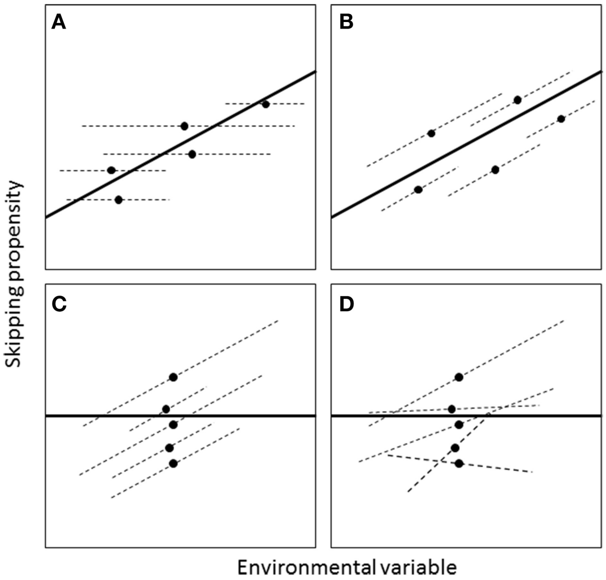

FIGURE 3 | Four different scenarios for how the effect of an environmental variable on skipping propensity may differ at the between- and within-individual levels (adapted from van de Pol and Wright, 2009). The relationships are assumed to be linear on the transformed (e.g., logit) scale. Each panel depicts five hypothetical individuals that vary both in their mean skipping propensity (black dots) and in the environmental conditions they experience (e.g., because they are born in different years or vary in lifespan). The dark lines are regressions fitted to the black dots and represent the between-individual effect. The dashed lines are within-individuals effects. In **A**, there is no relationship within individuals but an effect across individuals; in **B**, the within- and between-individual effects are the same; in **C** and **D**, the effect is present within but not across individuals. In **A–C**, there is no variation in within-individual slopes, but in **D** there is.

POPULATION-LEVEL ANALYSIS

The mean annual frequency of skipping was 0.07 and ranged from 0.02 to 0.14. The annual frequency of skipping was positively associated with wSST in the same year (**Figure 4A**, **Table 1**) and in the previous year (**Figure 4B**, **Table 1**). None of the other annual covariates were associated with annual skipping frequency (**Table 1**).

INDIVIDUAL-LEVEL ANALYSES

The GLMM with skipping as the binary response indicated that the effect of wSST was present within individuals (effect of wSST_dev: $\chi^2 = 9.66$, $df = 1$, $P = 0.002$) but not across individuals (effect of wSST_mean: $\chi^2 = 2.25$, $df = 1$, $P = 0.13$). The estimate from the GLMM for the term wSST_dev was 0.38 ± 0.12, which compares with an overall effect of winter range SST in the population-level analysis of 0.37 ± 0.08 (**Table 1**), indicating that the cross-sectional relationship mirrors the underlying

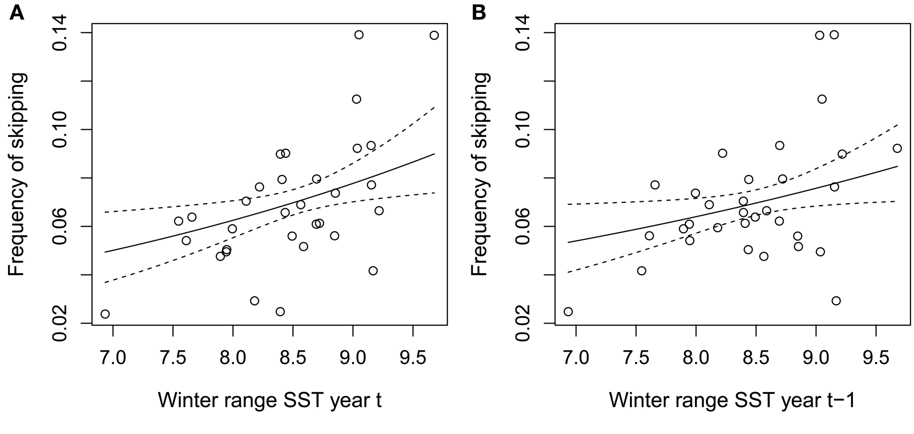

FIGURE 4 | Annual skipping frequency as a function of (A) winter range SST in year *t* and (B) winter range SST in year *t*-1. Regression fits with confidence bands are shown (back-transformed from logit scale).

within-individual effect. The best random effects structure was one with uncorrelated random intercepts and slopes. A likelihood ratio test indicated that this model was better than one with just random intercepts ($\chi^2 = 4.98$, $df = 1$, $P = 0.026$), while a model with correlated random intercepts and slopes was not supported ($\chi^2 = 1.08$, $df = 1$, $P = 0.30$). Sex did not have an effect on skipping propensity ($\chi^2 = 1.75$, $df = 1$, $P = 0.18$). The overall quadratic effect of years since ringing (**Figure 5**) was highly significant ($\chi^2 = 81.89$, $df = 2$, $P < 0.001$), but the linear component was not significantly different from zero ($\chi^2 = 0.002$, $df = 1$, $P = 0.96$). The between-individual variance in skipping propensity (variance in intercepts) was much larger than the between-year variance (2.86 vs. 0.02, both on logit scale; variance in slopes = 0.49). These results indicate that the individual-level patterns are most consistent with scenario D in **Figure 3**.

Table 1 | GLM results for the population-level analysis of annual skipping frequency.

Variable	Estimate	Standard error	LRT	*P*
Intercept	−7.62	0.89	–	–
Winter range SST (year *t*)	0.37	0.08	28.69	< 0.001
Winter range SST (year *t*−1)	0.21	0.08	7.78	0.005
Local spring SST (year *t*−1)	–	–	1.34	0.25
Population size	–	–	0.82	0.37
Local spring SST (year *t*)	–	–	0.54	0.46
Winter NAO index (year *t*−1)	–	–	0.28	0.60
Winter NAO index (year *t*)	–	–	0.16	0.69

Estimates and standard errors are shown only for those terms retained in the final minimum adequate model. LRT, likelihood ratio test statistic, assumed to follow a χ^2 distribution; P, p-value from LRT.

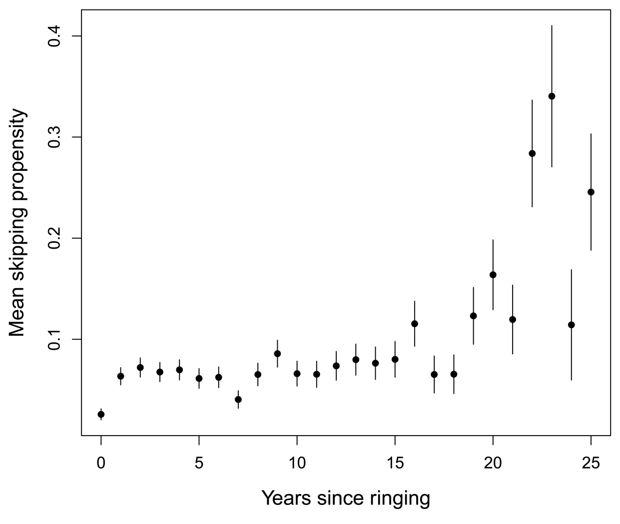

FIGURE 5 | Mean skipping propensity as a function of years since ringing (proxy for age). Data points are means ± standard errors for each age class.

Individuals that skipped breeding in year t had lower breeding success in year $t + 1$ than individuals that bred in year t but failed, which in turn had lower breeding success in year $t + 1$ than individuals that bred successfully in year t (**Figure 6A**, effect of previous status: $\chi^2 = 406.47$, $df = 2$, $P < 0.001$). Sex had no effect on breeding success ($\chi^2 = 0.15$, $df = 1$, $P = 0.70$). The quadratic effect of years since ringing (our proxy for bird age) on breeding success in year $t + 1$ was highly significant ($\chi^2 = 54.05$, $df = 2$, $P < 0.001$), with breeding success being lower at older minimum inferred ages (**Figure S1**). Individuals that skipped breeding in year t had a higher probability to skip in year $t + 1$ than individuals that bred but failed, which in turn had a higher probability to skip in year $t + 1$ than individuals that bred successfully in year t (**Figure 6B**, effect of previous status: $\chi^2 = 379.98$, $df = 2$, $P < 0.001$), controlling for the significant quadratic effect of minimum inferred age ($\chi^2 = 36.94$, $df = 2$, $P < 0.001$).

Among those individuals with complete breeding histories, those that skipped breeding more frequently produced fewer chicks on average across their breeding lifespans (**Figure 7A**), controlling for the fact that individuals with longer breeding lifespans had higher LRS (**Figure 7B**). The GAMs indicated that these effects were slightly non-linear (effect of skipping frequency: estimated $df = 2.55$, residual $df = 3.19$, $\chi^2 = 285.6$, $P < 0.001$; effect of breeding lifespan: estimated $df = 6.11$, residual $df = 7.27$, $\chi^2 = 2899.9$, $P < 0.001$; overall deviance

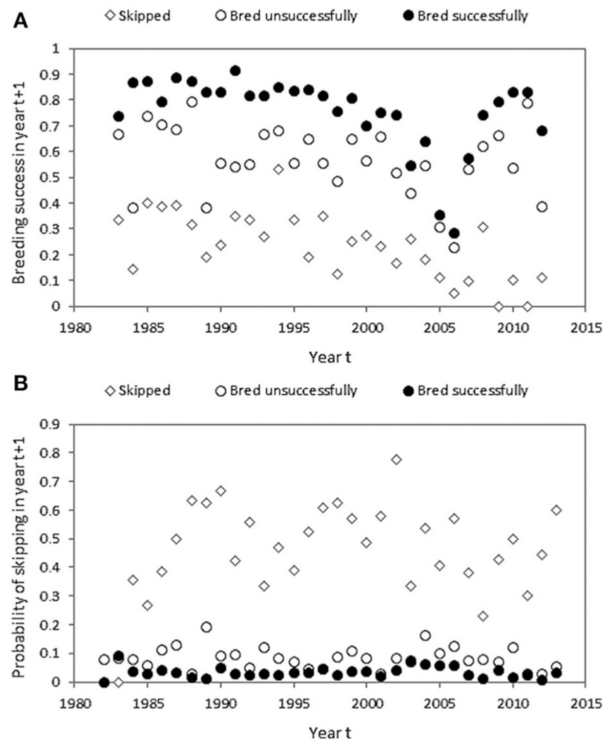

FIGURE 6 | (A) Breeding success in year $t + 1$ conditional on previous status in year *t*. **(B)** Probability of skipping breeding in year t+1 conditional on previous status in year *t*.

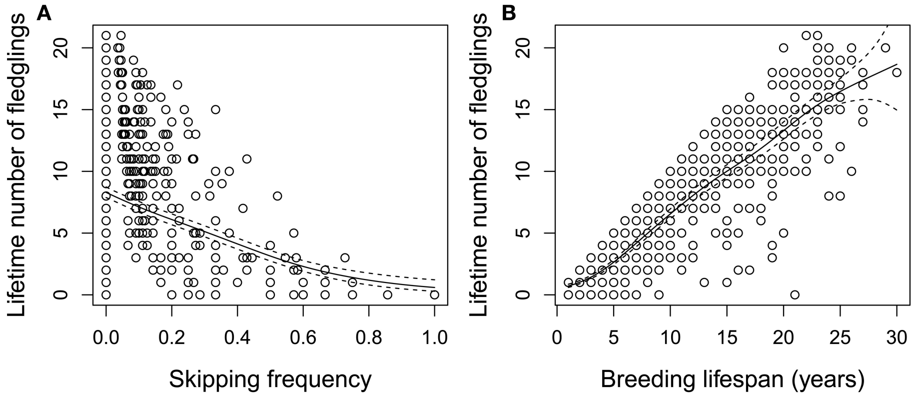

FIGURE 7 | (A) Lifetime number of fledglings as a function of skipping frequency (fraction of breeding lifespan where adult did not breed) for individuals with complete life histories ($n = 660$). **(B)** Lifetime number of fledglings as a function of breeding lifespan for same individuals. Predicted fits with confidence bands from generalized additive model are included.

explained = 85.1%). An asymmetric non-linear relationship between skipping frequency and breeding lifespan was found (**Figure S2**; estimated $df = 2$, residual $df = 2$, $\chi^2 = 30.9$, $P < 0.001$; deviance explained = 5.0%): individuals that skipped approximately 30% of the time had the longest breeding lifespans, while both individuals that skipped very infrequently and those skipping more frequently lived less long.

DISCUSSION

A relatively low absolute rate of skipping was found for guillemots on the Isle of May, with only 7% of birds skipping on average across the study period. Nonetheless, skipping was more frequent in years where SST in their wintering area in the southern/western North Sea were high the preceding winter and also the one before i.e., ca.15 months prior to the breeding season. Ringing recoveries and tracking studies indicate that guillemots from the Isle of May disperse widely throughout the North Sea during the winter months, with the core of the winter distribution centering on the southern and western North Sea (Reynolds et al., 2011; Harris et al., in press). North Sea temperatures have increased gradually over the past several decades in line with rising global air temperatures, but the rates of warming observed in the southern North Sea (most of which is <50 m deep) are among the highest documented anywhere in the world (Rayner et al., 2003; Heath et al., 2012). A direct effect of higher SSTs on breeding propensity seems less likely than indirect effects mediated via changes in the food web, particularly given that lagged effects of wSST were also found. The little information available on the winter diet of guillemots indicates that many fish species are taken, in particular clupeids, gadids, and sandeels (e.g., Blake et al., 1985; Harris and Bailey, 1992; Sonntag and Hüppop, 2005). The mechanisms by which increases in wSST might filter through the marine food web to affect the breeding propensity of guillemots are unclear but recruitment rates of lesser sandeels (*Ammodytes marinus*), which are an important prey species for guillemots during the breeding season but may also be taken during winter months, correlate negatively with winter SSTs in the North Sea (Arnott and Ruxton, 2002). Herring (*Clupea harengus*) are another oil-rich small pelagic fish taken by guillemots during winter months (Blake et al., 1985; Harris and Bailey, 1992; Sonntag and Hüppop, 2005) and positive correlations between SSTs and herring recruitment and stock biomass have been reported in the Barents Sea (Hjermann et al., 2004). These findings and others indicate that changes in SST and other physical oceanographic variables can have complex food web effects (Durant et al., 2004; Frederiksen et al., 2007). The net impacts on the body condition and hence breeding propensity of piscivorous seabirds may in general be difficult to predict.

In long-lived species with low annual reproductive output population growth rate is often most sensitive to changes in adult survival and these species are expected to favor self-maintenance over reproduction when conditions are poor (Curio, 1988; Linden and Møller, 1989; Sæther and Bakke, 2000). Fitness in marine top predators may therefore be maximized by minimizing interannual variance in adult survival: so-called life-history buffering against environmental variability (Morris and Doak, 2004; Forcada et al., 2008). Recent work on Antarctic mammals and seabirds has shown that variation in annual breeding propensity can also strongly influence individual fitness and population growth (Jenouvrier et al., 2005b; Forcada et al., 2008). In the case of Antarctic fur seals *Arctocephalus gazella*, increased ecosystem fluctuations associated with increased climate variability since 1990 seems to have reduced their capacity for life-history buffering, as evidenced by an increasing impact of SST variation (which affects abundance and predictability of krill, a key food source for fur seals) on adult survival and breeding propensity (Forcada et al., 2008). Cubaynes et al. (2011) found that a higher fraction of red-footed boobies (*Sula sula*) skipped breeding in El Niño years (associated with high SSTs), which are predicted to become more frequent or intense as result of global warming (Jackson, 2008). Similarly, increases in the mean or variance of pre-breeding SSTs could lead to a loss of life-history buffering abilities in guillemots with possible consequences for population numbers and structure. On the other hand, annual rates of skipping are relatively low in this population and the breeding propensity of guillemots appears to be less sensitive to environmental fluctuations than that of European shags on the Isle of May, where up to 60% of adults may skip breeding in extremely poor years when crashes in population size also occur (Aebischer and Wanless, 1992). Cormorant species in general are prone to such periodic population crashes and rates of non-breeding are also typically highly variable (Duffy, 1983; Boekelheide and Ainley, 1989; Nur and Sydeman, 1999). Thus, population impacts of climate change mediated via changes in breeding propensity will depend on the life history strategy and ecological constraints of the species in question; some species likely have greater scope for regulating breeding effort than others.

A relationship between climate and skipping frequency was present within individuals, as evidenced by a significant effect of wSST_dev in the individual-level GLMM. No across-individual relationship was found between mean skipping propensity and wSST_mean; such a relationship could have arisen if individuals consistently spent the winter in different areas, or lived through different periods, and hence experienced warmer or cooler temperatures on average. Individuals varied in their sensitivity to wSST (as in **Figure 3D**) in that variation among individuals in the slope of their skipping-wSST relationship was greater than expected by chance. Such a pattern could reflect individual variation in cue sensitivity, individual differences in the extent to which the environment imposes constraints on breeding propensity, or both. We cannot distinguish definitively in this observational study whether cues or constraints are more important, but the constraints hypothesis seems more likely. First, some individuals were consistently more likely to skip breeding than others and were also more likely to breed unsuccessfully if they did breed the year after having skipped (**Figure 6**). Skipping tends to occur after a bird loses its breeding site to another individual and hence may be socially-induced (Harris and Wanless, 1995), but our analysis indicates that environmental factors (i.e., wSST) also play a role. One possibility is that certain individuals may be in poorer body condition following a difficult winter than others and hence be less capable of defending their nest site against incursions (fights are energetically costly) and so be evicted by a competitor. Non-breeding adult black-legged kittiwakes at a colony in Brittany (France) were shown to have lower survival rates than breeders (Cam et al., 1998) and to be more likely to skip again the following year. Our guillemot studies and the studies of Cam et al. (1998) thus suggest persistent between-individual phenotypic differences that influence a range of fitness components such as breeding propensity, breeding success and adult survival (see also Le Bohec et al., 2007; Robert et al., 2012). Understanding how such "quality" effects arise in the first place, are maintained throughout the lives of individuals and whether they are transmitted from parents to offspring constitutes a major challenge for evolutionary ecology in general (Wilson and Nussey, 2010; Bergeron et al., 2011).

Second, if individuals base their decision of whether to breed or not on predictive cues then one would expect some fitness advantage to skipping in poor years. The most obvious such advantage would be an increase in survival probability from one breeding season to the next compared to individuals that did breed, as predicted by the life history buffering hypothesis. A multi-year study of king penguins *Aptenodytes patagonicus* found that non-breeders and breeders had similar survival rates, but breeders were less likely to breed again the following year than non-breeders, suggesting the existence of reproductive costs and hence benefits of prudent skipping (Le Bohec et al., 2007). Cam et al. (1998), on the other hand, found that non-breeding kittiwakes survived less well than breeders, as did previous work on Isle of May guillemots (Harris and Wanless, 1995). In the current study we did not test for survival rate differences between individuals skipping vs. those breeding, but examined overall lifetime breeding success. Lifetime fledgling production declined monotonically with skipping frequency, controlling for the positive effect of breeding lifespan (**Figure 7**). If skipping when conditions are poor is advantageous, then one would expect a hump-shaped relationship between individual-level skipping frequency and lifetime number of fledglings, because individuals that never skip might suffer survival or future reproductive costs, while those that skip too frequently ("over-responders") would likely also raise fewer chicks on average. We found no such optimum. Again, this points toward the constraints rather than restraints (adaptive life history buffering) hypothesis.

Third, it is difficult to imagine that environmental cues are available to individuals during the winter or early spring (when guillemots may be far away from the breeding colony) that reliably correlate with environmental factors determining the fitness consequences of breeding decisions. A string of years of poor breeding success occurred at this colony from 2004 to 2008 (**Figure S3**), associated with poor feeding conditions around the breeding colony (Ashbrook et al., 2010). Skipping frequency was also noticeably higher during this period (**Figure 2A**), which would be consistent with the restraint hypothesis, i.e., birds "chose" to skip when breeding conditions were perceived in advance to be poor. Indeed, wSST (the putative cue) is correlated negatively with annual breeding success ($r = -0.51, P = 0.003$) and annual skipping frequency and breeding success are also negatively correlated ($r = -0.69$, $P < 0.001$). However, correlations between wSST, skipping propensity and breeding success do not constitute strong evidence that wSST acts as a cue for adaptive restraint and could instead reflect carry-over effects of winter conditions on both skipping propensity and breeding performance of individuals that do lay an egg (e.g., mediated via changes in body condition). The costs, in terms of residual reproductive value, of breeding under poor conditions are paid after the breeding season, not during it. If these future costs depend on the environment (e.g., survival chances of breeders are lower than non-breeders in harsh winters) then one would expect flexible skipping rules to evolve, but only if environmental cues perceived prior to the breeding season predict post-breeding survival chances, or future breeding success. Rephrased in the language of adaptive plasticity theory, the environment of decision making must predict the environment of selection (Gavrilets and Scheiner, 1993). If such cues are not available or reproduction costs are independent of the environment, then selection would instead favor a fixed, environmentally-insensitive rate of skipping (i.e., flat reaction norms). Nonetheless, the notional cost of responding to a weakly predictive cue by not breeding (in terms of foregone offspring production when conditions turned out to be good) may be considerably less than the cost of making a bad decision, i.e., breeding under circumstances that turn out to be bad and hence jeopardizing one's own survival. Such asymmetry in fitness outcomes under good vs. bad conditions may favor the evolution of risk-averse strategies (Bårdsen et al., 2008), and hence flexibility in breeding propensity may be adaptive even when environmental cues are only weakly informative of future costs. Given the lack of any discernible fitness benefits of skipping in our case, however, we tentatively infer that the observed relationship with winter SST reflects (individual-specific) constraints on breeding condition, rather than adaptive restraint in response to a cue. An interesting alternative, which we cannot fully exclude, is that individuals use their own body condition (which may be affected by environmental variation) as a cue and skip breeding if they are below a certain threshold (i.e., condition-dependent decision making). If inter-individual variation in condition is large, a positive relationship between current breeding and future breeding (and hence LRS) may be found, because those individuals that are in good condition breed now and are successful again later. Those skipping, however, may still have made an adaptive choice under their specific circumstances (particularly if poor body condition is associated with higher post-breeding mortality risk) and might have had even lower LRS if they had instead bred. The fact that individuals that never skipped had shorter lifespans (see **Figure S2**; i.e., breeding lifespan was maximal at a skipping frequency of approximately 30%) is consistent with this hypothesis. It remains possible, therefore, that differences between studies in the apparent adaptive benefit of skipping could reflect differing amounts of inter-individual heterogeneity in body condition (or other physiological cues) in different study systems.

Finally, skipping became more frequent in very old individuals (those with a minimum inferred age of circa 15 or more, **Figure 5**). Increased frequency of skipping in the oldest age classes has also been reported in great skuas *Catharacta skua* (Catry et al., 1998), European shags (Harris et al., 1998) and short-tailed shearwaters *Puffinus tenuirostris* (Bradley et al., 2000). These patterns collectively point toward reproductive senescence effects in long-lived seabirds and clearly warrant further investigation.

LIMITATIONS OF THE APPROACH

In this study we made a number of simplifying assumptions that allowed us to analyze skipping events as a binary variable in a GLMM framework. First, we assumed that known individuals were detected during the breeding season in our study area (if present) with a probability of 1.00. That is, if a ringed bird returned to the breeding colony in a given year we were 100% confident that we would indeed detect it as a breeder or a non-breeder. All breeding pairs are monitored intensively in our study plots throughout the breeding season and non-breeding individuals are easy to resight from the hides as they simply linger around the study area without a breeding site. While it is remains possible that birds could come ashore elsewhere in the colony (and go undetected) and then return to the study area in the future, we have no record of this in 30 years of intensive searching for ringed birds. Moreover, it is extremely unlikely that any of our ringed birds not resighted in a given year bred on a different island or on the mainland since, as far as we are aware, there is no record of a guillemot changing colony once it has bred. Thus, we can be confident that our estimates of skipping frequency are not biased substantially by true detection probabilities that could be slightly lower than 1.00. Nevertheless, we acknowledge that our study system may be unusual in this regard (in that both breeders and non-breeders present at the colony can be resighted easily) and in many other systems (e.g., nocturnal burrow-nesters) detection probabilities will be much lower. In such cases, our GLMM approach should not be applied as failing to account for variation in detection probability (and possible effects of covariates on this) could result in severely biased estimates of skipping frequencies and incorrect inferences regarding the effects of covariates. A multi-event modeling framework (e.g., Cam et al., 1998; Forcada et al., 2008; Cubaynes et al., 2011; Sanz-Aguilar et al., 2011) would be more appropriate in these circumstances, although it would be interesting to test the relative performance of both techniques in a simulation study to elucidate the extent of such biases.

A second major assumption we made was that skipping events were defined conditional on future resighting: if an individual was missing in year *t* and never seen again, this was not classed as a skipping event. This means that skipping frequency may have been slightly under-estimated, especially in the last 2 years of the study, as some of these individuals might have actually been alive in year *t* but did not return to breed. Adult survival rates would then also be slightly underestimated, depending on the prevalence of skipping in the final year of life, for the same reason. In this study we used resighting histories to estimate skipping rates but not adult survival rates, but we acknowledge the above biases. While these should not have had a strong influence on our findings, such biases could be larger in other study systems and we again advise caution in applying the GLMM approach in cases where detection probabilities are lower or where additional information is unavailable (e.g., non-breeders cannot be observed or the occupancy of previous nests of non-breeders cannot be confirmed). Statistical inference and model selection with GLMMs are constantly being refined (e.g., Bolker et al., 2009; Link and Barker, 2009). As always, GLMMs should be applied cautiously, particularly when *P*-values are marginal and further confidence in findings will be instilled when different approaches (e.g., forwards vs. backwards selection) produce the same answers.

Finally, we acknowledge that correlative studies are by their nature limited and experimental studies are required to rigorously test whether skipped breeding is adaptive or not, i.e., individuals must be "moved" experimentally from their hypothesized adaptive optimum to quantify the fitness consequences of breeding decisions. This is very challenging in the case of skipped breeding as skippers would need to be forced to breed without altering other aspects of phenotype (or environment) that might influence the fitness outcome. Correlative studies, especially those that use long-term and information-rich datasets, nonetheless provide good information on possible trade-offs because in some years, or for some groups of individuals, extreme environmental conditions might indeed push individuals to make non-optimal decisions.

In conclusion, we have documented a clear link between skipped breeding in common guillemots and climate that suggests that skipping may become more frequent in a warmer, or more climatically variable, future. While we cannot definitely say whether skipping reflects an adaptive response to predictive cues or environmental constraints on breeding propensity, our results collectively point more toward the latter, particularly given that the lifetime reproductive output of individuals declined as a function of the fraction of years skipped.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fevo.2015.00001/abstract

Figure S1 | Breeding success in year $t + 1$ as a function of years since ringing (proxy for age) in year t.

Figure S2 | Breeding lifespan as function of mean skipping frequency at the individual level. Predicted fits with confidence bands from generalized additive model are included. Data were grouped for ease of plotting into 14 classes along the x-axis, but the GAM fit is based on the raw (unbinned) data.

Figure S3 | Annual mean breeding success (fraction of egg layers that successfully raised a chick) as a function of year.

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The role of climate and food availability on driving decadal abundance patterns of highly migratory pelagic predators in the Bay of Biscay

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Within the current context of changing ecosystems, many organisms are experiencing phenological changes in the timing of migration. Here, we assessed whether the abundance patterns of two trans-equatorial migrating pelagic seabirds, the great shearwater and the sooty shearwater (*Puffinus gravis* and *Puffinus griseus*, respectively), have changed over recent decades in the Bay of Biscay (BoB) in relation to the main drivers shaping their migratory journey: climatic factors and food availability. Specifically, we studied the staging dynamic by estimating dates of arrival and departure, staging duration and abundance during a 16-year temporal window (1995–2010) based on monthly at-sea observations performed onboard a commercial ferry. Climatic effects were studied at two temporal scales: oceanic winds and global oscillations indices (North Atlantic Oscillation–NAO) that represent climate variability at short and long time scales, respectively. Based on oceanic winds, we also estimated a hypothetical cost of flying on a monthly basis considering wind speed and the angle between flight and wind direction. Our results showed that both great and sooty shearwaters were influenced by the large scale NAO index but the shape of the relationship was different, while the sooty shearwater was also influenced by food availability. Thus, each species might rely on different cues before and during their migration to adjust to optimal flying conditions and foraging grounds. Both species shape their arrival in the BoB with periods of potential minimum flying costs, following their migration from the western to the eastern North Atlantic. We foresee that the quantification of flying costs can integrate different processes at the level of migration and provide a wider understanding of the migratory dynamic of pelagic predators within current changing ecosystems.

Keywords: oceanic winds, North Atlantic Oscillation, energetic ecology, trans-equatorial migration, pelagic seabird, food availability

Introduction

Many organisms are experiencing phenological changes in their life cycles and the alteration of seasonal timing has been an evident change in recent decades (Thackeray et al., 2010). This is especially true for migrating birds as a result of present climate change that have promoted shifts in the timing of migration (Gordo, 2007). Within the marine seascape, the majority of system components are changing rapidly with an increased risk of fundamental and irreversible ecological transformation (Hoegh-Guldberg and Bruno, 2010). Decades of ecological research on marine ecosystems has shown that climatic variables are primary drivers of distribution and dynamic of pelagic organisms (Roessig et al., 2004). In this sense, global climatic indices have received much attention due to their ability to capture a large part of the inter-annual climatic variations over large areas and temporal scales (see review in Stenseth et al., 2002; Gordo, 2007). In particular, the North Atlantic Oscillation (NAO), is linked to large-scale patterns in winter conditions in north-western Europe, and has been found to be correlated with many aspects of the biology of a wide range of marine organisms (Frederiksen et al., 2004).

Oceanic winds are a major component of the seascape that has seldom been considered within the current context of changing ecosystems. Recent studies have evidenced a global increasing trend in wind speed, associated with long-term climatic oscillations (Young et al., 2011). These results have important consequences for highly migratory marine species that depend on wind for traveling and foraging, such as pelagic seabirds (Weimerskirch et al., 2000; Felicísimo et al., 2008). During the non-breeding season, highly migratory seabirds follow prevailing oceanic wind patterns to reduce flight costs on long-distance commutes (Shaffer et al., 2006; Felicísimo et al., 2008). Changes in wind patterns can cause shifts in foraging ranges and travel rates and may ultimately affect breeding performance (Weimerskirch et al., 2012). The trans-equatorial migrations of many species are also driven by highly seasonal food availability, enabling birds to exploit rich summer food supplies at both ends of their distributional range (Hedd et al., 2012; McKnight et al., 2013). Meanwhile, migrating birds move through different marine ecosystems and stop at a few key locations for increasing their refueling opportunities (McKnight et al., 2013), associated with major productivity hotspots such as coastal upwelling areas (Stenhouse et al., 2012; McKnight et al., 2013).

The Bay of Biscay (BoB) is an important migration flyway for Atlantic seabirds during the pre-breeding and post-breeding phases of their annual cycle (Brereton et al., 2003; Arcos et al., 2009). For numerous species, the BoB represents a key feeding area during certain periods of the year when seabirds, as well as other marine top predators, undertake seasonal feeding migrations into the area (Lezama-Ochoa et al., 2010; Stenhouse et al., 2012). There are two relevant shearwater species that perform trans-equatorial migrations that breed in the southern Atlantic Ocean: the great and sooty shearwaters *Puffinus gravis* and *Puffinus griseus*, respectively. After breeding, individuals of both species migrate to the productive waters of the western North Atlantic (Gulf of Maine, GoM) where they stay from June to August (Hedd et al., 2012). After this period, they continue the migratory journey toward the eastern North Atlantic following prevailing westerly wind patterns (Hedd et al., 2012). Thus, oceanic winds connect both sectors of the North Atlantic across middle latitudes (Hurrell and Deser, 2010), facilitating the flyway between the GoM and the BoB. Some individuals of both species might enter the BoB and stop there between August and October, before continuing their southward migration to reach their breeding grounds (Hobbs et al., 2003). The staging dynamic of southern shearwaters can vary from year to year, and the role of large- and short- scale climatic indices (e.g., NAO and oceanic winds, respectively) in driving these patterns have not yet been studied.

Here, we aimed to assess whether the abundance patterns of trans-equatorial migrating pelagic seabirds have changed over the past two decades in relation to the main drivers shaping their migratory journey: climatic factors and food availability. Based on long-term systematic at-sea surveys, we studied the annual staging dynamic of great and sooty shearwaters in the BoB by estimating dates of arrival and departure, staging duration and abundance patterns covering a 16-year temporal window (1995–2010). Climatic effects were studied at two different temporal scales: oceanic wind patterns and global oscillations indices (NAO) that represent climate variability at short and long time scales, respectively. In addition, the role of food availability was jointly analyzed by using a unique long-term series of anchovy biomass (AB) in this biogeographic area. Based on oceanic winds, we also estimated the cost of flying on a monthly basis following Louzao et al. (2014). We hypothesized that shearwaters might minimize the cost of flying by adjusting their arrival to the BoB during an optimal temporal window. Combining different long-term physical and biological datasets can provide a comprehensive picture of the effect of changing ecosystems on highly migratory predators.

Materials and Methods

Seabird Observations

Monthly at-sea observations were performed onboard a commercial ferry, the Pride of Bilbao, crossing the English Channel and BoB between July 1995 and August 2010 (**Figure 1**). Since surveys spatial coverage corresponded to the internal sector of the BoB, we referred to the term BoB to the geographic limits between 6.18° and 0.94° W and 43.33°-50.78° N corresponding to the longitudinal and latitudinal ranges of ferry surveys, respectively. On each trip, effort-based seabird observations were carried out by a team of three experienced volunteer observers, with two observers at a time. A two and a half day ferry trip was performed monthly between the harbors of Portsmouth and Bilbao. Recording was made from a fixed position on the bridge of the ship, at a height of 32 m and speed of 15–22 knots. For each seabird sighting species name and number seen were recorded. At 15–30 min intervals or whenever the ships course changed, a range of variables were measured including the ship's speed and course, and sea/weather variables such as sea state

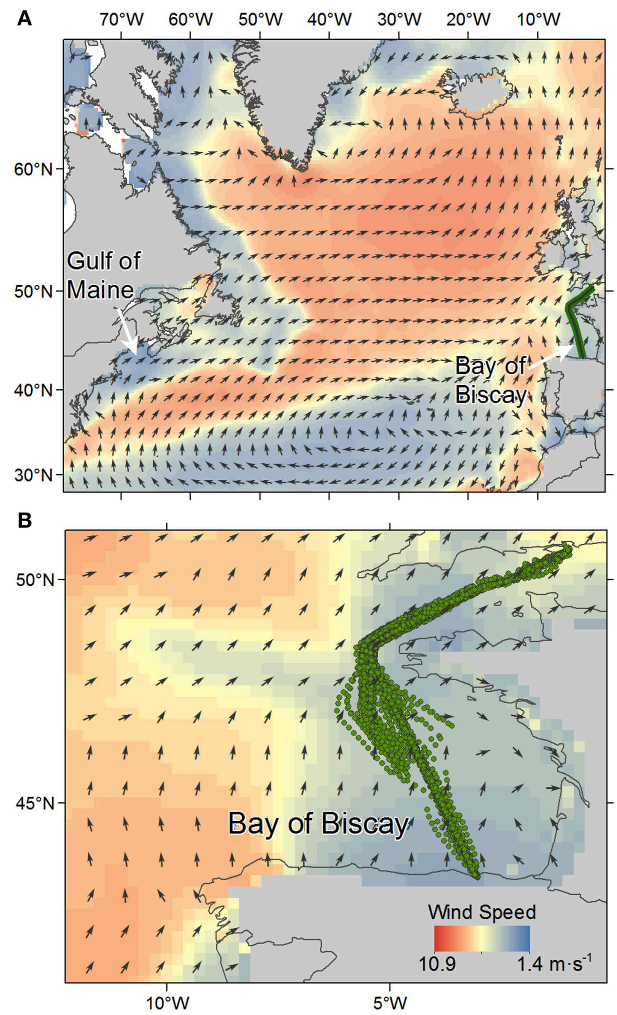

FIGURE 1 | (A) Map of the North Atlantic showing overall mean wind speed for August (1995–2009). Wind speed is graded in color. Arrows show wind direction. The main prevailing wind speed and direction is shown illustrating the facilitated flyway between the Gulf of Maine and the Bay of Biscay (BoB). Green line marks ferry trackline for surveys. **(B)** Survey map showing the effort during the 16-years study period in the BoB.

and visibility. Observations periods with sea state higher than Beaufort scale 5 were removed.

Observations were performed over different recorded time periods with a median of 30 min (range: 1–270). In order to compare periods of similar searching effort we selected observation periods ranging between 20 and 40 min. By multiplying the speed and the observation time, we estimated the distance traveled (km). The mean distance traveled per observation period was 17.02 km (range: 6.69–28.12). For this study, we considered the distance traveled as an index of survey effort. When comparing temporal differences in the sampling effort, we did not observe differences among years neither between months and years (Figures S1A,B, respectively). Regardless of the year, survey effort was higher between spring and summer months, whereas survey effort was lower during autumn and winter months. Thus, the observation effort was comparable between years and months.

We then estimated the encounter rates, dividing the number of birds observed by the distance traveled. The encounter rate was used as an index of seabird abundance, thus higher encounter rates were indicative of higher numbers of birds per km traveled. Lower encounter rates were indicative of the opposite pattern.

Climatic Indices and Food Availability

In the case of global climatic indices, the NAO index is estimated from differences in sea level pressure between two distant meteorological stations at Lisbon, Portugal and Stykkisholmur, Iceland (Hurrell and Deser, 2010). Positive NAO values are related to strong westerlies across the middle latitudes of the North Atlantic towards Europe (Hurrell and Deser, 2010). Thus, we expected that positive NAO values would be related to higher abundance of highly migratory shearwaters into the BoB. We used wintertime NAO value (mean value from December to March) since it can leave persistent surface anomalies in the seascape that might significantly influence the marine ecosystems throughout the year (Hurrell and Deser, 2010) (**Table 1**).

Regarding short-term climatic indices, we analyzed the role of oceanic winds across the North Atlantic (longitude range: 15°–55° W; latitudinal range: 40°–55° N) (see **Figure 1**, **Table 1**). We used the Blended Sea Winds containing globally gridded, high resolution ocean surface vector winds on a global 0.25° grid (http://www.ncdc.noaa.gov/oa/rsad/air-sea/seawinds.html). The wind speeds ($\mathrm{m\,s^{-1}}$) and directions were generated by blending observations from multiple satellites and reanalysis products, respectively. Oceanic wind data was downloaded from the NCDC/NOAA website at http://coastwatch.pfeg.noaa.gov/erddap/griddap/ncdcOwMon.html. Oceanic winds are described using the vector of the wind speed in $\mathrm{m\,s^{-1}}$ and the direction. Similarly, wind speed can be resolved into two perpendicular components. Zonal u and meridional v winds represent the west-east and north-south direction and are represented by positive values toward the north and east, respectively (more information at http://mst.nerc.ac.uk/wind_vect_convs.html).

Regarding food availability, great and sooty shearwater feed on small pelagic fish (Ronconi et al., 2010). We used a fishery-independent dataset, the biomass index for the European anchovy *Engraulis encrasicolus* in the BoB, calculated through the daily egg production method as an index of food availability based on oceanographic cruises (**Table 1**). These cruises have been carried out annually in May at the peak spawning period since 1987, covering the whole spawning area of the anchovy in the BoB (Santos et al., 2011). To ensure that spring Anchovy Biomass (AB) was correlated with anchovy landings during the late summer period, we estimated the non-parametric Spearman-rank correlation coefficient r_s between (1) the AB and the historical anchovy landings of May ($r_s = 0.37$, $S = 2049.81$, $P = 0.05$), as well as (2) anchovy landings between May and August ($r_s = 0.60$, $S = 1287.61$, $P < 0.001$) to ensure the positive underlying biological relationship. Fishing data were extracted from the International Council for the Exploration of the Sea (ICES) reports (**Table 1**). August was chosen as a representative

TABLE 1 | Description of the dataset used for understanding the role of climate and food availability on driving decadal abundance patterns of highly migratory marine predators in the Bay of Biscay.

Dataset	Covered area	Source	Time window	Sampling rate
Predator observations	Bay of Biscay	MarineLife	1995–2010	Monthly
Oceanic winds	North Atlantic	[a]NCDC/NOAA	1995–2010	Daily/Monthly
NAO	North Atlantic	[b]NOAA Climatic Center	1981–2010	Monthly
Anchovy biomass estimates	Bay of Biscay	[c]BIOMAN oceanographic surveys	1987–2013	Annual

[a] *http://coastwatch.pfeg.noaa.gov/erddap/griddap/ncdcOwMon.html*
[b] *ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/nao_index.tim*
[c] *http://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2014/WGHANSA/01%20WGHANSA%20Final%20Report.pdf*

month of the summer period since it corresponded to the month of first detection of both shearwaters in 46% of the cases, followed by July (27%), September (15%) and October (12%) (see Results). Even the time lag between the biomass estimation (spring) and the study period (late summer), we considered that the AB was a more robust index of small pelagic fish availability than fishing landings in the BoB during the summer period (c.f. Alheit et al., 2014).

Estimation of Flying Costs

We used the flying cost function developed by Louzao et al. (2014) to estimate the cost of traveling across middle latitudes of the North Atlantic. The flying cost function is based on the effect of wind speed w and the angle between flight and wind direction θ based on Weimerskirch et al. (2000), González-Solís et al. (2009). Considering wind speed when estimating flying cots is important for the energy budget during flying activities (González-Solís et al., 2009; Raymond et al., 2010). The flying cost function is expressed by the following equation:

$$c = 30 + 2.381e - 09^{*}\theta - 9.667e\text{-}01^{*}w + 1.093e\text{-}02^{*}\theta^{*}w \quad (1)$$

where c is the flying cost (i.e., energy expenditure with arbitrary cost units ranging from 0 to 60), w represents the wind speed (ranging from 0 to $30\,\mathrm{m\,s^{-1}}$) and θ is the angle between flight and wind direction (ranging from 0° to 180° indicating that birds were flying with tail and head winds, respectively). The intercept at 30 is related to intermediate flying cost units when w and θ are 0° and 90°, respectively (i.e., in the absence of wind and when birds are flying with cross winds; see Figure 1 in Louzao et al., 2014). From this intermediate reference level, energy expenditure decreases when birds are flying from cross winds to tail winds at increasing wind speed. On the contrary, energy expenditure increases when birds fly from cross winds to head winds at increasing wind speed.

Flight costs were estimated monthly using wind speed and direction at the original spatial resolution of 0.25° through a zonal hypothetical flyway across the North Atlantic at the latitude of 45° N from January 1996 to December 2009 (see Figure S2). Monthly wind directions showed that westerlies were the predominant wind direction in this biogeographic area independently of the month of the year and wind speeds were higher during winter months (see Figures S3, S4, respectively). The hypothetical flyway was established based on empirical evidences of southern shearwater migration through the North Atlantic (Hedd et al., 2012). We only focused on the flyway across the North Atlantic between longitudes ranging from 55° to 15° W without considering the departure from the Gulf of Maine (GoM; the main staging area in the Northwest Atlantic) and arrival point to the center of the BoB. The flying cost function was applied to flying activities and, in turn, we assumed that shearwaters were mostly flying from the GoM to the BoB. This assumption is in accordance with empirical evidences of sooty shearwaters that spend a high proportion of the day (78.4 ± 4.2%; 10.1 ± 0.7 $\mathrm{hd^{-1}}$) and over half of the night (58.5 ± 9.1%; 6.4 ± 1.0 h $\mathrm{night^{-1}}$) flying during northward and southward migrations (Hedd et al., 2012). See Figure S5 for an illustrative example of c, w, and θ values for a given month through the hypothetical flyway. We summed the flying cost estimated along the zonal flyway and used it as a measure of flying cost index.

Data Analysis

First, we described the annual timing of highly migratory shearwaters in the BoB by estimating (1) the first month of detection (i.e., month of arrival), (2) the last month of detection (i.e., month of departure), and (3) the staging duration. We tested the relationship between the first month of detection and the staging duration by estimating the Spearman rank correlation coefficient and applying a permutation test to estimate whether correlations were stronger than expected.

Then, we investigated the role of the NAO, oceanic winds and food availability driving the abundance patterns of southern shearwaters entering the BoB during the late summer period (1996–2009) using Generalized Additive Models (GAMs). For each species, the response variable was the number of shearwaters from the first month of detection to September, when all birds that flew to the BoB are assumed to have arrived but when they have not started to migrate south to their breeding grounds (Cuthbert, 2005). Explanatory variables included normalized values of NAO winter index, food availability (AB), as well as the monthly zonal winds u from the previous month of first detection to the previous month of September (see below). We hypothesized that the role of zonal winds would be more critical than wind speeds or meridional winds in facilitating the arrival of shearwaters to the BoB due to the longitudinal flyway across the middle latitudes of the North Atlantic. Collinearity between predictors was checked with the Variation Inflation Factor (cutting point of 5). No variable was removed since VIF was lower than 5 in all cases.

GAMs were carried out using the *mgcv* package (Wood and Augustin, 2002) and limiting the smoothing splines to a maximum of three degrees of freedom. Models were compared using Akaike's Information Criterion corrected for small sample sizes (*AICc*) and the model with the lowest *AICc* value was considered the best compromise between model deviance and model complexity. When models were within 2 points of *AICc*, they were considered statistically equivalent (Williams et al., 2002). Models were first ordered by their *AICc* value and among equivalent models the best model was chosen as the one with highest explained deviance. Shearwater abundance was modeled by including the log-transformed distance traveled (i.e., effort in km) as an offset in order to minimize estimation biases due to surveyed effort, following a negative binomial distribution. This model was selected over the Poisson distribution since the *AICc* value was lower for the negative binomial distribution. The following equation represented the full model for each species:

$$A_i = \alpha + f(NAO_i) + f(AB_i) + f(u_i) + offset\,(log(Effort)) + \varepsilon_i \qquad (2)$$

where A stands for abundance patterns of shearwaters each month between the month of first detection to September i from 1996 to 2009 ($n = 26$), whereas ε represents the residuals.

Finally, we analyzed the influence of flying costs along the hypothetical zonal flyway driving abundance patterns of southern shearwaters in the BoB over the period January 1996–December 2009. We hypothesized that the abundance of shearwaters (i.e., the encounter rate) for a given month was influenced by the flying cost (*FC*) estimate from the previous month (*t - 1*). For great shearwater, this hypothesis was supported by the higher r_s between the encounter rate of a given month and the *FC* of the

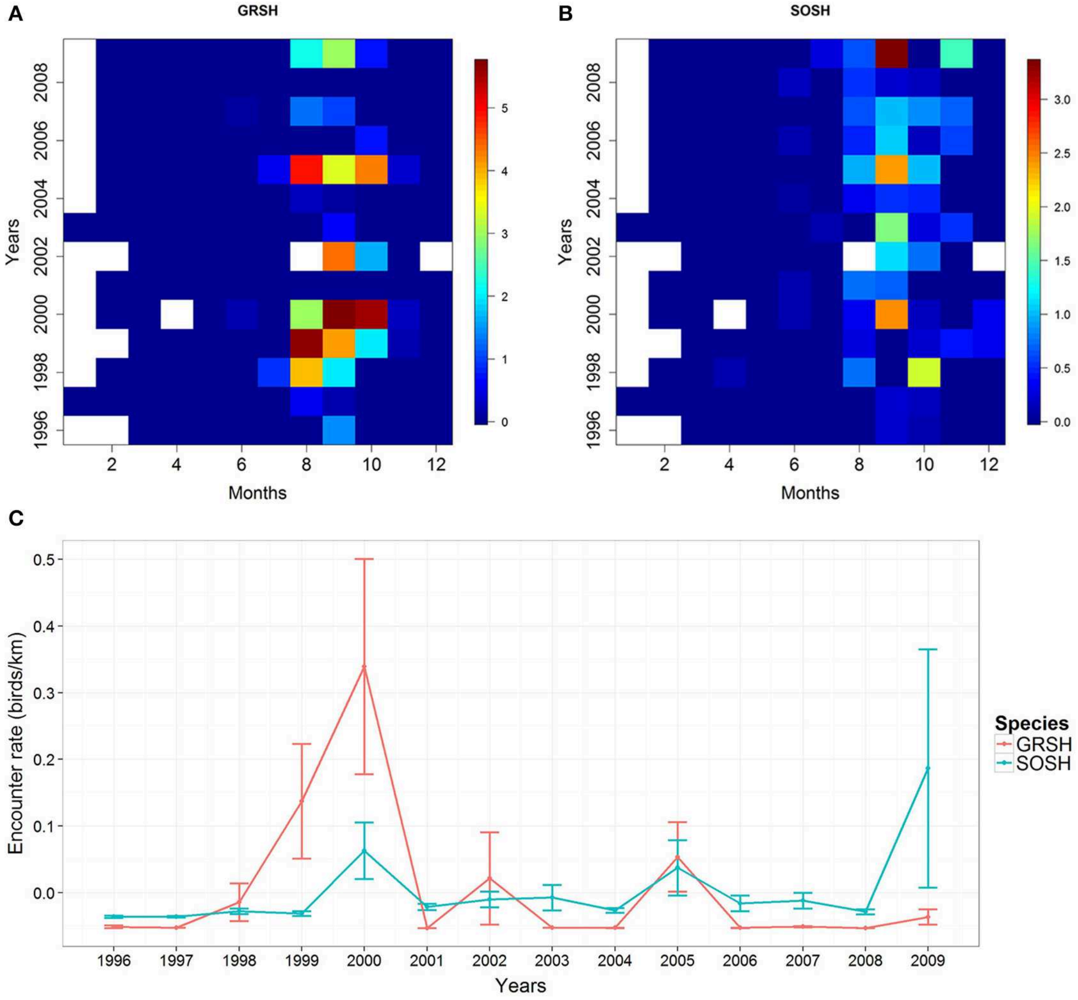

FIGURE 2 | Temporal trends of log-transformed encounter rate (ER, number of birds/traveled km) for (A) great shearwaters (GRSH) (B) sooty shearwaters (SOSH) in the Bay of Biscay and (C) Decadal trends of encounter rates (birds km^{-1}) for both species. Blank values correspond to non-surveyed months. Encounter rates were normalized for visualization purposes.

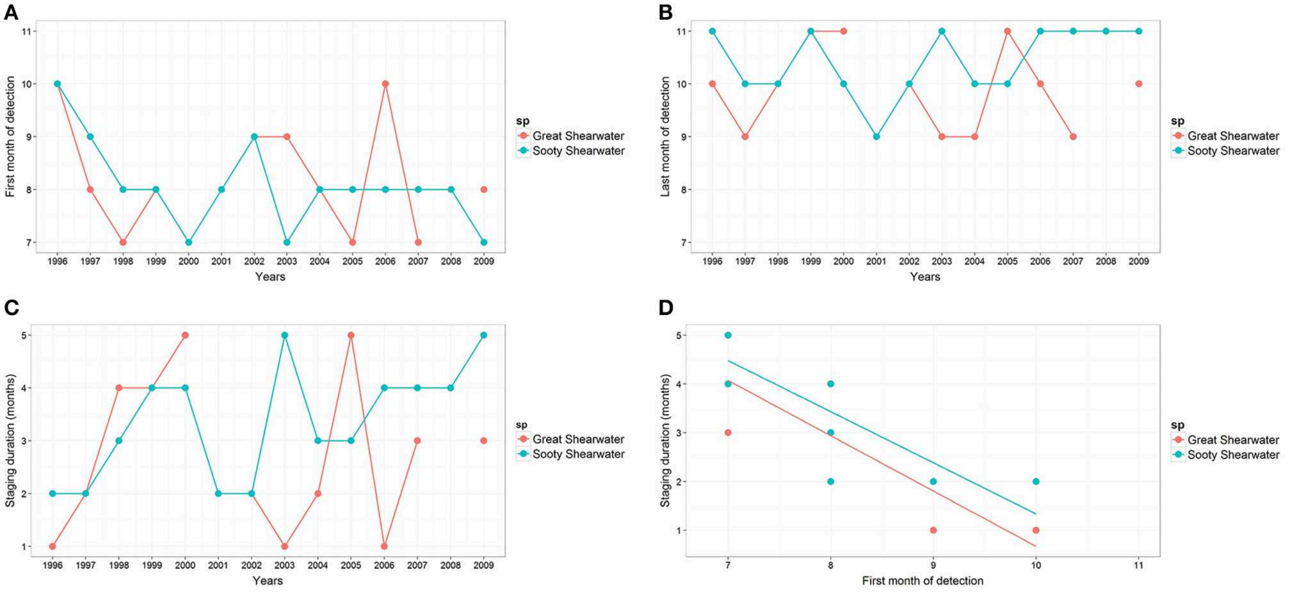

FIGURE 3 | Staging dynamic of transequatorial migrating seabirds in the Bay of Biscay described by (A) the first and (B) last months of detection, (C) staging duration (months) and (D) the relationship between both of them. GRSH, great shearwater; SOSH, sooty shearwater. Note that GRSHs were not detected in 2001 and 2008.

previous month ($r_s = 0.16$, $S = 395681.8$, $P = 0.074$) than the r_s between the encounter rate and the *FC* of the same month ($r_s = 0.03$, $S = 339152.3$, $P = 0.74$). A similar correlation pattern was found for sooty shearwater ($r_s = 0.16$, $S = 667586.1$, $P = 0.009$ for the encounter rate and FC of the previous month; $r_s = -0.21$, $S = 566948.8$, $P = 0.923$ for encounter rate and FC of the same month). This relationship was tested using GAMs and is represented by the following expression:

$$A_i = \alpha + f(FC_i) + offset\ (log(Effort)) + \varepsilon_i \quad (3)$$

where A stands for abundance patterns of shearwaters every month i from January 1996 to December 2009 ($n = 167$), whereas ε represents the residuals. We did not restrict the analysis to any specific period of the year when shearwaters were most likely to occur in the BoB, but tested the direct influence of lower flying cost months (explanatory variable) in facilitating the arrival of a higher number of shearwaters (response variable). Shearwater abundance was modeled by including log-transformed traveled distance (i.e., effort in km) as an offset in order to minimize estimation biases due to surveyed effort, following a negative binomial distribution. GAMs were performed following the procedure previously described and we only compared two candidate models: the null model and the one including the flying costs. The model with the lowest *AICc* value was considered the best compromise between model deviance and model complexity. All data processing and analysis were performed within the R environment (R Core Team, 2014).

Results

We observed a total of 8630 great shearwaters (GRSH) and 612 sooty shearwaters (SOSH) during 105408 km traveled and 3030 h of observations. Note that no GRSH were detected in 2001 and 2008 (see **Figures 2A,B**). Overall encounter rates (mean ± SD) for GRSH and SOSH were 0.091 ± 1.728 and 0.006 ± 0.149 birds km^{-1}, respectively. Encounter rate values for both species were higher in 2000 and 2005 across the study period, as well as in 2002 for GRSH and 2009 for SOSH (**Figure 2C**). We found a non-significant positive correlation between the annual encounter rate of both species ($r_s = 0.40$, $S = 272.80$, $P = 0.156$).

Both species were mainly present in the BoB from July to November (**Figures 2A,B**). The timing of arrival and departure ranged from July to October and September to November, respectively (**Figures 3A,B**). However, observed patterns for SOSH were more regular (above 50% of the first month of arrival was in August, and months of departure were in October and November). The detection months in the BoB varied from 1 to 5 months for GRSH, while detection months were from 2 to 5 months for SOSH (**Figure 3C**). The first detection month was significantly negatively correlated with the staging duration for both species ($r_s = -0.88$, $S = 538.624$, $P < 0.001$ based on a permutation test for GRSH; $r_s = -0.827$, $S = 2049.81$, $P < 0.001$ for SOSH; **Figure 3D**). Therefore, these results indicate that the earlier shearwaters were detected in the BoB, the longer the detection period. Cumulative higher encounter rates (1996–2009) were recorded during the months of August and September for GRSH and September for SOSH (**Figures 2A,B**). Annual encounter rates for both species varied significantly between years for both species (Kruskal-Wallis test for GRSH $H_{12,\,6193} =$

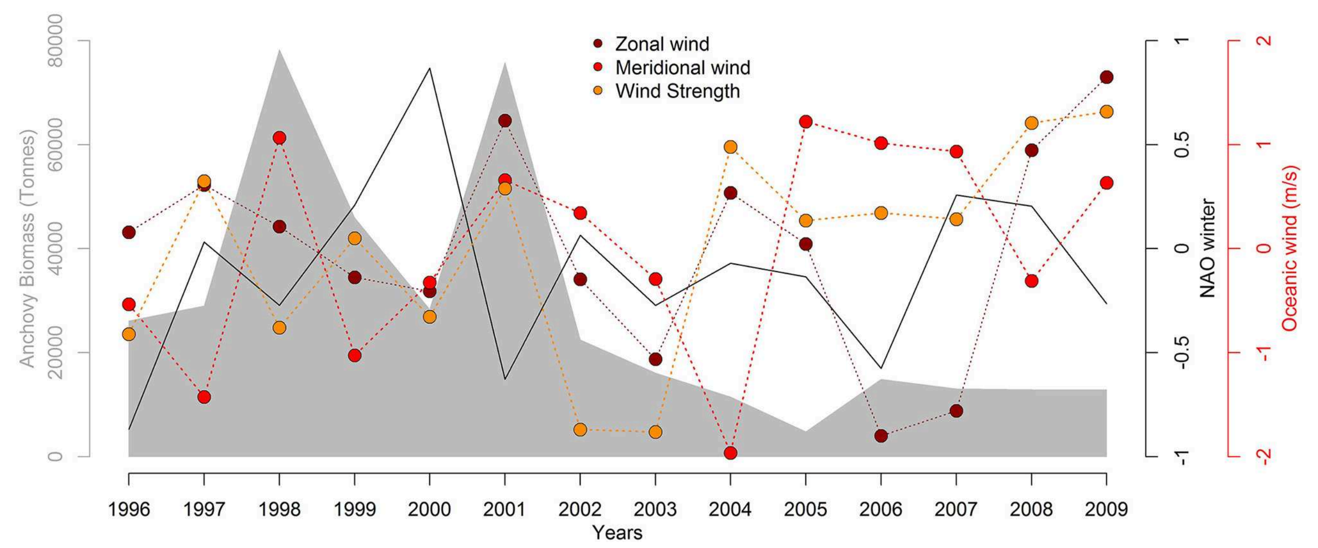

FIGURE 4 | Decadal trends of anchovy biomass estimates (gray shaded area represented in the left y-axis), winter values of the North Atlantic Oscillation index (NAO, solid black line represented in the first right y-axis) and oceanic winds (zonal, meridional, and wind strength indicated by dark blue, blue, and light blue dotted lines, respectively, with values represented in the second right y-axis). Oceanic winds have been normalized by subtracting the mean and dividing by the time series standard deviation. Wind August values are shown only for illustration purposes since it was the most representative month of first summer detection for both great and sooty shearwater species (47% of all cases).

TABLE 2 | Output of Generalized Additive Models showing the ranking of the candidate models based on the corrected Akaike Information Criteria (AICc).

Species	Model	Parameter	AICc	ED	ΔAICc
GRSH	**2**	**NAO**	**280.1850**	**0.1724**	**0.6872**
	4	U	281.0677	0.0805	1.5698
	1	NULL	279.4979	0.0113	0.0000
	7	NAO + U	281.8664	0.1461	2.3685
	3	AB	281.9412	0.0166	2.4434
	5	NAO + AB	283.3281	0.1743	3.8302
	6	AB + U	283.6137	0.0892	4.1158
	8	NAO + U + AB	283.9345	0.1345	4.4367
SOSH	**5**	**NAO + AB**	**247.3674**	**0.6410**	**0.0000**
	8	NAO + U + AB	251.8272	0.6526	4.4599
	2	NAO	254.7199	0.4019	7.3525
	3	AB	258.608	0.1561	11.2406
	7	NAO + U	259.6517	0.4488	12.2844
	6	AB + U	261.3013	0.1618	13.9339
	1	NULL	262.7228	−0.0562	15.3554
	4	U	265.1799	−0.0406	17.8125

Models are first ordered by the AICc value and among equivalent models the best model is the one with highest explained deviance. Selected models are in bold. ED, Explained deviance; NAO, North Atlantic Oscillation; U, zonal wind; AB, Anchovy Biomass; GRSH denotes great shearwater and SOSH sooty shearwater.

237.08, $P < 0.001$; Kruskal-Wallis test for SOSH $H_{12,\,6193} = 72.03$, $P < 0.001$).

For the time series of global and local environmental drivers, normalized mean values are given in **Figure 4** for the study period (1996–2009). Regarding climatic indices, NAO winter (December–March) values showed high inter-annual variability ranged between −0.867 and 0.867, with maximum and minimum values observed in 2000 and 1996, respectively. For local environmental drivers, food availability expressed as AB peaked in 1998 and 2001, with the lowest value in 2005. Wind speed ranged between 6.15 and 9.28 m s^{-1}, whereas zonal and meridional winds ranged 1.23–4.86 m s^{-1} and −0.42–2.01 m s^{-1}, respectively. In the case of oceanic winds, we were interested in analysing the correlation between zonal winds and both NAO and AB. The zonal wind was only negatively correlated (not statistically significant) with NAO values, whilst no correlation was found between NAO and AB in the case of both species (see Figure S6).

Regarding abundance patterns of these highly migratory shearwaters, the model containing the NAO winter index was chosen as the best model for GRSH apart from the additive effect of AB for SOSH (**Table 2**). Abundance of GRSH increased with increasing winter NAO values, explaining 17% of the observed abundance variability (**Table 2**, **Figure 5**). For SOSH, abundance was higher at intermediate NAO winter values, whilst there was a decreasing effect of AB which explained 64% of observed variability in abundance (**Table 2**, **Figure 5**). Our modeling approach did not identify zonal wind as an important factor driving the staging dynamic of migrating shearwaters into the BoB.

Potential flying cost estimations during the study period showed that higher costs for crossing the North Atlantic occurred in August (see Figure S7). GAM analysis showed that shearwater monthly abundance was better explained by the potential flying costs of the preceding month rather than the null model in the case of both species (**Table 3**, **Figure 6**). With more than 3500 units of flying costs across the North

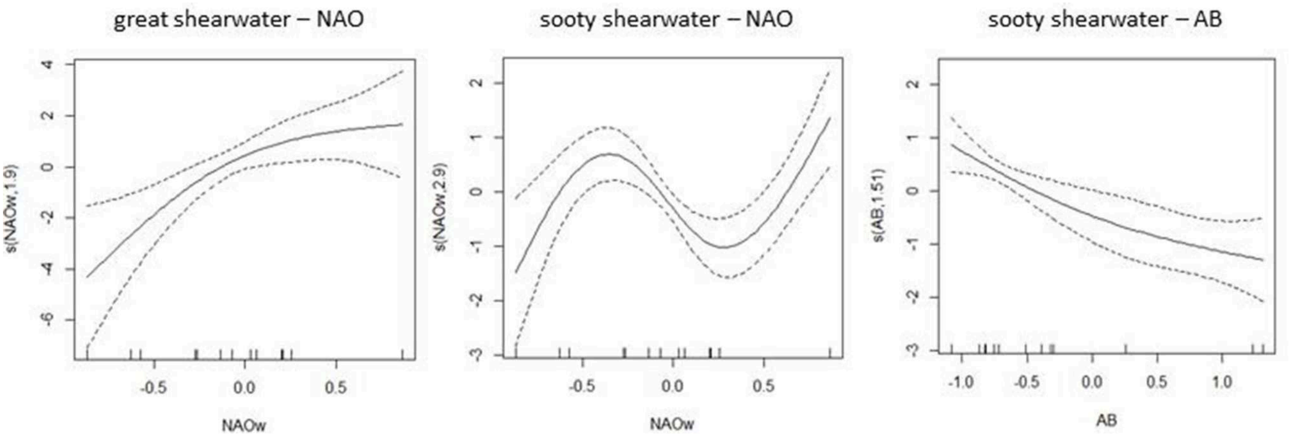

FIGURE 5 | Smooth functions fitted to the best relationships between great and sooty shearwater abundance and environmental variables: NAO winter index (December to March) and less importantly the anchovy biomass estimation (AB). Models were first ordered by the AICc value and among equivalent models the best model was the one with highest explained deviance (see results in **Table 2**). Dotted areas represent the 95% confidence interval. Tick marks on the horizontal axis show the distribution of observations. The vertical axes describe the smoother term and estimated degrees of freedom.

TABLE 3 | Summary of Generalized Additive Models exploring the relationship between monthly abundance patterns and potential flying costs (FC) of the preceding month for great and sooty shearwaters, respectively, from January 1996 to December 2009.

Species	Model	Parameter	AICc	ED	ΔAICc
GRSH	**2**	**FC**	**497.941**	**0.2481**	**0.000**
	1	NULL	503.061	0.1151	5.120
SOSH	**2**	**FC**	**472.004**	**0.2329**	**0.000**
	1	NULL	474.605	0.1610	2.601

Candidate models are ordered based on the corrected Akaike Information Criteria (AICc). Selected models are in bold. ED, Explained deviance; GRSH and SOSH denote great and sooty shearwaters, respectively.

Atlantic, predicted shearwater abundance in the following month decreased progressively in the BoB. In other words, shearwaters tend to arrive in the BoB when potential migration/flying costs across the North Atlantic were lower, associated with lower average wind speeds (**Figure 7**). These models accounted for the 24.8 and 23.3% of the explained deviance of GRSH and SOSH abundance, respectively.

Discussion

In this study, we provide new insights into the role of decadal climatic effects driving migratory seabird movements across the North Atlantic. Both shearwater species were influenced by large scale NAO climatic index, but the shape of the relationship was different and the SOSH was also negatively influenced by food availability in the BoB. Abundance of GRSH was higher with increasing winter NAO values while SOSH abundance was higher at intermediate values. Thus, our predictions were partially fulfilled since higher NAO values were related to higher abundance of highly migratory shearwaters. This could be explained by higher NAO values related to stronger westerlies across the middle latitudes of the North Atlantic toward Europe (Hurrell and Deser, 2010) and, in turn, facilitating the arrival of southern shearwaters. The large-scale winter NAO index (December-March) can leave persistent surface anomalies in the seascape that might significantly influence the marine ecosystems throughout the year (Hurrell and Deser, 2010).

In addition, we also observed differences in abundances as well as the timings of arrival and departure: GRSH were more abundant than SOSH but the arrival of the former seemed to be more variable, supported by previous results (Hobbs et al., 2003; Ocio et al., 2011). This could be related to the different shape of the relationship between each species abundance and NAO values. Even if both species might likely rely on different cues during the migration, they shape their arrival in the BoB during periods which minimize flying costs across the two extremes of the North Atlantic. Indirectly, distribution patterns of both species might be related to oceanic winds, since positive NAO values are related to westerly (positive zonal) winds across middle latitudes of the Atlantic (Hurrell and Deser, 2010). Thus, stronger westerly winds might facilitate the arrival of higher numbers of highly migratory shearwaters into the BoB. The indirect effects of oceanic winds might be related to the shorter spatiotemporal variability captured by oceanic winds, while climatic indices integrate environmental information simultaneously over several months.

Great and sooty shearwaters entering the BoB can be detected during a time period of 5 months from July to November. Recent tracking information has shown that southern shearwaters might not approach the BoB during certain years after staging in the GoM from June to August (Welch and Ronconi, pers. commun.). These birds might follow a mid-ocean route in their southward return to the breeding grounds in the South Atlantic (Bourne, 1986). In fact, numbers of southern shearwaters in the northwest Atlantic seem to be higher than in the noreast Atlantic (Bourne,

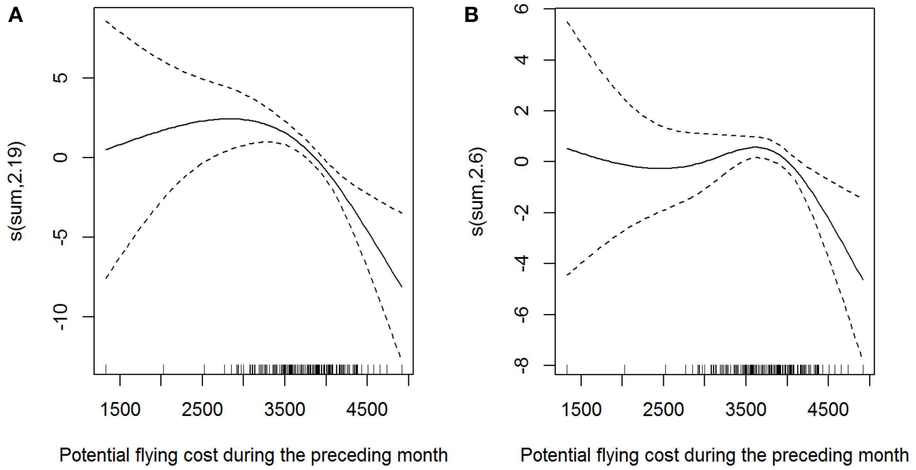

FIGURE 6 | Generalized Additive Model output exploring the relationship between monthly abundance patterns and potential flying costs of the preceding month for (A) great and (B) sooty shearwaters, respectively, from January 1996 to December 2009. Dotted areas represent the 95% confidence interval. Tick marks on the horizontal axis show the distribution of observations. The vertical axes describe the smoother term and estimated degrees of freedom. These models accounted for the 24.8 and 23.3% of the explained deviance of GRSH and SOSH, respectively.

1986). Therefore, shearwaters might detour to the BoB during certain environmental conditions related to food availability and/or lack of favorable wind conditions (Dias et al., 2012). In addition, another alternative hypothesis was suggested by Bourne (1986) in that most southern shearwaters entering the BoB to feed in upwelling areas might be non- or pre-breeders (Bourne, 1986, but see Romay et al., 2009). In the case of great shearwaters, breeders return synchronously to their burrows in mid-September (Cuthbert, 2005) and, in turn, bird observed in the BoB after this period should be considered as non-breeders.

Since shearwater at-sea observations were restricted to the internal BoB at a monthly temporal scale, our results are limited in precisely describing the timing of migratory flows. Cumulative higher encounter rates were recorded during the months of August and September for GRSH and September for SOSH. Observations from the northernmost headland in Spain (i.e., Estaca de Bares which is an important gateway for Atlantic seabirds, http://www.seawatchingestaca.com/) has shown the apparent existence of different migratory flows for GRSH: a less and more important in September and the first half of November, respectively (Sandoval et al., 2009, 2010). In the case of SOSH, the main migratory flow was identified from mid-September to mid-October (Sandoval et al., 2009). Thus, observations from the internal BoB were unable to detect the migratory flow of GRSH during the first half of November observed in the southwestern sector of the BoB, which might correspond to non-breeding individuals (Bourne, 1986; Cuthbert, 2005).

Surprisingly, we found a negative relationship between the abundance of sooty shearwaters and fish abundance, while no relationship was found between great shearwaters and fish abundance. We expected to obtain (if any) a positive relationship between shearwater and fish abundance and our results could be in part related to the difficulty of identifying the factors influencing the decision of arriving/leaving specific wintering areas during the non-breeding. When studying the joint effects of climate and food abundance during breeding, closely related species such as the Cory's shearwater *Calonectris diomedea* did show an important combined effect of climate (i.e., NAO) and food availability (wind effects were not included) on the behavior and foraging range (Paiva et al., 2013). Previous winter negative NAO values may cause a decrease in food availability in foraging grounds and force shearwaters to exploit remote areas and consequently show lower reproductive rates (Paiva et al., 2013). Thus, the distribution patterns of breeding adults might be more affected by small-scale environmental conditions around their nesting grounds, while during the non-breeding season they would be more affected by large-scale environmental conditions. This is partially supported by previous studies showing that global climatic effects have an important effect at the long-term population level (e.g., adult survival) (Sandvik et al., 2005; Genovart et al., 2013). These studies highlighted that adult survival is mainly influenced by large scale climatic oscillations and prey availability is generally a worse predictor, though climatic factors could have an indirect effect possibly through the food chain.

Here, we have studied the role of different environmental drivers affecting the decadal abundance patterns of southern hemisphere breeding shearwaters in the BoB. Within the foraging process, environmental drivers are extrinsic factors that constrain decision-making, while internal state (i.e., physiology that drives the organism to fulfill energetic requirements) governs the decision of foraging destinations (i.e., where and when to move, Nathan et al., 2008). Thus, both extrinsic and intrinsic factors play an important role and are intimately interlinked (Owen-Smith et al., 2010). To further advance our knowledge of migration ecology, we foresee that the quantification of energy costs can be a valuable index integrating different processes at the level of migration. By quantifying the energy needed for pelagic birds to move, we will be able to understand how foragers may move across the landscape in order to maximize net energy

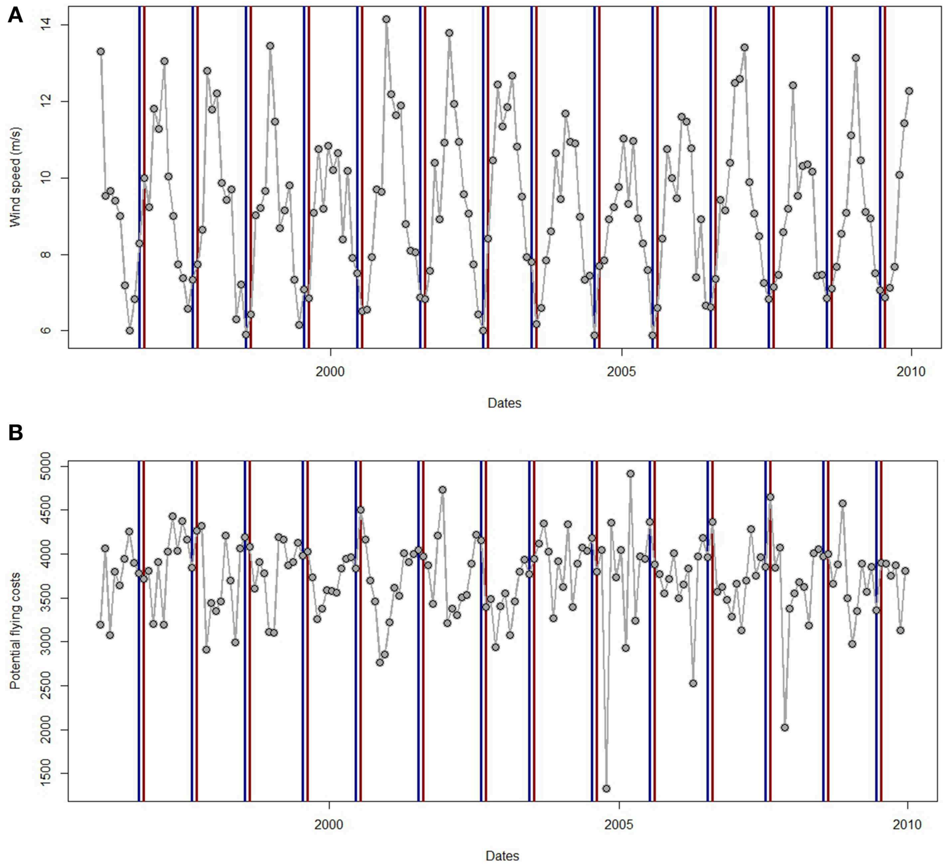

FIGURE 7 | (A) Time series of monthly wind speed and **(B)** potential flying cost (FC) from January 1996 to December 2009. Blue and red lines represent the month preceding the staging period and the month arriving to the Bay of Biscay for sooty shearwaters since time series are the same for great shearwaters.

gain (Louzao et al., 2014). We acknowledge that we have only considered a small portion of the migratory dynamic, but we have provided an energetic understanding of Southern Hemisphere breeding shearwater migratory dynamics in the North Atlantic.

Long-term time series data are crucial for understanding the effects of changing ecosystems on wide-ranging predators, since the first response of animals might be related to changes in foraging traits (e.g., distribution), while demographic effects might be evidenced in the long-term (Weimerskirch et al., 2012). Research efforts studying climate effects have focused more on population-level parameters such as population size, breeding performance and survival rates (Frederiksen et al., 2007). The study of the at-sea distribution of marine predators is more challenging but can be overcome due to the advent of tracking technologies. Therefore, integrative studies combining observations from systematic cruises and tracking devices may be able to provide a comprehensive picture of the effect of changing ecosystems on widely distributed marine predators.

Acknowledgments

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Supplementary Material

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fevo.2015.00090

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Climate change and the increasing impact of polar bears on bird populations

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The Arctic is becoming warmer at a high rate, and contractions in the extent of sea ice are currently changing the habitats of marine top-predators dependent on ice. Polar bears (*Ursus maritimus*) depend on sea ice for hunting seals. For these top-predators, longer ice-free seasons are hypothesized to force the bears to hunt for alternative terrestrial food, such as eggs from colonial breeding birds. We analyzed time-series of polar bear observations at four locations on Spitsbergen (Svalbard) and one in east Greenland. Summer occurrence of polar bears, measured as the probability of encountering bears and the number of days with bear presence, has increased significantly from the 1970/80s to the present. The shifts in polar bear occurrence coincided with trends for shorter sea ice seasons and less sea ice during the spring in the study area. This resulted in a strong inverse relationship between the probability of bear encounters on land and the length of the sea ice season. Within, 10 years after their first appearance on land, polar bears had advanced their arrival dates by almost 30 days. Direct observations of nest predation showed that polar bears may severely affect reproductive success of the barnacle goose (*Branta leucopsis*), common eider (*Somateria mollissima*) and glaucous gull (*Larus hyperboreus*). Nest predation was strongest in years when the polar bears arrived well before hatch, with more than 90% of all nests being predated. The results are similar to findings from Canada, and large-scale processes, such as climate and subsequent habitat changes, are pinpointed as the most likely drivers in various parts of the Arctic. We suggest that the increasing, earlier appearance of bears on land in summer reflects behavioral adaptations by a small segment of the population to cope with a reduced hunting range on sea ice. This exemplifies how behavioral adaptations may contribute to the cascading effects of climate change.

Keywords: cascading effects, colonial breeding birds, depredation, global warming, polar bear, seabirds, sea ice

Introduction

Understanding causes and consequences of climate-related shifts in ecosystem functioning, as well as the role of focal species in these processes, is currently a dominant theme in ecology. In the Arctic, temperature has increased at a rate two to three times faster than at southerly latitudes (Post et al., 2009). As a consequence, the rapid environmental changes that are taking place can be directly attributed to global warming (Gilg et al., 2012). The decrease in the extent of sea ice is on the order of 5% per decade in the Arctic (Liu et al., 2004; Serreze et al., 2007), and it is expected that this trend of disappearing sea ice will continue with the strongest losses predicted in the southern Arctic seas, including the Barents Sea area. Changes in the physical environment linked with global warming have become evident in the marine food web, for example, by shifts in the breeding phenology of sea birds (Barbraud and Weimerskirch, 2006; Moe et al., 2009). The Arctic terrestrial ecosystem has been affected as well, which includes changes in ecosystem functioning such as increased primary production (Madsen et al., 2011; Sistla et al., 2014).

One of the species directly affected by global warming is the polar bear (*Ursus maritimus*) whose life history is closely tied to sea ice (Lunn and Stirling, 1985; Ramsay and Hobson, 1991). Evidence is accumulating that polar bears are suffering from a warming climate and associated loss of sea ice habitat (Stirling et al., 1999; Derocher et al., 2004; Stirling and Derocher, 2012). It is expected that continued sea ice reductions will severely affect polar bear populations (Durner et al., 2009), which will force them into terrestrial ecosystems during the summer months in search of food (Stempniewicz, 1993; Drent and Prop, 2008; Rockwell and Gormezano, 2009; Smith et al., 2010; Hanssen et al., 2013; Prop et al., 2013; Iverson et al., 2014). Several studies have documented that polar bears on land can potentially have a large impact on their prey, in particular when bears feed on bird eggs (Drent and Prop, 2008; Smith et al., 2010; Prop et al., 2013; Iverson et al., 2014).

The occurrence of polar bears on land raises two fundamental questions. Firstly, what are the underlying causes of this shift? A major cause could be related to changes in sea ice conditions, as suggested by Iverson et al. (2014). Secondly, what is the role of polar bears as a novel top-predator in terrestrial habitats near the coast? To examine the role of polar bears in these terrestrial habitats, direct observations are needed, and these should be carried out including the periods before and after the appearance of bears.

In this paper, we document changes in the summer distribution of polar bears by exploring their relative presence at several locations on Spitsbergen and one location in Greenland. Based on the patterns of occurrence, which were collected over a period of >40 years, we assess the factors that may have contributed to the summer range expansion of polar bears. We test the hypothesis that the bear incursions on land are related to changes in sea ice conditions. Furthermore, we explore the effects of polar bears on the reproductive success of colonial breeding birds at one of our study locations.

Methods

Study Areas

Observations were collected along the west coast of Spitsbergen, which is the largest island in the Svalbard archipelago, and the east coast of Greenland. The study areas on Spitsbergen are composed of flat tundra stretches of up to 15 km wide, delineated by steep mountains and glaciers (Hisdal, 1998). Large fjords intersect the area, and islands are scattered along the coast, with many of these areas hosting breeding colonies of barnacle geese (*Branta leucopsis*), common eiders (*Somateria mollissima*) and glaucous gulls (*Larus hyperboreus*). Further bird nesting aggregations occur on tundra flats [e.g., colonies of pink-footed geese (*Anser brachyrhynchus*)], shore cliffs, and mountains (Kovacs and Lydersen, 2006).

Traill Island is part of the North East Greenland coastal fringe that is deeply indented by a network of long fjords. At the outer coast, the extent of annual landfast ice is delineated by a sharp ice edge that separates it from southward moving drift ice of varying extent, originating from the Arctic Ocean. The coastal zones contain breeding habitats for several bird species (Boertmann, 1994). In contrast to Svalbard, barnacle geese breed here exclusively on cliffs, and this applies also to small aggregations of glaucous gulls. Arctic terns (*Sterna paradisaea*), common eiders and long-tailed ducks (*Clangula hyemalis*) mainly nest on small rocky islands. These species may delay onset of breeding until ice breakup in mid-July.

We compiled data from a total of five locations in Svalbard and Greenland: Hornsund, Bellsund, Nordenskiöldkysten, and Kongsfjorden on the west coast of Spitsbergen (77–79°N); and Traill Island on the east coast of Greenland (72–73°N) (**Figure 1**). Descriptions of these locations are in Supplement 1.

Biological Data

Bear Occurrence

Observations were initiated in the 1970s or 1980s and continued until recently (**Table 1**). We restricted our analyses to June–July on Spitsbergen and 15 June–15 August in Greenland, where coastal ice breaks up later. The time spent by the biologists in the field averaged over the years and locations was 44 days, but this varied among years and locations (Supplement 1, Table S1).

The five locations differed in the way the observations were recorded and which data were obtained (**Table 1**). From all the locations, we had information on "annual bear presence," which is a binary variable denoting whether at least one bear had been observed or not. However, all polar bear observations were recorded in Nordenskiöldkysten, Kongsfjorden and Traill Island, which enabled us to calculate the number of bear days (e.g., two bear days may result from either two individuals being present for 1 day or one bear staying for 2 days).

Study localities may have differed in observation effort and detectability of bears. On Nordenskiöldkysten, daily observations were collected from several vantage points, including an observation tower that provided an extensive overview over the wide landscape. No observation towers were used at the other locations, but the nearby surroundings were scanned for polar bears as a measure of field safety. In all cases, the observations were done by experienced observers while doing fieldwork, typically on breeding birds. The spatial and temporal scale of the fieldwork was comparable between successive years within locations. We expect that any differences in detection probabilities were consistent over the years; thus, they should not affect any of the trends that we report.

Predation Rates on Birds

Polar bear predation rates on birds were obtained on Nordenskiöldkysten during the years 2004–2014 (all years except 2005–2006). On the island Diabasøya, which hosts the main bird colony of the area (Supplement 1, Figure S1), nests were monitored 6–16 h per day during the period that nesting geese or eiders were present. An observation tower on the mainland provided a good view of the island, which was 100 m off shore. Nests in view of the tower were mapped on high-resolution photographs of the island, which enabled us to assess the breeding history of individual birds. The species concerned were the barnacle goose, common eider and glaucous gull. As gull nests were not restricted to the island, all nests on rocky outcrops in adjacent bays visible from the observation tower were also recorded. Daily nest records included the following categories: settling (nest owners exhibit territorial behavior, and/or extensive nest building), incubating, nest predated (eggs or chicks taken by polar bear), nest successful (at least one egg hatching), and nest abandoned (nest owners abandon the nest territory, usually associated with removal of eggs by glaucous gulls). After the breeding season, all nests in the colony were mapped to determine the total number of nest sites for each species. Geese and eiders were only vulnerable to polar bear predation during the egg phase and during the first day after hatching, after which they departed from the colony; glaucous gulls had an extended period of predation as unfledged chicks stayed in the colony. Further details are given in Supplement 1 (Methods—Establishing predation rates).

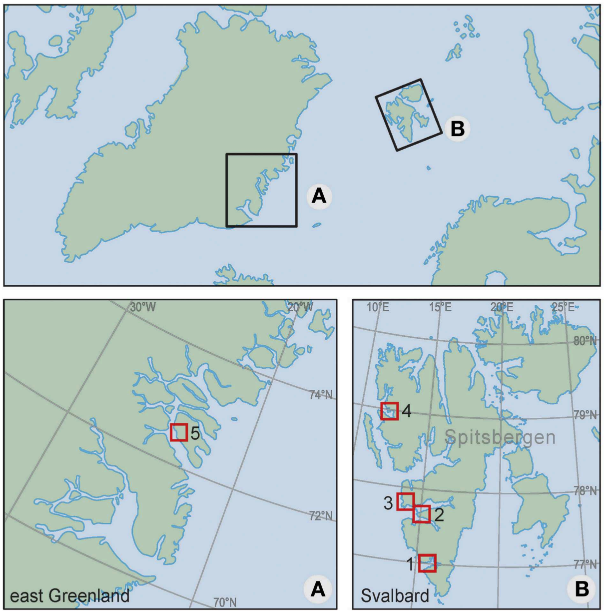

FIGURE 1 | Location of the study areas: (1) Hornsund, (2) Bellsund, (3) Nordenskiöldkysten, (4) Kongsfjorden (1–4 on Spitsbergen, Svalbard) and (5) Traill Island (east Greenland). Supplement 1 provides detailed maps of each of the areas (Figure S1), a photographic impression of the study animals (Figure S2), and a map indicating the locations of sea ice extractions (Figure S3).

We calculated two measures of predation intensity. (1) For each observation year (2004, 2007–2014), the closely monitored nests were used to calculate the proportion of predated nest attempts for species S as PNP_s = (number of nest predations$_s$)/(number of nest attempts$_s$). We obtained this measure only for barnacle geese and glaucous gulls as the number of common eider nests in view was too low to assume an unbiased sample. (2) In 2009–2014, we determined the number of bear predations by non-stop records of polar bear behavior in the breeding colony. For these years, we obtained a measure of predation intensity, which is different from the previous measure by considering the number of (physical) nest sites rather than nest attempts: the predation ratio PR_s = (number of predations$_s$)/(number of nests locations$_s$). This ratio may exceed 1.0 as a nest site may be used by several successive individuals, and thus potentially predated multiple times through the season. Further details are given in Supplement 1 (Methods—Establishing predation rates).

TABLE 1 | Summary of variables on biological data and sea ice acquired for the different locations.

	Nordenskiöldkysten	Kongsfjorden	Traill Island	Hornsund	Bellsund
BIOLOGICAL DATA DURING SUMMER					
Bear presence (0 or 1)	1977–2014 (25)	1982–2014 (26)	1988–2013	1972–2012 (30)	1987–2010
Bear days	1977–2014 (25)	1982–2014 (26)	1988–2013		
Bear occurrence dates	2004–2014 (9)				
Bear predation rates on birds	2004–2014 (9)				
SEA ICE DATA					
Large-scale, at sea	1979–2013	1979–2013	1979–2013	1979–2013	1979–2013
Fine-scale, fjords/coastal	2004–2014 (9)	2008–2013	2008–2013	2008–2013	2008–2013

Listed are the time periods for when data was available. For incomplete time series, numbers of years with data are given in parenthesis. Locations are listed in order of data extent. See Methods and Supplement 1 for a full description of the variables. For location of the ice data areas, see Supplement 1, Figures S3 and S4.

Sea Ice Data

Large-Scale Conditions at Sea

To assess large-scale conditions of sea ice, we downloaded data on sea ice concentrations from the website of the University of Colorado [see Supplement 1 (Methods—Large-scale sea ice data) for link]. We extracted daily sea ice concentrations from the period 1979–2013 (**Table 1**) from four 25 × 25 km cells at each of six different locations: southwest Spitsbergen, west Spitsbergen, northwest Spitsbergen, north Spitsbergen, east Spitsbergen, and east Greenland (Supplement 1, Figure S3). Sea ice formation and disappearance follow a seasonal pattern with maximum concentrations in late winter (usually March) and minimum in autumn (usually September). We therefore structured each year of data as the period from 1 September to 31 August (Supplement 2, Figures S1–S6). By using a threshold sea ice concentration of 30% based on work in the Canadian Arctic (Iverson et al., 2014), we then calculated two sea ice indices. The ***length of the ice season*** was calculated as the number of days from the first day with sea ice >30% to the last day with sea ice >30%. The latter was also used to define the ***start of the ice-free season***. When sea ice concentrations were never above 30% during a year, start of the ice-free season was set at 0 (1 January). We also calculated ***monthly mean sea ice concentrations*** for April, May, June and July.

Fine-Scale Conditions in Fjords and Coastal Sites

As opposed to the large-scale data, fine-scale data on sea ice conditions were only available for the most recent years (**Table 1**). We downloaded ice maps for 2004 and 2007–2014 (April–July) from *www.met.no/Hav_og_is* to describe ice conditions in coastal areas in relation to the timing of bird breeding seasons. The maps are high-resolution sea ice concentration charts that are mainly based on weather-independent images from the Radarsat-2 satellite. The spatial resolution is sufficiently high (approximately 50 m) to analyze ice conditions in coastal areas, including fjords. Ice concentrations are classified by six categories. For the purpose of our study, we selected the three densest categories: dense drift ice (70–90% cover), very dense drift ice (90–100%), and fast ice. Ice data were analyzed for the coastal areas of Hornsund (southwest Spitsbergen), Bellsund/Van Mijenfjorden (west Spitsbergen), Kongsfjorden/Krossfjorden (northwest Spitsbergen), Woodfjorden (north Spitsbergen), Isbukta, Kvalvågen, Dunérbukta, and Sørporten (east Spitsbergen), and Traill Island (east Greenland) (see Supplement 1, Figure S4, for locations). Annual ice availability was characterized in two ways: (1) the ice data were aggregated by season to estimate the average amount of ice; and (2) the sea ice data were subjected to a non-linear (4-parameter) logistic regression (Sebaugh, 2011) to estimate the date of peak ice melt. To do this, we extracted the inflection point of the curves (the steepest part of the curve, midway the lower and upper asymptotes) in these regressions. In addition, the ice data were aggregated by 5-day periods to describe location-specific melt patterns.

Statistics

We used the program R (version 3.1.1, R Development Core Team, 2014) for statistical analyses. Linear models (*lm*) were used to test for temporal trends of the ice indices. Annual numbers of bear days were analyzed as a function of year and location by generalized linear models with a Poisson distribution. To account for overdispersion in the data, a quasi-GLM (*glm*, family = quasipoisson, link = log) was fitted to correct the standard errors (Zuur et al., 2009). Non-significant terms ($P > 0.05$) were dropped from the model to refit the model with the remaining terms.

Logistic regression (*glm*, family = binomial, link = logit) models were used to analyze annual polar bear presence (binary response, 0 = no bears observed, 1 = at least one bear observed) as a function of year, location and sea ice conditions. In order to choose one index among the closely related variables for large-scale sea ice conditions, we followed Iverson et al. (2014) and started with comparing models that related bear presence to location and the various sea ice indices (Supplement 4, Table S1). Length of the ice season was the ice index most strongly related to bear presence, and we used this variable in subsequent analyses. To test to what extent polar bear presence was associated with ice conditions, the first logistic regression model that we generated included length of ice season and location as explanatory variables. Length of the sea ice season and year were closely correlated (Supplement 3, Table S1), which precluded testing their effects simultaneously. Instead, we tested if polar bears responded to deviations in ice conditions from long-term trends by calculating detrended values of length of the ice season, using the residuals from the regression of length of the ice season with year. The second model, therefore, included year, location, and detrended length of ice season as explanatory variables.

To test for trends over the years in within-season patterns, we analyzed date of polar bear observations by a linear mixed model (*lme*) with year (centered at the mean) as covariate for the fixed variables. To account for within-year dependencies of observations, year was included as a random factor. Analysis was restricted to observations on Nordenskiöldkysten, the area with most detailed bear observations. A similar analysis was performed to test if bear occurrence was associated with variation in the date of peak ice melt as a measure of ice phenology (see above) in nearby fjords (Bellsund/Van Mijenfjord, indicated as W in Supplement 1, Figure S4).

The ratios of the numbers of predations and numbers of nests were compared among species by a Two-Way ANOVA including species and year as factors.

Results

Temporal Trends in Sea Ice Conditions

Large-scale sea ice conditions changed substantially during 1979–2013 in the study areas (**Figure 2**, Supplement 2, Figures S1–S6). Monthly sea ice cover dropped significantly over time for almost all months and all areas (Supplement 3, Table S1). In east Greenland, sea ice cover did not decrease over time in April or May but did so in June and July.

Length of sea ice season dropped over the years, on average by 3.5 days/year (Supplement 3, Table S1). The strongest decrease was in north Spitsbergen (–5.5) and southwest Spitsbergen

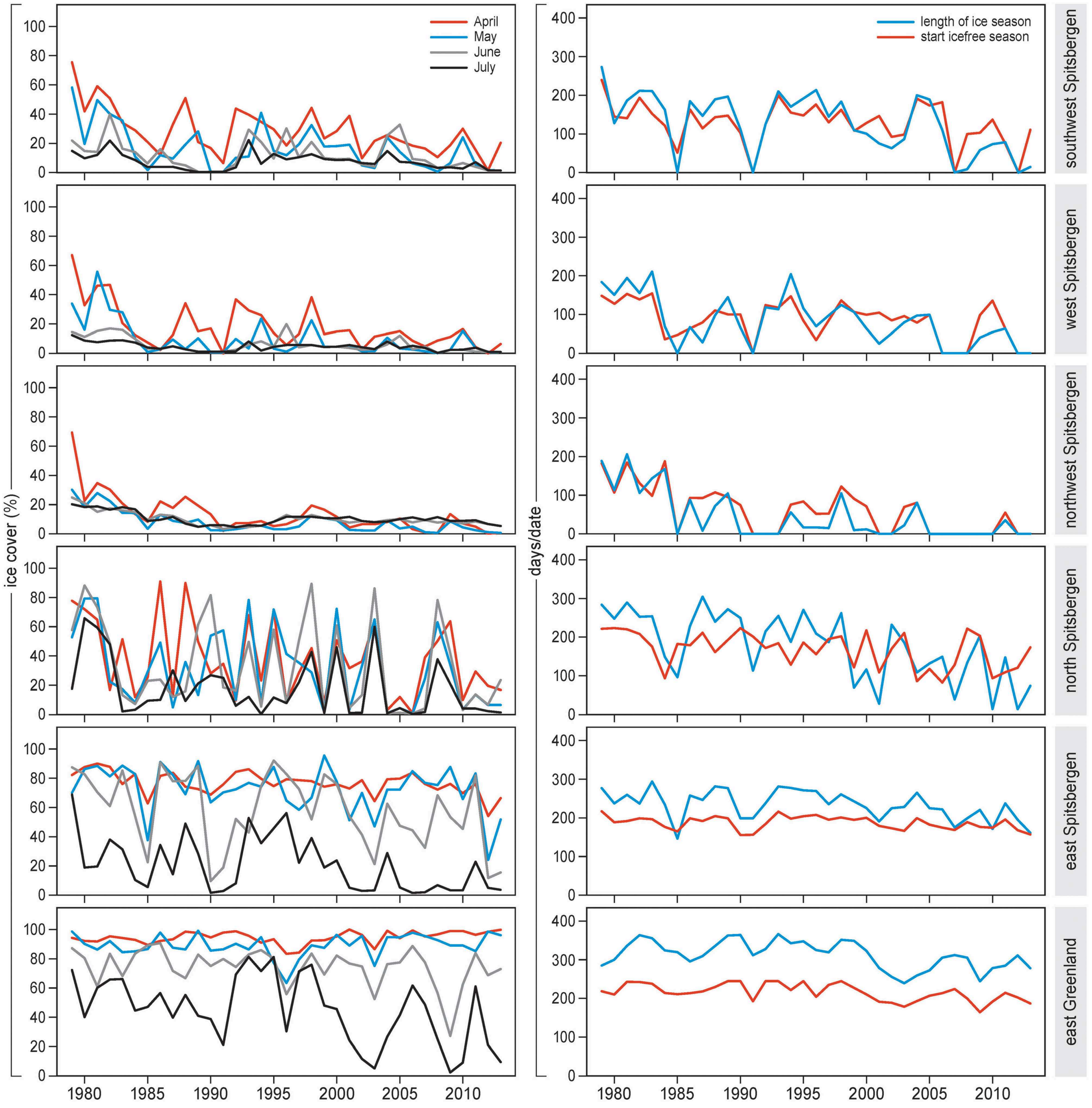

FIGURE 2 | Sea ice concentration (% cover) (left), length of the ice season (days) and start of the ice-free season (days from 1 January) (right) for the period 1979–2013 in selected plots off Spitsbergen (E, SW, W, NW, N) and Greenland (E). Ice concentrations are given for April, May, June and July separately.

(−4.2), and the weakest was in east Spitsbergen (−1.7) and east Greenland (−1.8).

Start of the ice-free season advanced by 2.0 days/year (see Supplement 3, Table S1). The strongest advancement was in northwest Spitsbergen (3.9 d earlier per year) and west Spitsbergen (2.3), and weakest in east Spitsbergen (0.6) and east Greenland (1.1).

Seasonal timing of the sea ice breakup varied among areas (**Figure 3**). Sea ice dropped below a concentration of 30% during the bird nesting season (=June to mid-July) in the open seas and coastal areas of north and east Spitsbergen and in east Greenland, and in the coastal area of west Spitsbergen. In other areas, sea ice breakup occurred before the nesting season.

Bear Observations

Annual Number of Polar Bear Days

Polar bears were only occasionally seen in the summers of 1980–2000 in the study areas on the west coast of Spitsbergen and

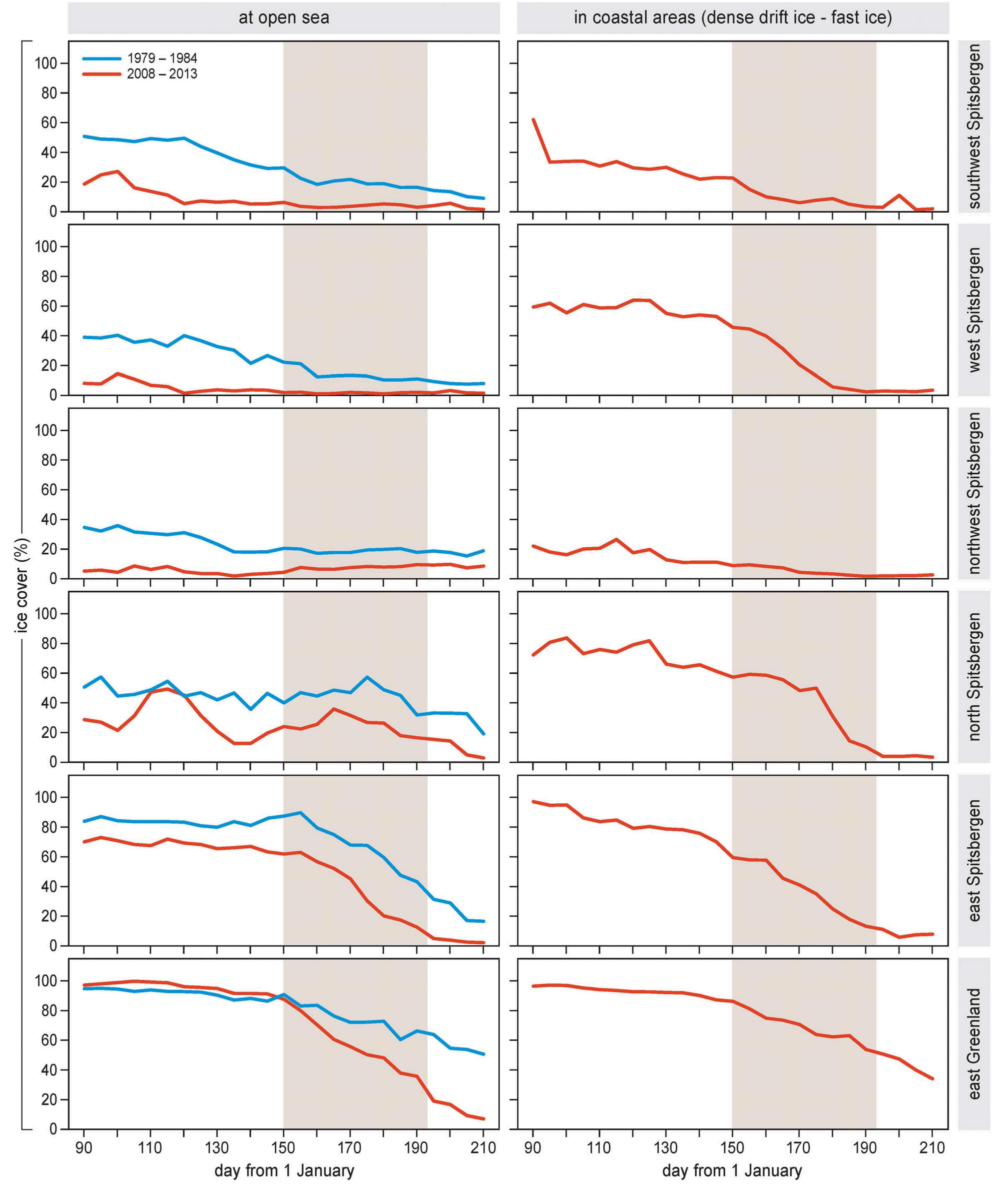

FIGURE 3 | Left panels. Large-scale sea ice concentration (% cover) throughout the months of April–July in areas off the coast of Spitsbergen and Greenland. Separately indicated are averages for 1979–1984 and 2008–2013. **Right panels**. Local sea ice cover (area covered by fast ice or drift ice denser than 70%) throughout April–July in the fjords or coastal sites of Spitsbergen and Greenland (2008–2013). Shading indicates the period of sea bird nesting (approximately 1 June–15 July for all areas).

east coast of Greenland. This changed drastically from the early 2000s onwards, when polar bears became regular summer visitors (**Figure 4**). Annual numbers of bear days increased exponentially, on average, by 15% each year (**Table 2**), a rate which did not differ between locations (the interaction term between year and location was not significant; **Table 2**). Bear numbers differed among locations, with those in Kongsfjorden and Traill Island being 31% and 61% of numbers on Nordenskiöldkysten (**Table 2**).

Annual Probability of Polar Bear Presence

The probability of polar bears being present was negatively related to length of the ice season (**Figure 5A**, **Table 3A**), indicating that more bears were encountered on land in years when the ice season was short. The intercept of the regression differed among locations, which underlines the additional importance of spatial variation. Polar bear presence was not related to detrended values of the length of the ice season (**Table 3B**). We, thus, did not find evidence that bears respond to

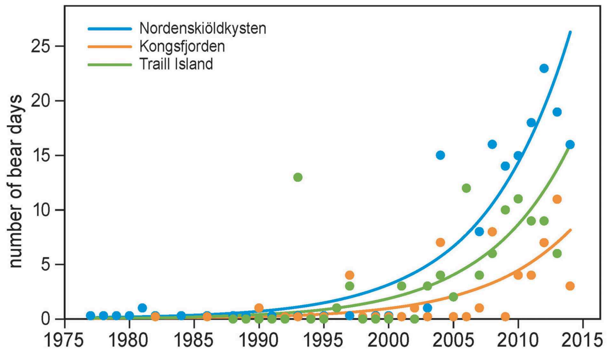

FIGURE 4 | The number of polar bear days in summer as a function of year and location. Locations are Nordenskiöldkysten and Kongsfjorden on Spitsbergen, and Traill Island in Greenland. The observation periods in summer were June–July on Spitsbergen and 15 June–15 August on Traill Island. The curves are based on the model in **Table 2**.

TABLE 2 | Modeling the number of polar bear days in June and July by study location and year (1972–2014).

Parameter	Estimate	*SE*	*t*-value	*P*
Intercept	1.08	0.305	3.53	<0.001
Year	0.15	0.025	5.92	<0.001
Location-NK	0			
Location-KF	−1.16	0.386	−3.01	0.004
Location-TI	−0.50	0.310	−1.61	0.112

Locations are Nordenskiöldkysten (NK), Kongsfjorden (KF), and Traill Island (TI). Data were analyzed by Poisson GLM and corrected for overdispersion by a factor 5.30. Non-significant terms were dropped from the final model. Model results are on a log scale. Location Nordenskiöldkysten was used as the reference category.

Residual deviance 200.21, df = 69.

Terms not included in the final model: Year × Location.

Year was centered at the mean value and the intercept must be interpreted accordingly.

year-to-year fluctuations in sea ice deviating from the long-term trend.

Associated with the ice effects, the probability of polar bears being present in summer increased steeply over the years (**Figure 5B**, **Table 3B**), with a similar rate of increase across locations (the interaction term between year and location was not significant). Notably, the significantly different intercepts for the locations (**Table 3B**) showed that polar bears appeared in each of the areas at different times (**Figure 5B**). Bears appeared first in Hornsund in the 1990s. Later, polar bears appeared in Bellsund, Traill Island, Nordenskiöldkysten, and Kongsfjorden (**Figure 5B**).

Within-Season Occurrence of Polar Bears

On Nordenskiöldkysten, polar bear occurrence shifted forward by 3.0 days/year ($SE = 0.83$; $df = 7$, $t = -3.64$, $P = 0.008$) during 2004–2014 (**Figure 6A**). With respect to the date of peak ice melt in adjacent fjords, the advancement was by 2.1 days/year ($SE = 1.36$; $df = 7$, $t = -1.52$, $P = 0.17$). In a year-by-year comparison, bear occurrence was not related to the date of peak ice melt ($df = 7$, $t = 0.31$, $P = 0.76$).

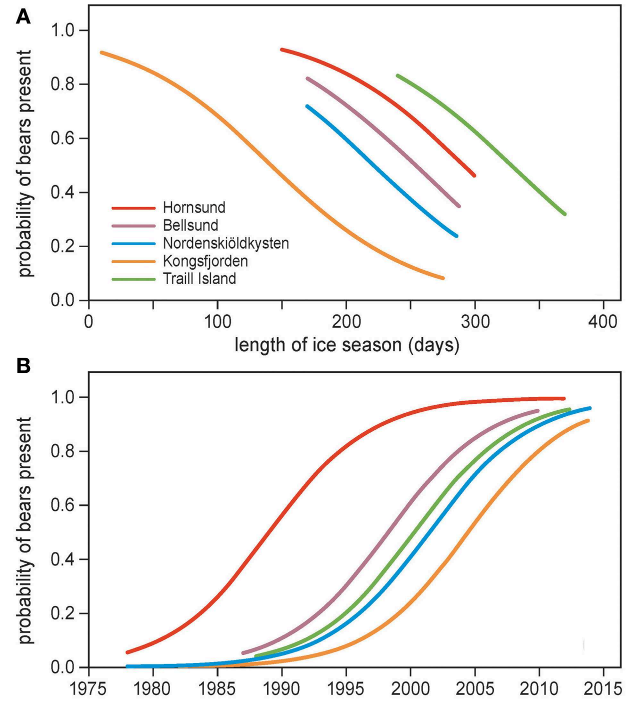

FIGURE 5 | Probability of polar bear encounter in summer as a function of (A) length of the ice season and location, and (B) year and location. Locations are Hornsund, Bellsund, Nordenskiöldkysten and Kongsfjorden on Spitsbergen, and Traill Island in Greenland. The observation periods were limited to June–July on Spitsbergen and 15 June–15 August on Traill Island. The curves are based on the logistic regression models in **Table 3**.

Polar Bear Predation in Bird Colonies

The number of barnacle goose nests in the main study colony on Nordenskiöldkysten fluctuated between 340 (2004) and 520 (2012), without a significant trend over the years ($y = 413.3 + 10.37 \times \text{Year}$ (centered at the mean), $R^2 = 0.241$, $P = 0.18$). During this period, the number of successful nests varied between 0 and 85, with the percentage of nests predated by polar bears ranging from 0 to 91% (**Figure 6B**). Highest predation occurred in the years when the first bears appeared in June, well before bird eggs hatched (Pearson correlation coefficient between predation rate and arrival date of the first bear = −0.75, $n = 9$, $P = 0.021$). The average predation ratio of barnacle goose nests (the ratio of number of predations and number of nest sites) was 0.93 (SD 0.28) (**Figure 7**).

The average number of common eider nests was 140 (SD 25.8) without a significant trend over the years 2009–2014 ($y = 144.9 - 2.31 \times \text{Year}$ (centered at the mean), $R^2 = 0.028$, $P = 0.75$). The predation ratio was 0.82 (SD 0.33), which is similar to that in the barnacle goose (**Figure 7**).

The average number of glaucous gull nests in the main study colony and surroundings was 45 (SD = 2.8). Gulls hatched their eggs approximately 1 week earlier than barnacle geese and common eiders, but this did not make them less vulnerable to polar bear predation. Gull chicks, which were reared in the colony, were easy prey for bears. During 2009–2014, the predation ratio was 0.93 (SD 0.08).

TABLE 3 | Modeling the probability of polar bear presence in June and July during 1979–2013 by (A) length of the ice season and study location, and (B) year, detrended length of the ice season and study location.

Parameter	Estimate	*SE*	*z*-value	*P*
(A)				
Intercept	5.294	1.281	4.13	< 0.001
Length of ice season	−0.018	0.005	−3.72	< 0.001
Location-HS	0			
Location-BS	−0.686	0.634	−1.08	0.279
Location-NK	−1.264	0.649	−1.95	0.051
Location-KF	−2.710	0.801	−3.38	0.001
Location-TI	0.671	0.708	0.95	0.343
Residual deviance = 144.5, *df* = 116.				
(B)				
Intercept	2.413	0.796	3.03	0.002
Year	0.253	0.045	5.65	< 0.001
Detrended length of ice season	−0.001	0.006	−0.20	0.845
Location-HS	0			
Location-BS	−2.319	0.969	−2.39	0.017
Location-NK	−3.136	1.116	−2.81	0.005
Location-KF	−3.918	1.097	−3.57	< 0.001
Location-TI	−2.843	1.008	−2.82	0.005
Residual deviance = 94.6, *df* = 115.				

Locations are Hornsund (HS), Bellsund (BS), Nordenskiöldkysten (NK), Kongsfjorden (KF), Traill Island (TI). Data were analyzed by GLM with a binomial distribution. Location Hornsund was the reference category in the analyses.

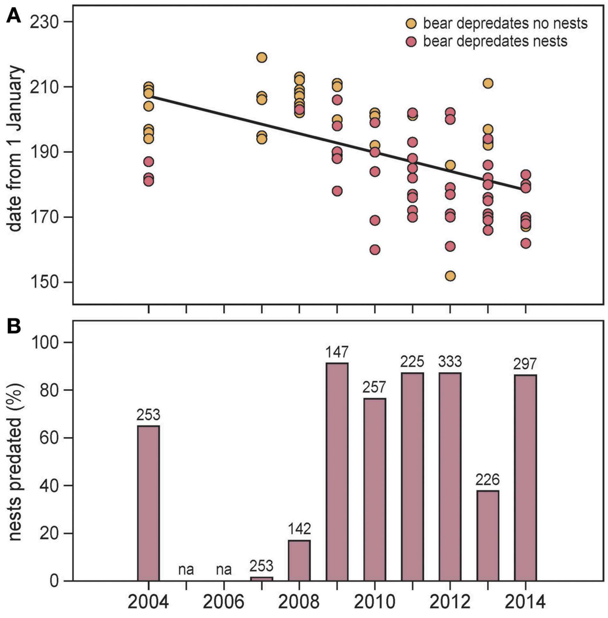

FIGURE 6 | (A) Occurrence of polar bears on Nordenskiöldkysten (west Spitsbergen) in summers 2004–2014 (no observations in 2005 and 2006). 95% of all nest predations took place between 9 June and 9 July (dates 160–190). Separately indicated are polar bears that predated bird nests and those that were not observed eating eggs. The regression line (based on all records in a linear mixed model) is $y = 190.1 - 3.01 \times \text{Year}$; $df = 7$, $t = -3.64$, $P = 0.008$; Year centered at the mean. **(B)** The proportions of barnacle goose nest attempts aborted by polar bear predation in the main study colony on Nordenskiöldkysten, 2004–2014. Numbers represent the sample size of intensively monitored barnacle goose nests included in the analyses. na means that no observations were available.

Discussion

When a new predator enters the scene, the delicate balance between predators and their prey may be perturbed (Bell et al., 2010; Sih et al., 2010). Polar bears colonizing coastal areas, from which they have been absent for a long time, is an example of this situation. Below, we discuss why polar bears have recently extended their summer range toward the terrestrial habitats of west Spitsbergen and east Greenland. We propose that the increased number of bears on land predating bird nests is due to the lack of sea ice on which bears can hunt seals in summer. This process may have been strengthened in west Spitsbergen by a recent expansion into areas that had been occupied by bears year round before humans arrived but thereafter became devoid of bears in summer. Lønø (1970) refers to an expedition led by Jonas Poole in June–July in 1610 to western Spitsbergen, where 27 polar bears were killed and 5 cubs were captured alive (confirming the account of the Willem Barentsz' voyage in 1596; de Veer, 1598). Although polar bears must have been common in summer in the area then, Lønø argues based on later reports from Norwegian trappers that they were rarely encountered in summer on the west coast in the 19th century. He also argues that a larger local stock of bears may have been present year round before the collapse of the walrus (*Odobenus rosmarus*) population.

Polar Bears on Land

The west coast of Spitsbergen has little sea ice in most years, and summer observations of bears in the periods free of sea ice have been relatively rare at least in the later decades of the 20th century. The east coast of Greenland hosts a polar bear population that used to roam the extensive drift ice offshore, only infrequently showing up at coastal tundra sites (Born et al., 1997; Wiig et al., 2003; Laidre et al., 2013). The bears that we observed during the past years were either in transit or they were extensively feeding on eggs in bird colonies. Incidentally, polar bears have also been observed feeding on carcasses of muskox (*Ovibos moschatus*) (Greenland) or reindeer (*Rangifer tarandus*) (see also Gormezano and Rockwell, 2013; Stempniewicz et al., 2014). The presence of polar bears in areas that used to be devoid of bears, often feeding on items that are regarded as relatively unimportant energy sources compared to their staple food (Derocher et al., 2004; Stirling, 2011), fits well with records from other parts of the Arctic (Schliebe et al., 2008; Smith et al., 2010; Iverson et al., 2014). This suggests that polar bears more frequently occurring on land is a circumpolar phenomenon.

We hypothesized that occurrence of polar bears on land is related to sea ice conditions. In line with earlier findings (Serreze et al., 2007; Moe et al., 2009) we report a high rate of sea ice disappearing. The large spatial variation in sea ice abundance and rate of disappearance over the years corresponds to patterns found at the scale of the entire Arctic (Cavalieri and Parkinson, 2012; Meier et al., 2014). Average annual reduction in length of the ice

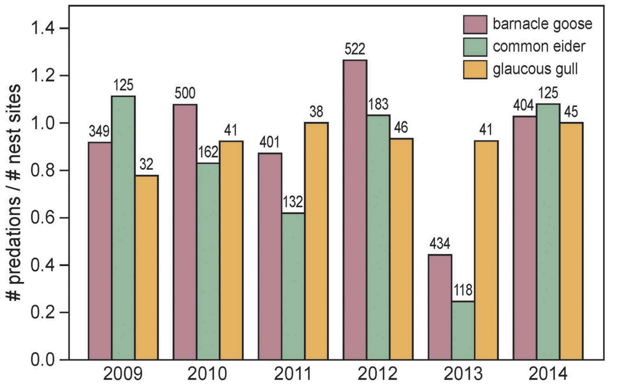

FIGURE 7 | Intensity of polar bear predation on barnacle goose, common eider and glaucous gull nests in the main study colony on Nordenskiöldkysten during 2009–2014, as measured by the ratio of numbers of predations and numbers of nest sites. A nest site may be used by successive nest owners, and, therefore, nests were predated up to three times within a single season. Indicated are the numbers of nests in the colony. Ratios do not differ among species [$F_{(2,\ 10)} = 0.58$, $P = 0.57$, while accounting for year effects].

season, a proxy of polar bear habitat availability, dropped by 3.5 days per year. Within our selection of study areas, the smallest reductions in ice season length occurred in east Spitsbergen and east Greenland. The area of east Spitsbergen is very important to the Barents Sea polar bear population (Lønø, 1970) due to the cold water and good access to sea ice much of the year. However, in summer and autumn, many of the bears that use this area in winter and spring will be further east and north on the pack ice (Mauritzen et al., 2001; Aars et al., 2009).

The number of bear days on land showed a consistent increase after polar bears colonized a specific area, although the data suggest a deceleration during the last couple of years of the study period. Given the high degree of seasonal site fidelity in polar bears (Mauritzen et al., 2001; Stirling et al., 2004; Zeyl et al., 2009; Lone et al., 2013), we suppose that a more or less permanent group of bears roamed the west coast of Spitsbergen in summer. If so, this group may be on the order of a few dozen individuals, based on the number of bears reported every year to the marine mammal sighting database (http://mms.data.npolar.no/) managed by the Norwegian Polar Institute. This number is also in accordance with a survey in August 2004 when 31 bears were counted along the coast of Spitsbergen (Aars et al., 2009), although numbers on land may have increased since then. We, thus, suspect that the number of polar bears along the west coast consists of a modest fraction of the Barents Sea population estimated at 2650 (Aars et al., 2009).

While some of the bears are likely local to the west coast of Spitsbergen year round, others may be visitors from the fjords in north Spitsbergen, and some are from east Spitsbergen. Visual observations and telemetry data show that polar bears move with drifting sea ice around the southern tip of Spitsbergen from east to west, and often eastwards into Hornsund where they may stay or cross the glacier back to Storfjorden on the east coast (Lydersen et al., 2002; unpublished data, Norwegian Polar Institute). This migration route linking the areas in east and west likely explains why Hornsund was the area where bears occurred earliest in the bird colonies.

Polar bear presence on land showed a strong negative relationship with the length of the ice season when accounting for variation among locations. This is on par with recent studies that showed a clear link between bear movements to terrestrial habitats and sea ice conditions (Cherry et al., 2013; Iverson et al., 2014; but see Stirling et al., 2004). That is not to say that sea ice conditions are the only factor determining polar bear numbers and distribution. We found that year of observation was a stronger predictor of bear presence than length of the ice season, even though both were closely correlated. This indicates that other factors contributed to the trend of increasing numbers of bears on land.

An important reason for an increasing number of bears on the west coast may be due to bears recolonizing areas where they used to be present before they were heavily hunted for about a hundred years, until 1973 (Lønø, 1970). Maternity denning in areas of west Spitsbergen has not been described in earlier literature despite several dedicated studies but has been recorded several times in recent years (Andersen et al., 2012). A recolonization may also be triggered by a likely increase in the population size at least until recently (Derocher, 2005). It seems, therefore, that an increasing number of bears have started using the west coast, searching land for food when sea ice is absent.

The population in east Greenland is still hunted, although not at the intensity as in Svalbard in former days (Rosing-Asvid, 2002), and the increased occurrence on land is, thus, not likely to be explained by recolonization. Instead, a shift in habitat use may be associated with a decrease in sea ice habitat; thus, bears are forced onto land for longer periods than in earlier years. It seems, therefore, that large-scale processes, such as climate and subsequent habitat changes, are a common driver but that population history plays an additional role.

Habitat choice depends on the quality of each of the habitats considered (Fretwell and Lucas, 1970), and any change in quality is reflected in allocation of time over the habitats (Mauritzen et al., 2003; Schreiber, 2012). Thus, the changes in polar bear numbers that we observed might be due to—or strengthened by—developments in the recently colonized coastal habitat. Use of bird eggs as a food source for polar bears was already described by Lønø (1970) in Svalbard. It has been suggested that eggs allow individual bears to have a high energy intake (Rockwell and Gormezano, 2009). During the past decades, this potential food source became more widespread in the coastal zones of Spitsbergen (Drent et al., 1998) and Greenland (Madsen et al., 2011). Concurrent with the growth of the Svalbard goose populations, goose numbers in coastal areas have increased by a factor of three (barnacle geese) or four (pink-footed geese) (Mehlum, 1998; Goosemap et al., 2013; Black et al., 2014). Other alternative food sources may also further increase the value of the summer habitat to these bears. Increasing numbers of harbor seals (*Phoca vitulina*) have been spreading along the coasts of Spitsbergen in later years (Lydersen et al., 2002). Walrus haul-out sites are also increasing, due to a fast growing population (Kovacs et al., 2014). In Greenland, muskox carcasses may also be a source of energy for polar bears on land. Due to the increasing frost–melt events in winter during the last decades (Gilg et al., 2009), the number of available carcasses has increased (BS, unpublished data).

Earlier Arrival on Land by Polar Bears

Polar bears occurred at the coastal site of Nordenskiöldkysten earlier each year, and we have obtained evidence that bears arrived progressively earlier relative to the date of peak sea ice melt. Due to this rapid advancement, polar bear occurrence has undergone a striking change relative to the breeding season of colonial birds, in particular geese and eider. Initially, bears used to show up from the end of incubation onwards, whereas in most recent years, the first bears arrived during the early nest phase. This suggests that bears have adapted seasonal movements after experiences with new food resources. The phenomenon of bears returning to familiar, profitable sites is in agreement with the observation that polar bears repeatedly visit areas where they have been before (Mauritzen et al., 2001; Zeyl et al., 2009; Andersen et al., 2012; Lone et al., 2013). Our observations additionally suggest that polar bears adapt quickly once they have discovered new hunting opportunities. Indeed, there is strong pressure for early exploitation: (1) to hit the peak of egg availability; (2) to arrive before competing bears; and (3) to arrive before birds abandon their nests *en masse* as may happen at any time during inclement weather, which is what occurred during the breeding season of 2013.

Polar Bear Predation on Eggs

Polar bear predation was particularly severe on offshore island colonies of barnacle geese, common eiders and glaucous gulls. Some polar bears also preyed on aggregations of pink-footed goose nests further inland (Prop et al., 2013). Earlier arrival by bears in the colonies resulted in higher proportions of predated nests. Predation often led to nest territories being occupied by goose pairs that otherwise might have had difficulties in obtaining a nest site (Black et al., 2014), which increased the number of eggs available to bears later in the season.

Adult survival is a main determinant of population growth rates in long-lived species (Caswell, 2001). Reproductive costs are usually high due to impaired survival of successful pairs (Black et al., 2014). As such, a single predation event may not reduce the lifetime reproduction of an individual much because of the chances to reproduce another year. Breeding failure in Arctic-nesting birds is common, due to inclement weather or adverse snow conditions (Prop and de Vries, 1993; Yannic et al., 2014), and birds rely on the most favorable (and consequently most productive) years. However, polar bear predation will lower the reproductive outputs during favorable years. When possibilities to compensate an annual 10–15% mortality (Wilson et al., 2007; Allard et al., 2010; Black et al., 2014) are lost in any year, maintaining the local population at a constant level is unlikely. Surprisingly, the numbers of nests in the colony for either species remained relatively stable (**Figure 7**), which suggests that recruitment took place by birds arriving from elsewhere.

Polar bears act as top-predators in marine ecosystems or coastal ecosystems between sea and land. They have been documented to play a role in the population dynamics of light-bellied brent geese (*Branta bernicla hrota*) by visiting breeding locations in eastern Svalbard in years with dense sea ice in summer (Madsen et al., 1998). Our observations indicate that the ecological amplitude of polar bears in the Arctic ecosystem has broadened. We witnessed: (1) polar bears extending their range toward the coastal areas of west Spitsbergen and east Greenland; and (2) a persistent effect of polar bears on colonial breeding birds, including barnacle geese, common eiders and glaucous gulls, by high predation rates. We obtained evidence that these changes were driven by shifts in sea ice conditions, but we cannot rule out the possibility of a complex set of corroborating factors. Nevertheless, the number of polar bears exploiting the coastal habitat was small, and we suspect that there is little scope for further increase in numbers. This underlines the importance of the sea ice habitat to support current population levels of polar bears.

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Supplementary Material

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fevo.2015.00033/abstract

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Anthropogenic flank attack on polar bears: interacting consequences of climate warming and pollutant exposure

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Polar bears (*Ursus maritimus*) are subjected to several anthropogenic threats, climate warming and exposure to pollutants being two of these. For polar bears, one of the main effects of climate warming is limited access to prey, due to loss of their sea ice habitat. This will result in prolonged fasting periods and emaciation and condition related negative effects on survival and reproduction success. Prolonged fasting will result in increases of the tissue concentrations of persistent organic pollutants (POPs) in polar bears, and thus increase the probability for POP levels to exceed threshold levels for effects on health, and thus on reproductive success and survival. There are clear potentials for interactions between impacts of climate warming and impacts of pollutant exposure on polar bears. It is likely that that fasting-induced increases of POPs will add to mortality rates and decrease reproductive success beyond effects caused by loss of habitat alone. However, there is a lack of studies that have addressed this. Thus, there is a need to focus on population effects of POP exposure in polar bears, and to consider such effects in relation to the effects of climate induced habitat loss.

Keywords: arctic, pollution and global change, PCBs, ecology, climate change impacts

POLAR BEARS, CLIMATE WARMING, AND POLLUTION EXPOSURE

Polar bears (*Ursus maritimus*) have received considerable focus as a wildlife species impacted by climate change since projected sea ice loss is argued to restrict their access to seals on the ice, making their survival of global concern (Durner et al., 2009; Edwards et al., 2011; Molnar et al., 2011; Stirling and Derocher, 2012; Derocher et al., 2013). The polar bear is the single species among mammals and birds listed under the U.S. Endangered Species Act that attracts most public attention (Roberge, 2014), and a symbol-species of the potential devastating effects of global climate change on biodiversity and ecosystems. Modeling has shown that the southernmost polar bear populations are those that are most vulnerable, and will struggle to persist there throughout this century (Castro De La Guardia et al., 2013). Models have also predicted losses of polar bear sea ice habitats in the polar basin during this century (Durner et al., 2009) and indicated that two-third of the world's polar bears could disappear if greenhouse gas emissions continue as predicted (Amstrup et al., 2008).

However, climate warming is not the only anthropogenic factor that affects polar bear populations. Exposure to pollutants, hunting and increase in ecotourism and raw material exploration and exploitation are other major anthropogenic threats to this species (IUCN, 2014). Because of their high tropic position and food web biomagnification of persistent organic pollutants (POPs), and mercury (Hg), polar bears are exposed to high levels of these harmful compounds (Letcher et al., 2010; Sonne, 2010). Due to international regulations on production and use of POPs (www.pops.int) there have been significant decreases in levels of the conventional POPs in polar bears and their prey during the last decades, whereas brominated flame retardants (BFRs) and perfluoroalkyl substances (PFASs) overall have increased over the same period although some have started to decline in recent years (Bytingsvik et al., 2012a,b; Dietz et al., 2013c; Dietz R Rigét et al., 2013b; Riget et al., 2013). However, levels of most POPs such as polychlorinated biphenyls (PCBs), brominated flame retardants (BFRs), organochlorinated pesticides (OCPs) and perfluoroalkyl compounds (PFASs), are still high in polar bears, and often above threshold levels for physiological and toxicological effects reported in the literature for mammals (Letcher et al., 2010; Sonne, 2010). Furthermore, levels of Hg have been shown to increase in polar bears (Dietz et al., 2011) and there are increased concerns about the effects of metabolites produced by endogenous biotransformation of POPs (Letcher et al., 2010).

Many POPs and their metabolites, as well as mercury (Hg) have been shown to have endocrine disruptive effects, and are thus classified as endocrine disrupting chemicals (EDCs) (Colborn, 2004). In general, the endocrine system together with the nervous and the immune systems, form the main regulatory mechanisms in the animal body controlling all vital functions

(Lintelmann et al., 2003). Many POPs also interfere with immune function, lipid storage and metabolism and reproduction, and may perturb important processes during early growth and development (Letcher et al., 2010). There are concerns that effects on organisms caused by climate change and contaminant exposure interact, thus causing combined effects that may have large-scale ecological impacts (Jenssen, 2006; Schiedek et al., 2007; Wingfield, 2008; Noyes et al., 2009; Unep/Amap, 2011; Moe et al., 2013). The combined effects of these two anthropogenic factors on populations and ecosystems may be additive, or even synergistic. Herein, we focus on how POPs may interact with, and possibly enhance the effects of climate warming in polar bears. Insight into such combined effects caused by these two major anthropogenic stressors provides perspectives that are of importance for research and for conservation management of the species.

COMBINED EFFECTS ON ENERGETIC PROCESSES

In some regions periods of open-water force polar bears onshore during summer and autumn, and thus limit access to their most common high-energy containing prey, that mainly are ringed seals (*Pusa hispida*) (Stirling and Derocher, 2012; Derocher et al., 2013). During these periods they fast and rely on body lipid reserves for energy (Cherry et al., 2009). Climate warming causes earlier break-up of sea-ice and thus prolongs this fasting period in polar bears, resulting in increased mortality rates due to emaciation and starvation (Gagnon and Gough, 2005; Molnar et al., 2010, 2014; Stirling and Derocher, 2012). Because many lipid-soluble POPs are not excreted, fasting and especially emaciation will cause large increases of the concentrations of these compounds in blood and target tissues (Polischuk et al., 2002; Christensen et al., 2007; Helgason et al., 2013). Thus, prolonged fasting due to climate induced ice-loss and resultant lowered prey availability increases the likelihood for POPs levels to exceed threshold levels for effects. Many POPs have health effects that directly affect survival rates, such as their negative effects on the immune system (Vos et al., 2000). Thus, it is likely that fasting-induced increases of these compounds will increase the mortality rates beyond those predicted to be caused by the climate-induced prolonged fasting period alone (Molnar et al., 2010, 2014). It is also likely that fasting-induced increases of burdens of POPs that are reproductive EDCs will add to the predicted negative reproductive effects that lower body condition alone has on reproductive success of polar bears (Regehr et al., 2010); **Figure 1**.

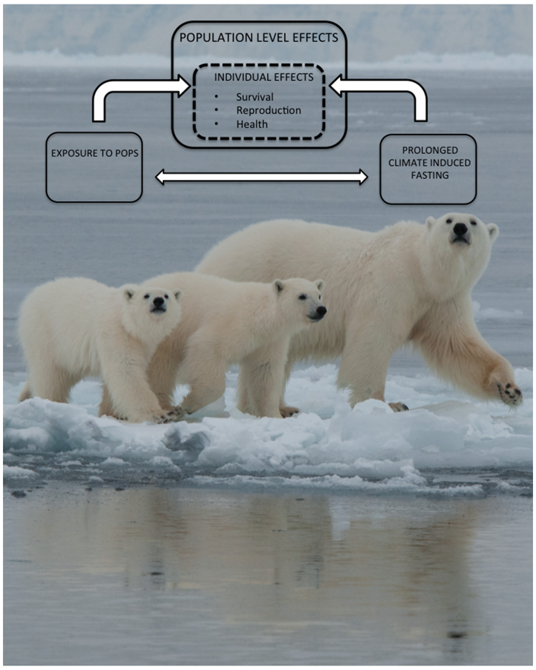

FIGURE 1 | Climate change induced fasting and exposure to persistent organic pollutants (POPs) are anthropogenic stressors that have the potential of affecting the individual health, reproduction and mortality of polar bears. Prolonged fasting may increase tissue concentrations of POPs and thus enhance negative fitness effects, whereas high levels of POPs may cause metabolic effects that interfere with fasting tolerance. Effects on the individual level propagate to population levels. Photo: Rune Dietz.

It is suggested that decreases of polar bear sea ice habitats will result in increased movement and migration rates and distances to remain on ice (Derocher et al., 2004; Durner et al., 2009), thus causing increased energetic requirements and feeding rates. In female polar bears it has been suggested that high movement rates and distances associated with occupying large home range sizes may result in high blood concentrations of PCBs (Olsen et al., 2003). This is because the high activity level associated with occupying large home range sizes requires high food intake, which causes high dietary intake of these persistent compounds (Olsen et al., 2003). It is therefore possible that long-range annual migrations mitigated by sea ice habitat loss will result in increased uptake and accumulation of POPs due to the increased feeding demands needed for longer migrations. In some regions, decline of sea ice extension has resulted in changes in the presence of seal species that polar bears depredate, and this has been shown to cause increased bioaccumulation of certain POPs (Thiemann et al., 2008; McKinney et al., 2009, 2013). Dietary shift toward feeding on plants, berries and caribou (*Rangifer tarandus*) and seabird eggs, respectively (Ramsay and Hobson, 1991; Gormezano and Rockwell, 2013a,b; Iles et al., 2013; Iverson et al., 2014), will most likely decrease and increase, respectively, the dietary uptake of POPs. Furthermore, climate warming induced immigrating warm-adapted fish species (Valdimarsson et al., 2012; Mackenzie et al., 2014) may act as biovectors that increases contaminant levels in marine arctic ecosystems (Macdonald et al., 2005; Carrie et al., 2010), ultimately causing increased bioaccumulation of these compounds in polar bears.

In polar bears, the thyroid hormone system is sensitive to the effects of several POPs (Skaare et al., 2001; Braathen et al., 2004; Gutleb et al., 2010; Knott et al., 2011; Villanger et al., 2011; Bytingsvik et al., 2013; Simon et al., 2013; Gabrielsen et al., 2015). The effects of EDCs on thyroid hormones appear to be particularly pronounced in female and subadult polar bears, whereas adult males appear to be much more resistant (Braathen et al., 2004; Villanger et al., 2011). In polar bears there are also indications that concentrations of T4 in muscle tissue and deiodinase activities in muscle, kidney and liver are influenced by circulating concentrations of POPs (Gabrielsen et al., 2015). Since thyroid hormones are involved in nearly all metabolic pathways (McNabb, 1995), EDC induced thyroid disruption may seriously interfere with energy expenditure during fasting. Thyroid dysfunction has also been linked to reduced fertility, increased rates of spontaneous abortion, premature delivery and low birth weight (Krassas et al., 2010). Because climate driven fasting and emaciation will increase contaminant loads in target tissues, the thyroid related effects might become "self-reinforcing" and thus escalate the negative effects on survival and reproduction.

The glucocorticoid endocrine system also plays an important role in metabolism and energetic processes (Hiller-Sturmhöfel and Bartke, 1998). In polar bears, the main glucocorticoid hormone in mammals, cortisol, has been reported to be influenced by plasma concentrations of pesticides and PCBs (Oskam et al., 2004; Bechshøft et al., 2012). Cortisol in polar bears is also influenced by climate conditions, indicating that the bears are under higher levels of physiological stress during years with less ice cover and thus less easy access to seals (Bechshøft et al., 2013). Pollutant exposure may thus add to the physiological stress encountered by polar bears during years with low ice coverage, enhancing the effects of climate warming.

Polar bears have an enrichment of genes associated with adipose tissue development that may be important in the adaptation to their lipid-rich diet and high blood concentrations of cholesterol and low-density lipoproteins (Liu et al., 2014). Recently, there has been an increased focus on the role of POPs on development of obesity in humans (Hotchkiss et al., 2008; Dirinck et al., 2013; De Cock and Van De Bor, 2014; Donat-Vargas et al., 2014). One mechanism for this effect may be that POPs causes "leptin-resistance" in adipose tissue, a typical metabolic alteration related to obesity (Ferrante et al., 2014). Furthermore, dietary exposure to PCBs may result in increased metabolic rates (Voltura and French, 2000). Since lipid storage and metabolism are important environmental adaptations in polar bears, disruption of these processes by POPs may seriously inflict on the ability of polar bears to tolerate prolonged fasting periods that are predicted to be associated with climate warming. If POPs increases metabolic rates, high body burdens of POPs are likely to induce higher rates of body mass loss, and thus increase mortality rates beyond those predicted to be caused by prolonged fasting alone (Molnar et al., 2010, 2014); **Figure 1**.

COMBINED EFFECTS ON REPRODUCTION AND IMMUNITY

Several POPs have been documented to have harmful effects on reproductive organs and hormones, and to adversely affect fertility and fecundity in mammals (Vos et al., 2000). In polar bears, POPs have been reported to affect reproductive hormones (Haave et al., 2003; Oskam et al., 2003) and to influence the morphology of male and female reproductive organs such as testicles, penis, uteri and ovary (Sonne et al., 2006). This may reduce their reproductive success (Sonne et al., 2006; Letcher et al., 2010). These morphological changes are probably a result of both pre- and post-natal effects and the pathways being via the hypothalamic-pituitary-axis likely with a thyroid cross-talk (Sonne, 2010). Although poor recruitment in the Svalbard polar bear population has been linked to their high burdens of reproductive EDCs (Derocher et al., 2003), it not possible to fully estimate the impact from these reproductive related disruptions and pathological conditions. It is likely that fasting-induced increases in reproductive EDCs will enhance the reported negative effects on reproductive success in polar bears caused by increasing duration of the ice-free period (Regehr et al., 2010)

Climate warming increases risks of disease spreading (Harvell et al., 2002), and may induce a shift in the micro-pathogen composition toward higher virulence (Shope, 1992; Burek et al., 2008). Polar bears may therefore become exposed to health challenges that they have not previously encountered (Sonne, 2010). Many POPs are immune toxic (Vos et al., 2000) and in polar bears inverse relationships between POP concentrations and immune globulins and cellular immune responses have been reported (Bernhoft et al., 2000; Lie et al., 2004, 2005). The combination of spreading of new diseases and micro-pathogens to the Arctic caused by global warming (Harvell et al., 2002) and a weakened immune system in polar bears caused by pollutant exposure will cause combined effects that can increase mortality rates. Polar bears also have low genetic diversity in their immune system, which is consistent with a long-term exposure to low levels of pathogens and parasites (Weber et al., 2013). Thus, contaminant exposure could depress their response toward micro pathogens and diseases even further, and thereby increase mortality rates. In addition, pathogens and diseases may affect reproductive rates (Sonne, 2010). It is likely that fasting will enhance immune related effects, both due to fasting-induced increases in POPs, and due to that fasting generally is associated with immunosuppression and poorer general health conditions (Sonne, 2010).

COMBINED EFFECTS ON NEUROLOGICAL PROCESSES, BEHAVIOR AND DEVELOPMENT

POPs can cause neurobehavioral effects, such as sexual and other reproductive behaviors, activity, motivation, communication, aggression, dominance and other social behaviors, as well as learning and other cognitive abilities (Zala and Penn, 2004). Field studies of behavioral effects of POPs in polar bears are, of natural causes, difficult to conduct. However, several POPs and methylmercury reported in brain tissue of polar bears, (Greaves et al., 2012, 2013; Krey et al., 2012; Dietz et al., 2013a) are known or suspected developmental neurotoxicants in humans and experimental animals (Grandjean and Landrigan, 2006, 2014; Fonnum and Mariussen, 2009; Mariussen, 2012).

POPs might affect brain function or development through many mechanisms, such as interacting with brain neurotransmitter systems (Fonnum and Mariussen, 2009). Also, the ability of some POPs to induce epigenetic changes could present a mechanistic pathway of neurodevelopmental perturbations (Mill and Petronis, 2008; Bollati and Baccarelli, 2010; Crews, 2011). Associations between neurochemical and epigenetic biomarkers and mercury levels in brain tissue have been reported for polar bears (Basu et al., 2009; Pilsner et al., 2010; Dietz et al., 2013a). Another proposed mechanism of developmental neurotoxicity is through thyroid hormone disruption, as these hormones are essential during fetal and early neonatal neurodevelopment (Crofton and Zoeller, 2005; Ahmed et al., 2008). Thus, the high levels of POPs reported in 4-month old polar bear cubs (Bytingsvik et al., 2012a,b) and their associated thyroid disrupting properties in cubs (Bytingsvik et al., 2013; Simon et al., 2013) raises concern for neurodevelopmental effects in polar bears.

The relative high concentrations of several POPs reported in polar bear brains may cause adverse effects, with a possible heightened susceptibility during the more sensitive fetal and neonatal stages of brain development (Rodier, 1995; Grandjean and Landrigan, 2006). Similarly to humans, this could alter behavioral traits and reduce cognitive abilities related to memory and learning in offspring. For polar bears, this could functionally reduce, e.g., hunting skills or alter mating behavior, and thus ultimately affect reproduction and survival.

COMBINED EFFECTS ON POPULATIONS, GENETICS, AND EVOLUTION

Several studies have documented that climate induced loss of sea ice has negatively affected the long-term survival and abundance of polar bears in some subpopulations (Regehr et al., 2010; Stirling and Derocher, 2012; Bromaghin et al., 2015). In contrast, there appear to be no documentation that POPs have caused decreases in polar bear populations. However, there are numerous reports that POPs affect fitness-related variables in polar bears at the individual level (Letcher et al., 2010; Sonne, 2010). Modeling of effects of POPs at the population level is thus warranted. The effects of both POPs and climate warming will affect density-dependent processes at the population level. Thus, mortality due to POP exposure and habitat loss caused by climate warming can separately and/or combined, reduce competition for food and thus reduce starvation in surviving animals.

The divergence of polar bears from brown bears (*Ursus arctos*) has taken 480-340 thousand years (Edwards et al., 2011; Liu et al., 2014). It is also indicated that polar bears were adapted to arctic marine diet and life 130-110 thousand years ago (Lindqvist et al., 2010), indicating an unprecedented time for rapid evolution of less than 20,500 generations (Liu et al., 2014). Furthermore, dispersal events driven by climate fluctuations has caused opportunistic mating between these two species, suggesting that interspecific hybridization may be a mechanism by which polar bears deals with marginal habitats during previous non-anthropogenic periods of environmental deterioration (Edwards et al., 2011). The history of the large-scale environmental changes caused by anthropogenic pollution is short in relation to their evolutionary history. Whereas polar bears most likely have experienced rapid and dramatic climatic fluctuations during the past hundreds of thousand years, exposure to anthropogenic POPs have occurred for less than 100 years. Although Atlantic tomcod (*Microgadus tomcod*) inhabiting waters highly polluted with PCBs and dioxins, genetically evolved AhR resistance over the time-span of three decades (Wirgin et al., 2011), it is very unlikely that a similar rapid evolution will occur in a polar bears.

Morphometric differences in the size and shape of individual polar bear skulls collected in 1892–1932, which is prior to the major anthropogenic environmental changes, as compared to in skulls from 1961 to 2002 were suggested to be a combined consequence of exposure to POPs and climate induced changes in the availability of food resources (Pertoldi et al., 2009). These combined effects may also have affected the polar bears' genetic composition and effective population size (Pertoldi et al., 2009). An epigenetic study documented Hg-associated DNA hypomethylation in brain stems of male polar bears (Pilsner et al., 2010). Epigenetic responses do not represent a permanent redirection of phenotype in the same way as mutation and natural selection (Burggren and Crews, 2014), and are "turned off" in downstream generations when the environmental stressor that created them diminishes or disappears (Burggren, 2014). However, multi-generation *in utero* exposure to a stressor (such as Hg and POPs) may cause long-lasting transgenerational effects (Burggren and Crews, 2014). It should also be noted that although in mammals, epigenetic markers are erased before being re-established, a process referred to as "reprogramming," recent studies show that some epigenetic marks escape epigenetic reprogramming (Mendizabal et al., 2014).

CONCLUDING REMARKS

According to the points discussed above, there are clear potentials for interactions between impacts of climate warming and impacts of pollutant exposure on polar bears. However, there is a lack of studies that can confirm or discard the presence of such interactions. Of particular concern are the interacting effects of the climate induced prolonged fasting periods and the resultant increased POP levels in polar bears. We hypothesize that fasting-induced increases of POPs will add to mortality rates and decrease reproductive success beyond effects caused by loss of habitat alone. When considering the numerous fitness-related traits reported to be influenced by POPs, there is a need to focus on population effects of POP exposure in polar bears, and to consider such effects in relation to the effects of habitat loss.

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REVIEW
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A review of the battle for food in the Barents Sea: cod vs. marine mammals

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Cod, harp seal and minke whale are the main top predators in the Barents Sea ecosystem. In the last decade, the abundance of cod has increased considerably, and is at a record high level. In spite of this, the growth and condition of cod has remained rather stable, although some decrease is seen in size at age of large, mature cod. During the same period, the abundance of harp seals has declined whereas the minke whale stock has been at a stable level. The body condition (blubber thickness) of these two mammal stocks has, however, decreased, with the strongest decrease observed for harp seals. A possible hypothesis for explaining this is that cod outperform the marine mammal stocks in the competition for food. The main advantages for cod are most likely larger availability of food (mainly capelin) during winter-spring than for marine mammals, as well as a wider range of prey species being available to cod than to marine mammals. Harp seals are more dependent on prey items found close to the ice edge than the other two predator stocks are, which could partly explain why the performance of harp seals is worse than that of the two other main top predators in the area.

Keywords: cod, harp seal, minke whale, Barents Sea, competition, top predators

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Introduction

The abundance of high trophic level or apex predators such as marine mammals and large piscivorous fish have varied substantially worldwide over the past five decades (e.g., Pauly et al., 1998; Myers and Worm, 2003; Estes et al., 2011). Current trends in harvested fish populations appear to be diverging among regions; stabilizing in some regions but continued to decline in others (Worm and Branch, 2012). As for marine mammals they are either protected or harvested at very low and sustainable levels. In the North Atlantic there has been an increasing trend in whale species such as fin whales and humpback whales (Haug et al., 2011), while there are examples of both increasing (harp seals; ICES, 2013a; Øigård et al., 2014a) and decreasing (hooded seals; Øigård et al., 2014b) seal stocks. Although the ecological consequences of such predator changes vary among ecosystems (e.g., due to functional diversity of top predators) several studies point out that cascading effects through the entire food web is a likely outcome (Pauly et al., 1998; Frank et al., 2005). Understanding the role of high trophic predators and how they respond to changes in the resource availability is important to predict future functioning of ecosystems.

The Barents Sea ecosystem (BSE) is a shallow (average depth 220 m, depth range 20–500 m) high latitude shelf sea that supports major fisheries and where the productivity is high but vary considerably between years (e.g., Wassmann et al., 2006) that supports major fisheries. The

BSE has been displaying decadal shifts in species abundance and trophic control the past four decades (e.g., Wassmann et al., 2006; Johannesen et al., 2012) where climate change, particularly increasing temperatures and effects on sea ice cover and distribution, appears to have noticeable effects on the distribution and abundance of species (Wassmann et al., 2006; Dalpadado et al., 2012). There has been a gradual shift toward more Atlantic species the past decade (Fossheim et al., under revision), most likely as a result of warming and reduced ice coverage.

The BSE is an important feeding area for several migratory and resident apex predators (Dolgov et al., 2011). The three most important are cod *Gadus morhua*, harp seals *Pagophilus groenlandicus* and common minke whales *Balaenoptera acutorostrata* (Bogstad et al., 2000; Wassmann et al., 2006; Dolgov et al., 2011). There are several other piscivorous fish and marine mammal species that reside in the Barents Sea (see e.g., Dolgov et al., 2011; Haug et al., 2011), but we have decided to not take them into consideration in this paper as their impact on fish stocks probably is much less conspicuous than that of cod, harp seal and minke whale due to their stock sizes and diet compositions.

The Northeast Arctic cod is by far the most abundant, and hence, conspicuous piscivorous /planktivorous fish species in the Barents Sea ecosystem, with a total biomass of about 3 million tons at present (ICES, 2014a). The biology of this stock is described in detail e.g., by Yaragina et al. (2011). The abundance and spatial distribution of this stock has increased considerably in recent years, both due to a combination of favorable climatic conditions and good management (Kjesbu et al., 2014). Cod is also the most important commercial valuable fish stock in the area. Similar to cod, harp seals and minke whales exploit several trophic levels in Arctic systems, and because of their large body size, high metabolic demands and abundance, they are thought to have an important top-down effect on the structure and function of the food web (see Bowen, 1997; Bogstad et al., 2000; Folkow et al., 2000; Nilssen et al., 2000; Wassmann et al., 2006; Kovacs et al., 2009). They have also been target species for important hunting activities for a long period of time (Øien et al., 1987; Skaug et al., 2007; Haug et al., 2011).

Food-limitation, which is one of the most common density dependent factors in nature, appears to have affected both the harp seal and whale populations but hardly the cod population. The growth and body condition of cod have remained relatively unchanged the past decade despite a major increase in abundance whereas the body condition of harp seals (Øigård et al., 2013) and, to some extent also, minke whales (Hiroko Solvang, Institute of Marine Research, Norway, pers. comm.) has declined in the same period despite stable or declining stock sizes.

The purpose of the paper is to explore possible mechanisms why cod, harp seal and minke whale have reacted differently and discuss the short and long-term outcome of the competition. Will the cod outperform the sea mammals in the struggle for food?

Predator-Prey Relationships

Oceanographic Conditions in Recent Years

The temperature in the Kola section (monthly observations from a transect from 70°30′ to 72°30′ N along 33°30′ E, depth range 0–200 m) in the southern Barents Sea is often used as an indicator of the oceanographic conditions in the area (Tereshchenko, 1996, www.pinro.ru). The temperature has been at a historic high level in the last decade (**Figure 1**). The ice coverage in the Barents Sea (Special Sensor Microwave/Imager (SSM/I) passive microwave remote sensing data from the National Snow and Ice Data Centre, USA (http://www.nsidc.org); Cavalieri et al., 1996; Meier et al., 2006) has also decreased considerably (**Figure 2**; McBride et al., 2014), and the Barents Sea was for instance completely free of ice in early autumn in 2013 (**Figure 3**).

Prey Items

Figure 4 shows the development in abundance of the main fish prey stocks in the Barents Sea (also including shrimp *Pandalus borealis*—the main commercial shellfish stock in the area). The total abundance of these prey items has been relatively stable over the last decade.

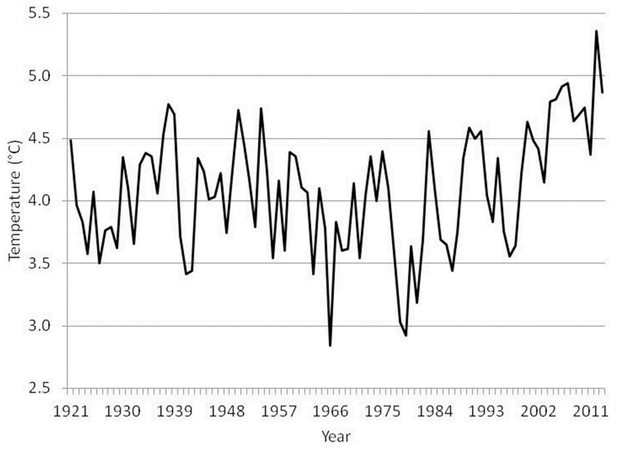

FIGURE 1 | Temperature (°C) in Kola section (0–200 m) during the period 1921–2013 (annual averages of monthly observations).

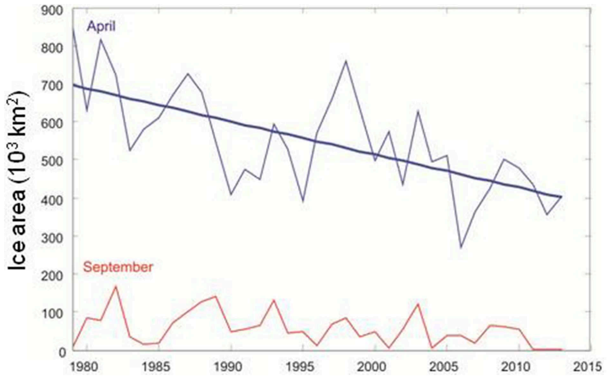

FIGURE 2 | Ice coverage (1000 km^2) in the Barents Sea in April and September 1980–2013.

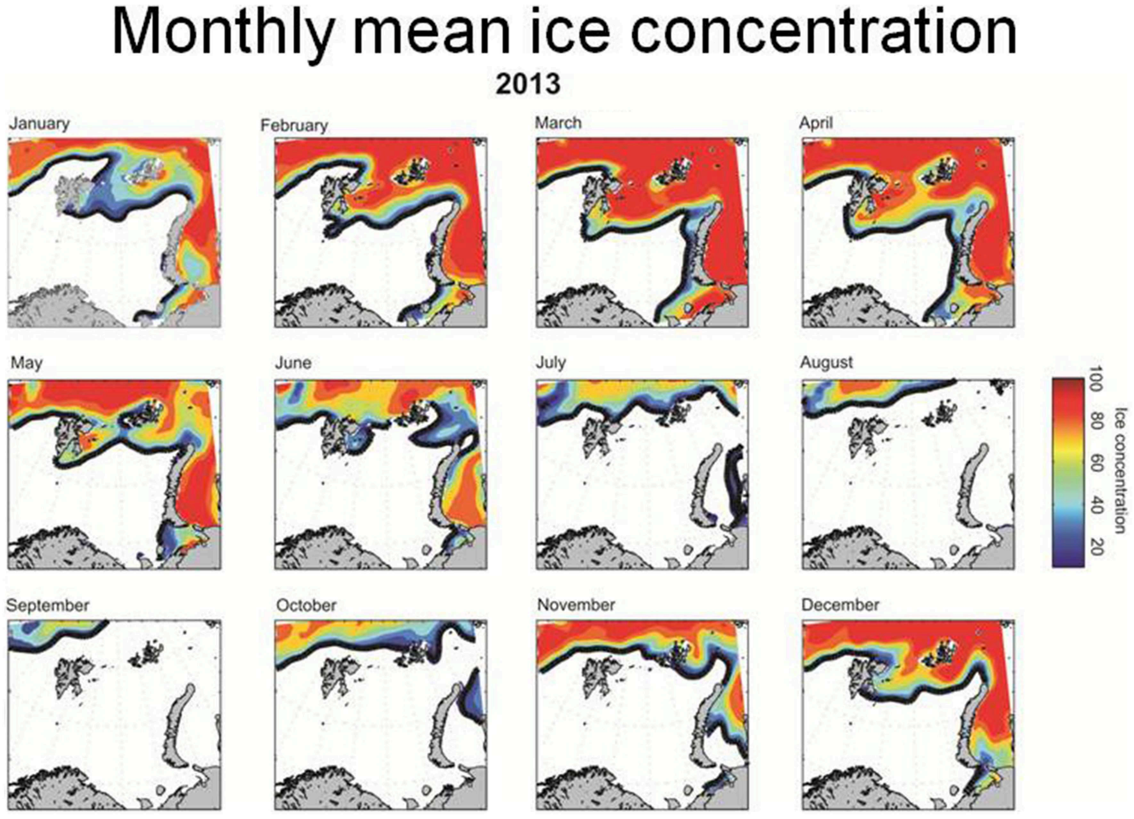

FIGURE 3 | Monthly ice coverage in the Barents Sea in 2013.

Capelin (*Mallotus villosus*) is regarded as the most important forage fish species in the Barents Sea despite major decadal fluctuation in stock size (**Figure 4**). In periods, this stock completely dominates the pelagic fish biomass; the biomass has historically been estimated to exceed seven million tons. However, on three occasions during the last 30 years, each spanning about 5 years, the stock dwindled and reached a level two orders of magnitude lower (Gjøsæter, 1998; Gjøsæter et al., 2009). The spatial distribution and size of the capelin stock has been monitored since the early 1970s (acoustic surveys). In cold years the capelin stock is normally distributed to the north of the polar front during autumn, and in periods it has extended to the ice edge. In recent warm years, when the ice edge is north of the Barents Sea, capelin have been observed both north of the shelf edge i.e., north of the Svalbard and Franz Josef peninsulas at 81°N (Ingvaldsen and Gjøsæter, 2013), and also in the northern Kara Sea (ICES, 2014a; **Figure 5**). Ingvaldsen and Gjøsæter (2013) suggested that this north- and eastward expansion of the capelin feeding area could be attributed to both density dependent and environmental factors because there has been an eastward shift in water masses and plankton fields due to ocean warming.

Polar cod (*Boreogadus saida*) is another forage fish species inhabiting the Barents Sea and the adjacent areas north and east of the Barents Sea. The size and distribution of the stock has been monitored since 1986, but since an unknown part of the stock is distributed outside the survey area, it is unknown how well the acoustic indices reflect the true stock size. Hop and Gjøsæter (2013) compared the distribution and ecological role of polar cod and capelin, and found that polar cod is distributed in colder water than capelin and therefore further to the north and east. The observed distribution of polar cod has been more static than that of capelin, but it should be noted that the northern and eastern border of the polar cod distribution is poorly defined. In recent years, the abundance of polar cod in the Barents Sea has shown a serious decline, perhaps as a result of loss of habitat (ice). Polar cod is known to be more associated with ice than is capelin, both during the juvenile stage, when drifting sea ice mostly serves as habitat, and during the adult stage, when ice associated fauna constitutes a part of the food base (Hop and Gjøsæter, 2013).

Among fish prey, juvenile herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) may also play important roles as forage fish in periods (**Figure 4**). They reside in the Barents Sea 2–3 years and then join the adult stocks found in the Norwegian Sea prior to maturation. These species mainly occupy the southern (herring) and south-western (blue whiting) parts of the Barents Sea.

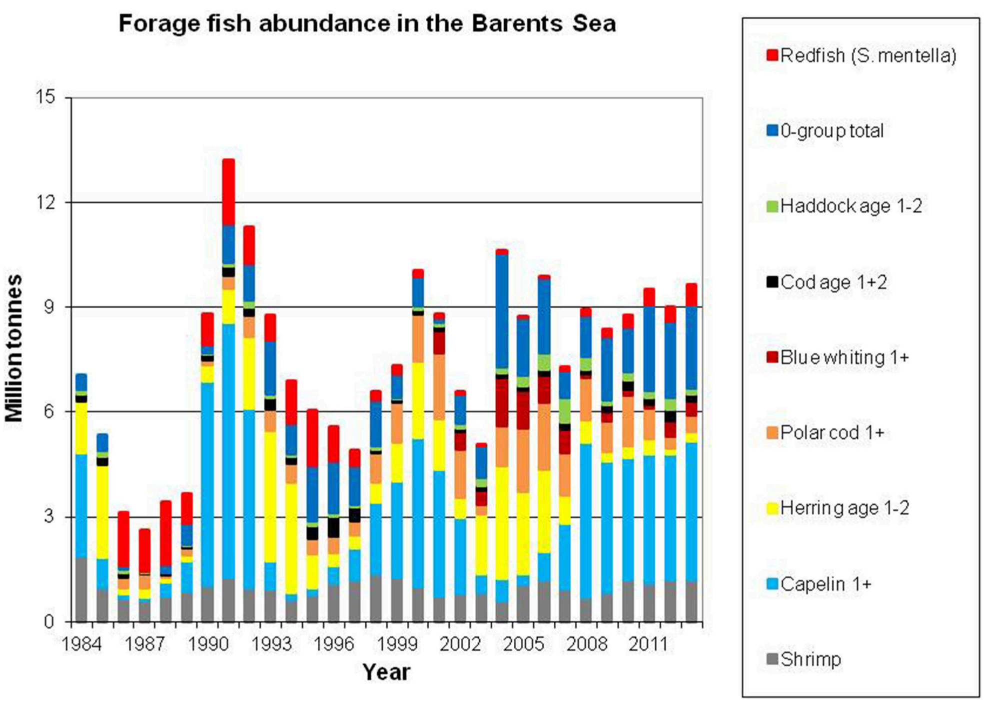

FIGURE 4 | Abundance of main fish prey stocks, as well as shrimp. Data sources: Capelin: acoustic estimates in September, age 1+ (ICES, 2014a); Herring: VPA biomass estimates of age 1 and 2 herring (ICES, 2014b) using constant weights at age (10 g for age 1 and 44 g for age 2); Polar cod and blue whiting: acoustic estimates in September, age 1+ (Prokhorova, 2013); 0–group: estimates of biomass of cod, haddock, herring and capelin, corrected for catch efficiency (ICES, 2014a); Cod and haddock age 1+2: VPA biomass estimates of age 1–2 (ICES, 2014a) Redfish (*Sebastes mentella*): survey biomass of 5–24 cm fish (bottom trawl swept area), scaled to adjust for catchability and vertical distribution (ICES, 2014a) Shrimp: biomass (bottom trawl swept area, ICES, 2013b), scaled to adjust for catchability).

The deepwater redfish (*Sebastes mentella*) played an important role as food for cod during the 1980s and beginning of the 1990s when the abundance of preferred prey was low and the abundance of redfish was high. The dietary importance of redfish has been low the past two decades, when the stock size was heavily reduced (ICES, 2014a). Deepwater shrimp (*Pandalus borealis*) is also important food for cod, and have constituted a much more stable proportion of the diet during the study period compared with the other food items. The amount of shrimp has increased in recent years but their distribution area has shifted eastwards. It is uncertain whether this is a result of higher temperatures in the near-bottom layers.

The youngest age group (0-group) of various fish species might be considered as another "stock" of forage fish. The young stages of cod, haddock (*Melanogrammus aeglefinus*), polar cod, capelin and herring, as well as numerous other fish species in the Barents Sea, inhabit the upper 50 m of the water column the first 6 month of life (summer and fall). They are distributed over most of the Barents Sea but the highest densities are normally found in the central part of the sea (Eriksen et al., 2012). The abundance of this "stock" has not changed much the past decade (Eriksen et al., 2012). Also, juvenile cod are eaten by adult cod as well as harp seals and minke whales, and this food source has been abundant and increasing during the last decade.

Macrozooplankton, mainly pelagic amphipods and krill are important prey for all these three predator species. The production and standing stocks of zooplankton is more difficult to monitor than fish and sea mammals, and there are probably spatial shifts and geographical variation that are difficult to trace but may be important when considering the importance of these prey groups. The total abundance of amphipods has shown a decreasing trend over the last couple of decades (Figure 8B in Dalpadado et al., 2012). Krill abundance estimated from the Russian autumn (October-December) survey (Figure 3 in Zhukova et al., 2009) is at present at or slightly above the long-term mean (McBride et al., 2014), and krill abundance estimates from the joint ecosystem survey (Prokhorova, 2013) also indicate that krill abundance in the last decade has been above average.

The Predators, their Biology and Feeding

Cod

The Northeast Arctic Cod (NEA cod) is a large, mainly demersal, fish that may attain sizes of 1.5 m and 40 kg and an age of 20 years. The annual growth rate is about 10 cm until maturation thereafter the growth slows down. Average age and size at maturation is about 7 years and 70 cm. The NEA cod spawns along the west and northwest coasts of Norway; the Lofoten area is the most important spawning area. The fish

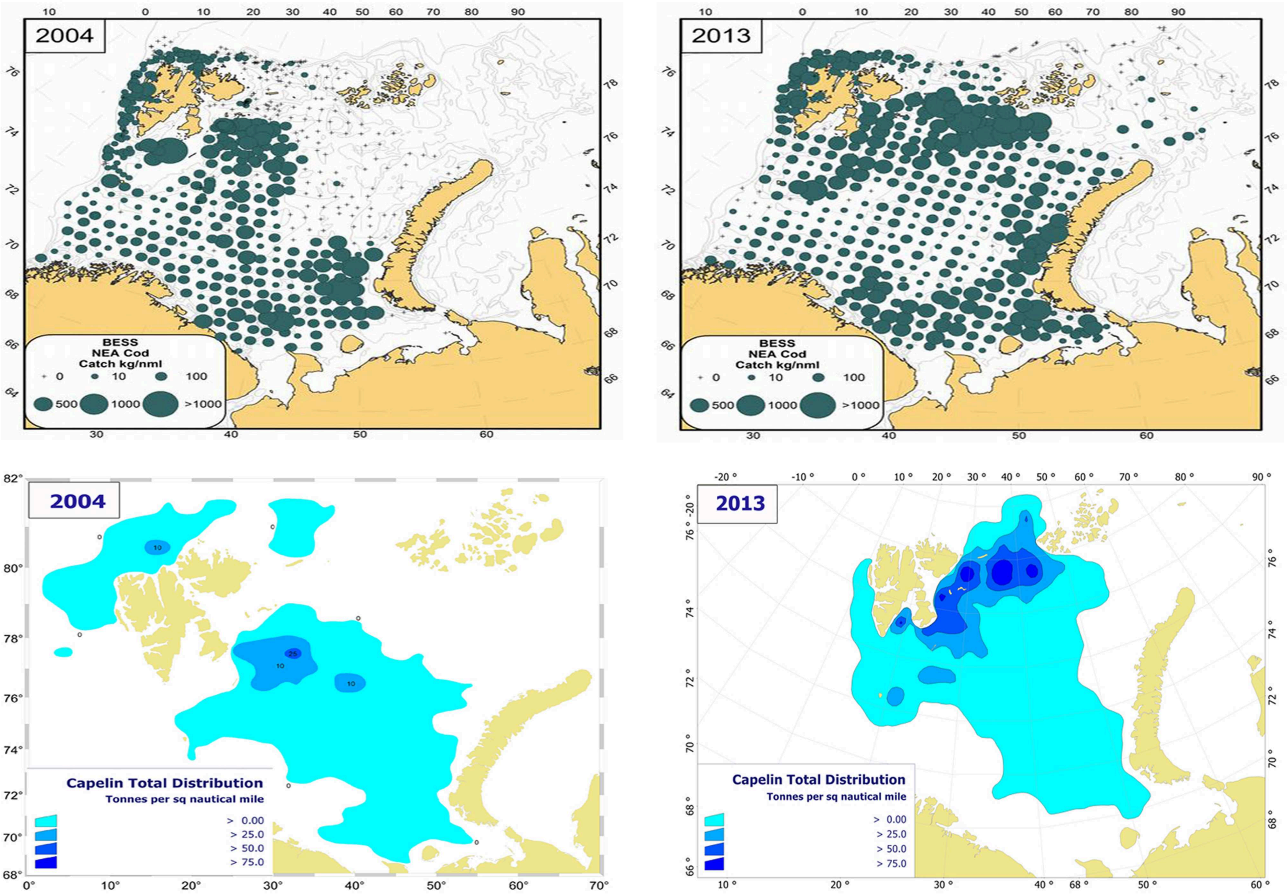

FIGURE 5 | Spatial distribution of cod (upper panels) and capelin (lower panels) in August-September 2004 and 2013, from the Norwegian-Russian ecosystem survey. Cod: bottom trawl catches (kg/nm), capelin: acoustic estimates (tons/nm^2).

larvae are transported to the Barents Sea by the currents and enter the south-western Barents Sea. They spend their first years mainly in the southern and central parts of the Barents Sea. The adult individuals have a more northern distribution in the Barents Sea. They perform seasonal spawning and feeding migrations during early spring and summer, respectively.

Although cod is considered a bottom-dwelling fish, acoustic observations and analysis of data storage tags (e. g., Heffernan et al., 2004), as well as analysis of stomach content (e.g., Bogstad and Mehl, 1997), have shown that cod frequently use pelagic habitats to feed on pelagic prey. The abundance of large cod (age 7+) has increased much since 2000 whereas the abundance of medium-sized (age 3–6) increased strongly until 2009 and then declined to levels observed prior to 2000 (**Figure 6**; ICES, 2014a). The peak in abundance of age 3–6 cod around 2009 is due to the very abundant 2004 and 2005 year classes. During the last decade, the geographical distribution of cod has expanded north- and eastwards both in autumn (**Figure 5**) and winter (Johansen et al., 2013; Mehl et al., 2013).

Cod is regarded as a generalist feeder, particularly on a population level, with a diverse food base including pelagic and demersal fish, shrimp, epi-benthos and zooplankton. Age groups 1 and 2 feed mainly on crustaceans (**Figure 7**). Capelin is the main prey item for age groups 3+ (**Figure 8**), however, large cod (age 7+) is far more piscivorous, feeding on cod, haddock and long rough dab (*Hippoglossoides platessoides*), compared with smaller cod (age 3–6) (**Figure 9**). Details about the feeding of cod in the Barents Sea can be found in Dolgov et al. (2011).

Harp Seals

Harp seals are highly migratory animals with a generalist foraging behavior. The two stocks inhabiting the Barents Sea, whelp and molt on the pack ice off the east coast of Greenland (the Greenland Sea or West Ice stock), and in the White Sea and south-eastern Barents Sea (the Barents Sea or East Ice stock) (Lavigne and Kovacs, 1988; Sergeant, 1991). After the molt the Barents Sea stock disperse in small herds to feed, primarily around Svalbard and in the northern Barents Sea (**Figure 10**). The southward movement of the seals toward the breeding areas in the White Sea begins in November-December (Haug et al., 1994; Nordøy et al., 2008). Telemetry studies suggest that a major fraction of the West Ice stock forage in the northern Barents Sea during summer and autumn (Haug et al., 1994; Folkow et al., 2004;

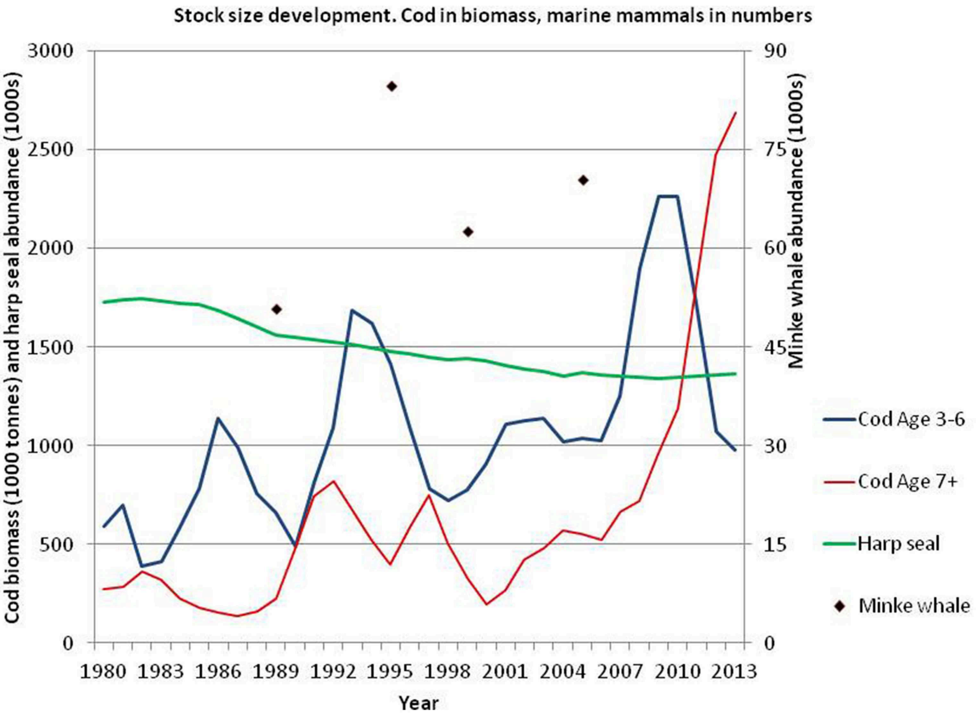

FIGURE 6 | Biomass (1000 tons) of age 3–6 and 7+ Northeast Arctic cod (ICES, 2014a) as well as abundance (1000s) of harp seals (Øigård et al., 2014a) and minke whales (Bøthun et al., 2009).

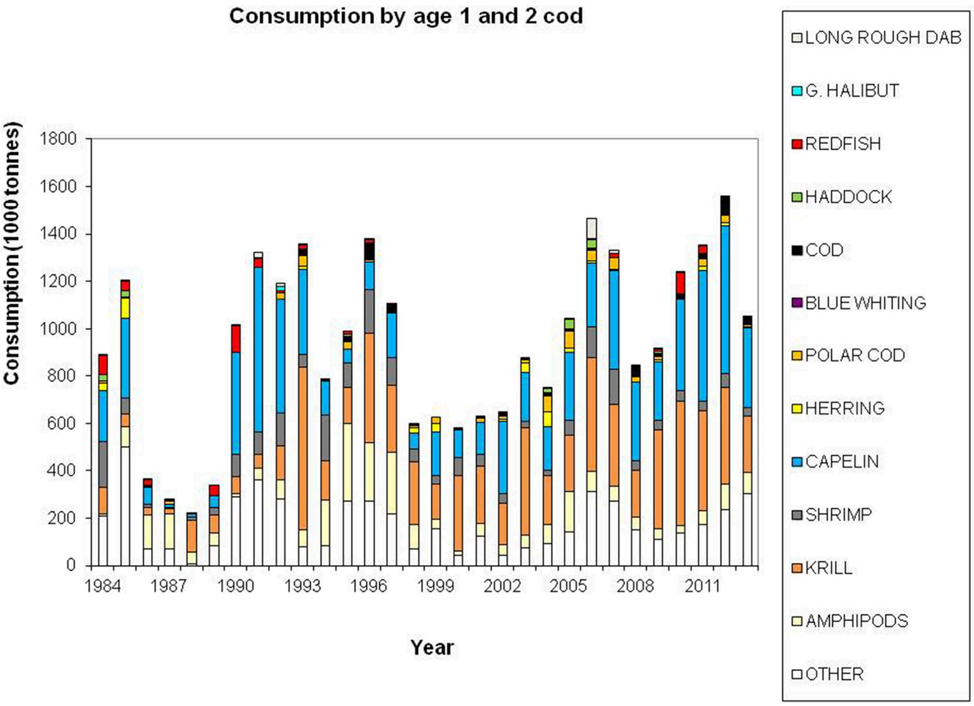

FIGURE 7 | Total consumption by age 1–2 cod based on calculations presented in ICES (2014a), using the method described by Bogstad and Mehl (1997). These calculations are based on stomach content data and a model for gastric evacuation rate, and the consumption is calculated by cod age group (1–11+), half-year and three areas in the Barents Sea.

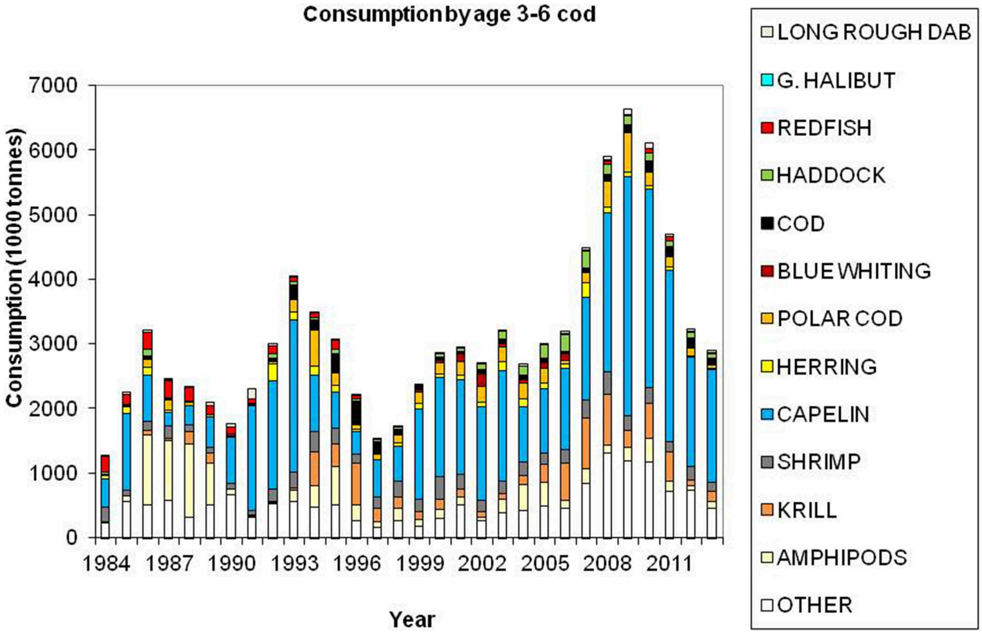

FIGURE 8 | Total consumption by age 3–6 cod based on calculations presented in ICES (2014a), using the method described by Bogstad and Mehl (1997). These calculations are based on stomach content data and a model for gastric evacuation rate, and the consumption is calculated by cod age group (1–11+), half-year and three areas in the Barents Sea.

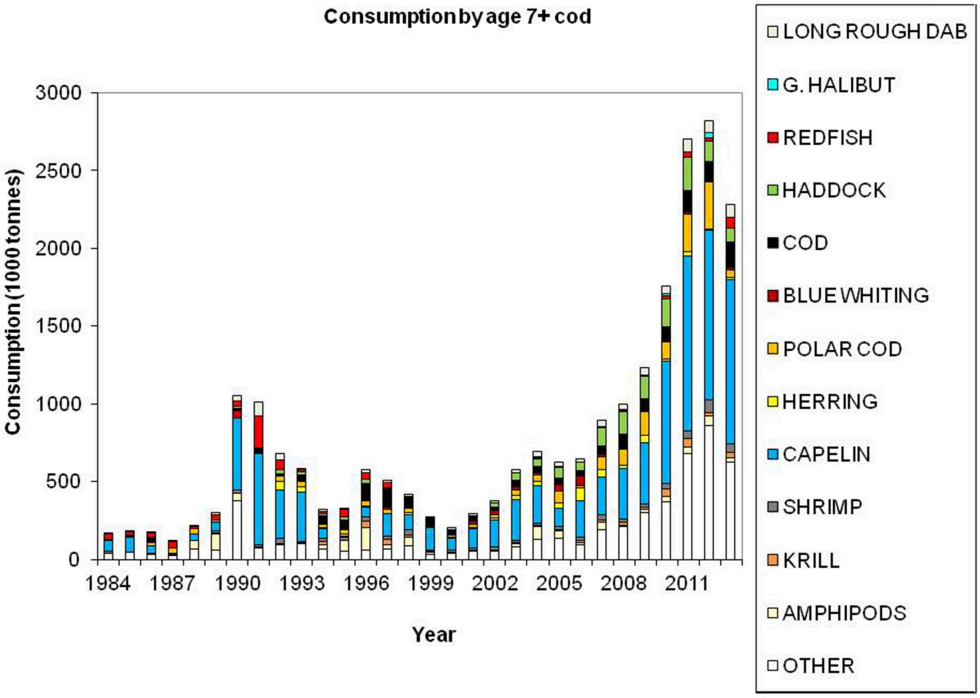

FIGURE 9 | Total consumption by age 7+ cod based on calculations presented in ICES (2014a), using the method described by Bogstad and Mehl (1997). These calculations are based on stomach content data and a model for gastric evacuation rate, and the consumption is calculated by cod age group (1–11+), half-year and three areas in the Barents Sea.

FIGURE 10 | Suggested gross annual migrations of the Barents Sea harp seal population between breeding in the White Sea in February-March and molting in May (black arrow), and between molting and breeding the following year (red area). The approximate extension of the breeding area is indicated as a yellow area, while the approximate extension of the molting area is indicated with dark blue. From Nordøy et al. (2008).

Nordøy et al., 2008). These data also show that there is major individual variation in diving behavior on a diurnal and seasonal time scale (Folkow et al., 2004; Nordøy et al., 2008). Seals tend to dive deeper during winter and daytime compared with the summer and night time. Further, harp seals appears to dive more frequently during early summer (June-July), when they have a low body condition and reside close to the pack ice, compared with other periods of the year. As the sea ice retreats the seals spend more time in the water, perhaps as a result of longer traveling distances between the ice-edge and the feeding areas (Nordøy et al., 2008). In fact, the East Ice seals were observed to spend at least 53% of the year in areas with less than 40% ice coverage (Nordøy et al., 2008).

Similar to cod, Barents Sea harp seals is regarded as generalist predators, at least on a population level, primarily feeding on the most available prey in the area and by doing so their diets vary much in both time and space (e.g., Nilssen et al., 1995a,b; Lindstrøm et al., 2013). Harp seals can potentially eat large prey but studies shows that they primarily feed on small specimens (10–25 cm) of gadoids such as polar cod, haddock and cod (e.g., Lindstrøm et al., 2013). The bulk of the harp seal diet is comprised of relatively few species, in particular capelin, polar cod, herring, krill *Thysanoessa* spp. and the pelagic amphipod *Themisto libellula* (Nilssen et al., 2000; Lindstrøm et al., 2013). The crustaceans appear to be of particular importance as food for harp seals during summer and autumn when they are feeding in the northern parts of the Barents Sea (July-October). As the ice cover expands southwards in late autumn and winter, the southward migrating seals appear to switch from crustaceans to fish (particularly capelin and polar cod) (Nilssen et al., 1995a; Lindstrøm et al., 1998). In the southernmost areas of the Barents Sea, where the seals occur during winter and early spring, herring may be an important forage fish (Nilssen et al., 1995b; Lindstrøm et al., 1998).

Nilssen et al. (2000) estimated the total food consumption by 2.2 million (c. 700 000 more than today) harp seals in the Barents Sea using a bioenergetics model. The annual food consumption was estimated to 2.69–3.96 million tons of biomass or more specifically 1.22 million tons crustaceans, 808,000 tons capelin, 605,000 tons polar cod, 212,000 tons herring and a mix of gadoids and other more Arctic fishes of ca. 500,000 tons. A small capelin stock (as in 1993–1996) made harp seals switch diet; the consumption of other fish species, in particular polar cod, other gadoids and herring increased.

The seals appear to target primarily the most lipid-rich prey during summer: krill, followed by other crustaceans and polar cod (see Grahl-Nielsen et al., 2011). Availability of high-energetic food in the northern areas in spring and summer presumably provide the energetic advantage necessary to account for the long migrations of harp seals from their more southerly located winter distributions.

There is a regular seasonal pattern of deposition of energy reserves as fat in the subcutaneous blubber layer (see Iverson, 2002). Barents Sea harp seals (see Nilssen et al., 1997) are generally thin in spring and early summer (May—June). Their condition improves over the summer, and the seals are very fat by September—October. The energy stores built up during the summer and autumn are maintained until February, but then the seals become thinner as the stores of blubber decrease rapidly during the breeding and molting period (March–June).

Common Minke Whales

The migration of minke whales into Norwegian waters, including the Barents Sea, starts in early spring (see Haug et al., 2011). In September-October a southward migration has been observed, however, old catch statistics reveal that minke whales have been caught in Norwegian waters nearly all year around, indicating that not all animals leave the northern areas in winter.

Minke whales have been the target species of Norwegian small-type whaling. Abundance estimates have been provided through dedicated sighting surveys, and the most recent estimate for the Barents Sea area is 81,400 (cv 0.23) (Skaug et al., 2004; Haug et al., 2011). Their general distribution and migration pattern is illustrated in **Figure 11**.

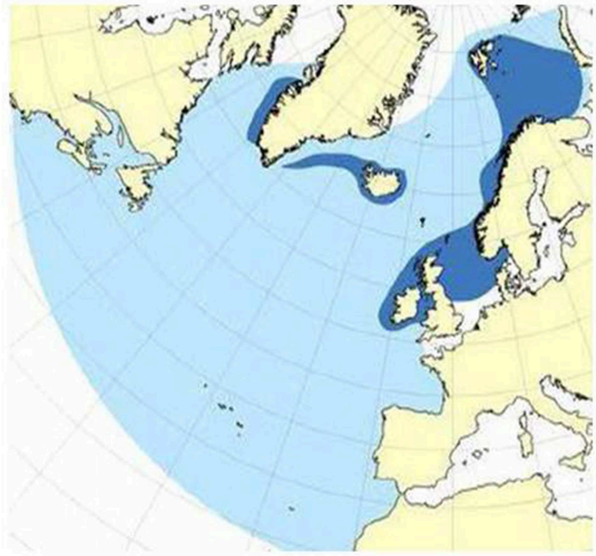

FIGURE 11 | General migration pattern of minke whales in the Barents Sea and adjacent areas. Summer feeding area (dark blue) and total distribution area (light blue).

By combining data on energy requirements, diet composition, and stock size, Folkow et al. (2000) estimated the total annual consumption of various prey species by minke whales during their assumed feeding period (mid-April to mid-October) in northeast Atlantic waters. In the period 1992–1995, a stock of 85,000 minke whales consumed more than 1.8 million tons (95% CI: 1.4–2.1 million tons) of prey per year in coastal waters off northern Norway, in the Barents Sea and around Spitsbergen: 602,000 tons of krill, 633,000 tons of herring, 142,000 tons of capelin, 256,000 tons of cod, 128,000 tons of haddock and 54,500 tons of other fish species, including saithe (*Pollachius virens*) and sandeel (*Ammodytes* spp.).

Minke whales have a very flexible foraging behavior and are normally able to switch among species without compromising the body condition. As a result their diets vary much in time (year and season) and space due to spatio-temporal variation in prey availability (see **Figure 12**). The whales exploit a variety of species and sizes of fish and crustaceans (Haug et al., 2002), however they appear to selectively forage on capelin, herring and occasionally krill (Lindstrøm and Haug, 2001). In extreme events such as in 1995–1996, when the abundance of capelin and herring was low simultaneously, the minke whales had to switch to krill and gadoid fish (cod and haddock) and as a result their body condition declined.

More recent studies (2000–2004 and 2010–2011) confirmed previous findings of significant differences in diet composition between areas and some differences between years (Windsland et al., 2007; Meier et al., in press). The importance of krill in the Barents Sea increased with latitude and dominated the Spitsbergen diet. Capelin dominated the diet around Bear Island and contributed considerable to the diet along the coast of northern Norway. In the latter area, herring and haddock were also a great part of the diet. The considerable size range of consumed prey (0.2—78 cm) confirms previous findings that minke whales are not particularly size selective (Windsland et al., 2007). The size of prey seems to be determined by the availability of different size classes, rather than selectivity by the whales (Lindstrøm and

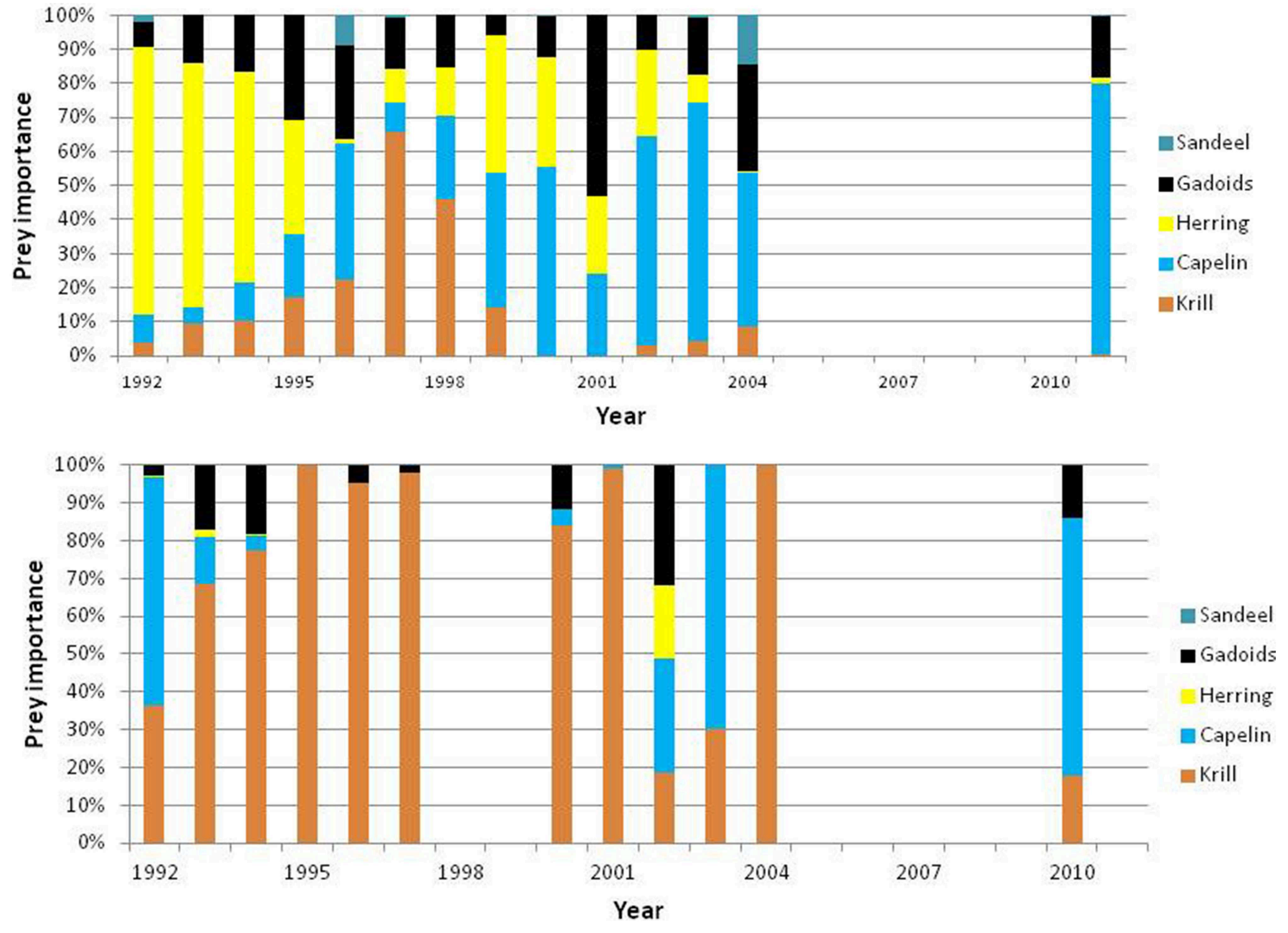

FIGURE 12 | Biomass-based diet composition of minke whales sampled in the northern (North) and southern (South) Barents Sea in the periods 1992–2004 and 2010–2011. Based on data from Haug et al. (2002), Windsland et al. (2007) and Meier et al. (in press).

Haug, 2001; Windsland et al., 2007). The age composition of the capelin consumed by the whales varied in space. It was mainly 3 or 4 years old capelin (i.e., mature, see Gjøsæter, 1998) in the southern Barents Sea, while capelin eaten north of the spawning grounds, around Spitsbergen and Bear Island, were considerably smaller with only ca. 50% being in the size range of mature fish (i. e., > 14 cm). The majority of herring eaten in the southern Barents Sea were below 20 cm (≤2 years old), whereas haddock taken in this area had a wide size distribution (from 5 to 65 cm) including both juvenile and large adult individuals, although both length and age analysis showed that the majority were smaller haddock.

In 2003—2013 the minke whale distribution was surveyed in August-September, along with the distribution of their main prey species, in joint Norwegian-Russian ecosystem surveys (e.g., Michalsen et al., 2013). During the first part of this period (2003–2007), the majority of minke whales were feeding in the northern Barents Sea, north of the polar front in association with high zooplankton (krill) concentrations in the productive marginal ice zone (Skern-Mauritzen et al., 2011). They were also predominantly north of the capelin, further indicating that capelin was not the major forage species, at least not in these years with low capelin abundances. Only a small fraction of the minke whales foraged in the southern Barents Sea, in areas inhabited by blue whiting and herring. Hence, there is likely a shift in whale distributions and diet from early summer, when diet samples are collected during the minke whale harvest, to late summer and early autumn when most whales feed in the north. Variations in diets between periods of the year were also demonstrated during dedicated ecological studies of minke whales in the Barents Sea in 1993–1994 (Haug et al., 1996).

Changes in Predator's Growth and Condition During Recent Years

The per capita consumption and growth of younger cod has been stable in recent years, while for older cod, this has decreased slightly in the last couple of years (ICES, 2014a, **Figure 13**). The condition factors show the same development (**Figure 14**). Although the condition factor of older fish has been slightly below the long-term mean in the last years, it is still well above the lowest levels experienced during the first capelin collapse in the late 1980s.

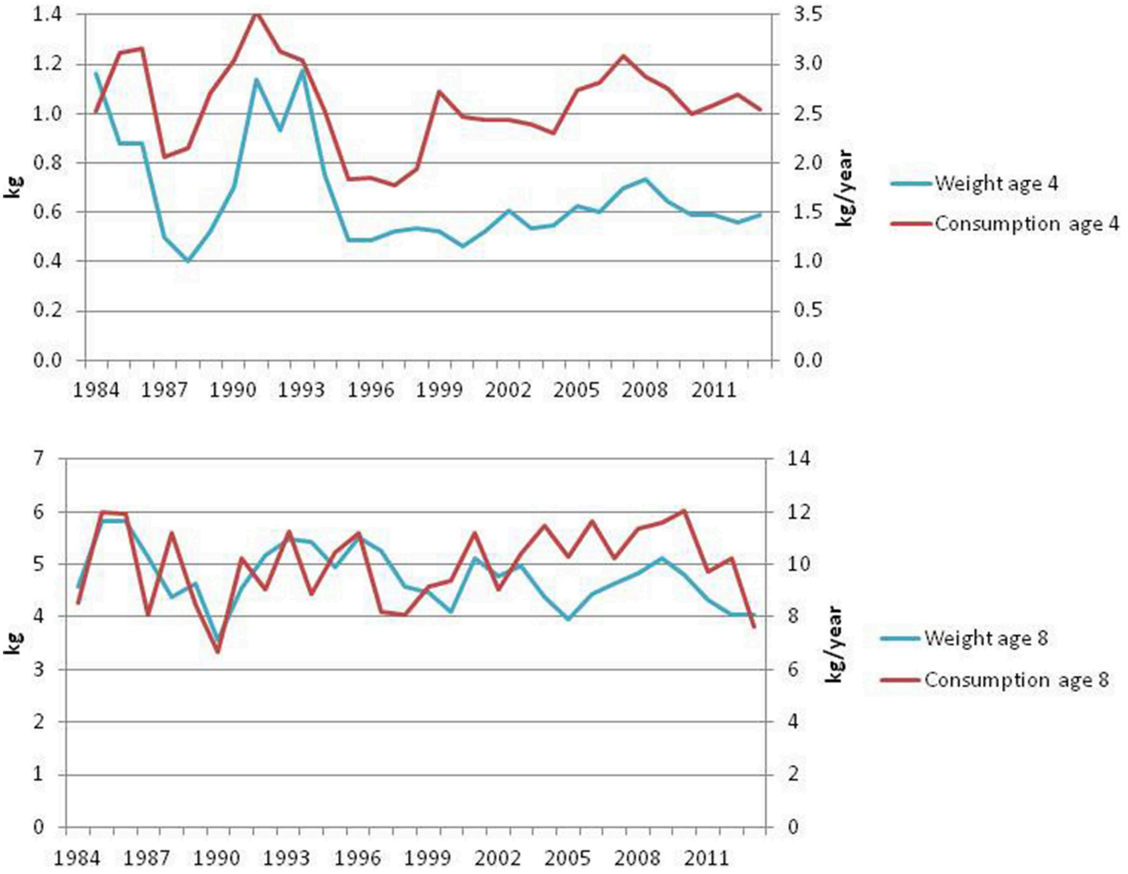

FIGURE 13 | Annual weight at age (kg) and per capita consumption (kg/year) for medium (age 4) and large (age 8) cod (ICES, 2014a).

Harp seal body condition, estimated from samples taken during spring in 1992–2011, exhibited a slow increase from 1992 to 2001, where after a significant decrease to a minimum in 2011 has occurred (Øigård et al., 2013, **Figure 14**).

Similar to other baleen whales, minke whales improve their body condition by increasing their fat deposits during the feeding period, and thereby store energy reserves for wintering and breeding at lower latitudes when their feeding activity is assumed to be low (Næss et al., 1998). Comparison of minke whales body condition in years of high and low abundances of immature herring showed that minke whales in the southern Barents Sea, particularly immatures and adult females, were in significantly better condition in years when the abundance of immature herring was high (Haug et al., 2002). A time series of blubber measurements, made dorsally right behind the blowhole as described in Haug et al. (2002), taken under commercial whaling in the period 1992–2013 shows a significant negative trend over the period with particular low values in 2013 (see **Figure 14**).

Discussion

Possible Mechanisms in Predation and Competition

How a stock develops over time depends on survival, feeding, and reproduction, and the population dynamics is a result of how these factors vary throughout the life-cycle and during the year. We here present the results in terms of total stock status (abundance, condition etc.) and try to relate that to processes (competition, predation etc.) going on in different seasons and for different life stages of the stocks under consideration.

A more recent study on harp seals body condition indicated that high abundance of krill impacted the seal condition positively, emphasizing the ecological significance of krill as key food for harp seals during summer (Øigård et al., 2013). High abundances of capelin, polar cod and cod, however, had a negative impact on the seal condition. Indirect effects such as competition between harp seals and prey for shared resources such as krill may have a negative effect on the condition with subsequent implications for the breeding success. Longer migration routes with increased energy expenditure, as a result of less ice, between the breeding/molting areas and feeding areas along the ice edge may certainly also have contributed to the reduced recent harp seal body condition.

The variation in blubber thickness within and between years is much more conspicuous for harp seals than for minke whales. This is to some extent expected given that minke whales are much larger animals and, as such, are expected to have less blubber thickness relative to their size (due to smaller surface-volume ratio). Also, the large-scale migratory behavior of minke whales may bias the blubber thickness toward less variability

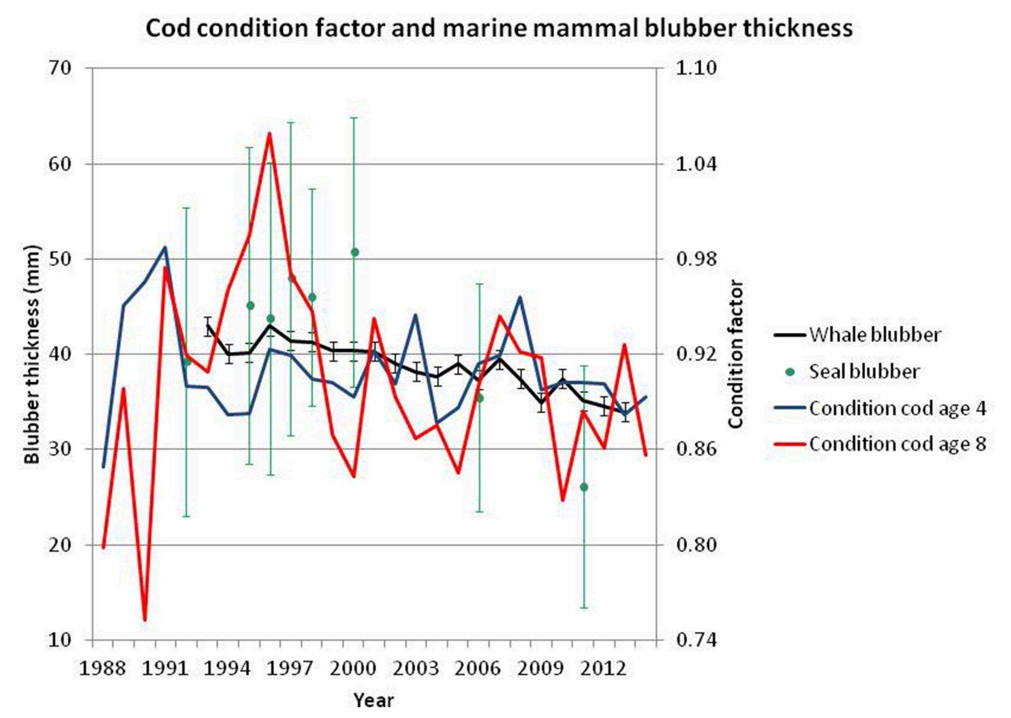

FIGURE 14 | Blubber thickness (mm, with 5–95% confidence intervals) for harp seal and minke whale (left axis) and condition factor (100000 × weight (kg)/L^3 (cm)) (right axis) for age 4 and 8 cod. Range of annual sample sizes (individuals measured): Harp seals 75–310, minke whales 216–635. The condition factor for age 4 cod is calculated from the winter survey (ICES, 2014a, Tables A5, A6), and for age 8 it is calculated from the Lofoten survey (ICES, 2014a, Tables A7, A8).

because lean minke whales may not be able to perform long-distance migrations or may migrate out of the Barents Sea due to bad feeding conditions thereby being under-represented in the catches. In contrast, harp seals are present in the Barents Sea all year round.

The distributions of cod, particularly medium and large individuals, and minke whales overlap to various degree during the year. The most intensive spatial overlap between the two predators occurs during summer and autumn in the central and northern parts of the Barents Sea. Given our dietary knowledge of these predators they compete (directly) for krill and capelin in these periods (Haug et al., 2002; Johannesen et al., 2012). A recent study in which the intra- and interspecific competition among top-predators (cod, minke whale and sea birds) was analyzed concludes that minke whales and cod compete for food and that their diets depend on the abundance of herring and capelin, respectively (Durant et al., 2014). That study further suggests that the diet overlap among these predators generally increase with changes in herring and krill abundances. Unfortunately, the harp seals were not included in that due to lack of synoptic (space and time) diet data. Harp seals are assumed to be distributed in open waters along and at moderate distances from the ice edge in the period June-October (Nordøy et al., 2008) and as such one would expect some degree of spatial overlap between harp seals and the two other predators (cod and minke whale), however, there is little empirical evidence to support that. It should be emphasized, however, that predators may still compete for food despite lack of spatio-temporal overlap between the predators as long as their diets overlap and they feed on the same stocks of prey. No direct diet comparisons between harp seals and cod have been conducted earlier but they share some preferred prey such as capelin, krill, amphipods and polar cod and as such there may be competition among them. In fact, a recent study (Øigård et al., 2013) suggests competition between harp seals and for example cod for shared resources, such as krill. Medium and large cod have similar geographical distributions during summer/autumn, although the areas close to the northern and northeastern boundary of the cod distribution are dominated by large cod. Predators of different size and feeding behavior probably also react differently to variable prey density; a possible reason why small/medium cod do better could be that they can utilize low densities of zooplankton which are not attractive for larger predators.

Spatial overlap between these predators also occurs during other parts of the year. Medium-sized cod and harp seal overlap to some extent close to coast of Norway/Russia in March/April when harp seals migrate back from the White Sea. During this period they feed on spawning capelin. It is also likely that there is overlap in distribution between minke whales and large (mature) cod in spring in the south-western Barents Sea when both are migrating northwards. However, the food abundance in that area at that time is likely to be fairly low.

If several stocks are found in the same geographical area, the main factors in their competition for prey are their vertical distribution relative to that of the prey, as well as their prey type preferences and ability (mobility, mouth opening etc.) to catch prey of different species and sizes.

To properly understand predatory interactions we need to understand the predator's potential predation space in 3D. Some benthic organisms are, however, available for cod, but not for seals or whales. In contrast to cod there is a trade-off between energy use and predation for sea mammals because they have to pay an energetic price for diving. Diet studies and diving experiments (Blix and Folkow, 1995; Haug et al., 2002) indicate that minke whales primarily feed in the upper 100 m of the water column. Measurements of dive duration have indicated that minke whales usually stay submerged in dives lasting between 4 and 6 min (Folkow and Blix, 1993). Harp seals use the entire water column but are obviously short-duration divers that normally stay submerged for less than 10 min which would leave very little time at depth if the animal chose to dive as deep as 300 m (Nordøy et al., 2008). It should be emphasized that there were few animals included in the mentioned study and the seals displayed major individual as well as spatio-temporal variation in dive behavior most likely due to spatio-temporal variability in prey availability. Nevertheless, more than 50% of all dives were shallower than 100 m. Diving behavior of both minke whales and harp seals seems consistent with animals primarily exploiting schooling fish or high concentrations of zooplankton.

The hunting pressure on harp seals decreased substantially in all areas around 1980 (ICES, 2013a) and as a result the populations increased in size. However, Barents Sea/White Sea harp seals has faced severe problems with a recent dramatic pup production decrease following a slow increase of the population from the mid-1970s (Skaug et al., 2007) to a current level of approximately 1.4 million individuals (ICES, 2013a). Problems with ice retreat seem to affect the Barents Sea/White Sea population in the same manner as observed in the Northwest Atlantic (Stenson and Hammill, 2014). Barents Sea / White Sea harp seals were observed to exhibit poorer body condition in recent years than 10–15 years ago by Øigård et al. (2013) who also observed possible links between the abundance of several distributional overlapping and food-competing fish species (cod, polar cod, capelin) and seal body condition (the more fish, the poorer seal condition). Similar body condition data are not available for the Greenland Sea harp seal population, but it is known that the two Northeast Atlantic harp seal populations share the same feeding grounds in the northern Barents Sea during their most intensive feeding period from July to November (Folkow et al., 2004; Nordøy et al., 2008).

Apparently, it may look as if the harp seal is paying a price of having a big cod stock; the body condition has declined much the past decade (Øigård et al., 2013). Similar observations has been made in common minke whales where there is a negative trend in body condition over the period 1992–2013, with particular low values in 2013 (Hiroko Kato Solvang, Institute of Marine Research, Norway, pers. comm.). While the stocks of fish in the Barents Sea, cod in particular, are at record high levels now (ICES, 2014a), the situation is the opposite in the Northwest Atlantic. For example the cod has been almost completely absent, due to the fisheries, the past two decades (Link et al., 2009; Hutchings and Rangeley, 2010). Furthermore, in 1991 there was a major reduction in capelin biomass in the Newfoundland—Labrador shelf area, and to date this stock has not recovered (DFO, 2010). Concomitant increases in the abundance of Northwest Atlantic harp seals has prompted modeling enquiries to assess whether these events were related (Buren et al., 2014): Cod biomass dynamics were best explained by a combination of fisheries removals and capelin availability, whereas seal consumption was found not to be an important driver of the cod stock. Buren et al. (2014) did, however, not assess if the currently generally low pressure on common prey species by cod might have some beneficial effects on harp seal growth and condition in the area. Long term fluctuations in body condition have been observed in Northwest Atlantic harp seals where adult seals were in poorer condition in the early 1990s (after the collapse of capelin and with cod on its way down, Buren et al., 2014) than in the mid 1980s before the fish stocks declined (Chabot et al., 1996).

Cod cannibalism decrease with prey size and medium sized cod (above 50 cm) are rarely exposed to cannibalism (Yaragina et al., 2009). All the major predator groups (medium/large cod, harp seal, and minke whale) may prey upon small fish. Only minke whales and some large cod appear to prey on larger fish above ca. 30 cm.

General performance of stocks will depend on the conditions they are exposed to throughout the year and throughout their distribution area. In the summer-autumn feeding period, it is not obvious that the food abundance and distribution of predators and prey has changed in a way that would favor cod, in particular medium sized cod, compared to harp seals and minke whales. The recent decline of polar cod in the Barents Sea (Prokhorova, 2013) is, however, more likely to affect the harp seals more than the other stocks due to the dietary importance of polar cod. Also medium-sized cod has been able to feed on capelin during the spawning migration each year, and the abundance of such cod has decreased toward an average level during the last couple of years. The abundance of large cod has increased so strongly during the last years that some reduction in individual growth rate is to be expected. The reduction in the herring stock during the last years (ICES, 2013b) would affect the minke whale stock considerably, as minke whales overlap considerably with young and, to a lesser degree, adult herring in the Barents Sea (Lindstrøm et al., 2002). Cod also feed on herring during cod spawning migration (Michalsen et al., 2008), but this is a fairly small part of the total cod consumption and a decline in adult herring abundance would thus have a minor direct impact on cod.

Macro-zooplankton is seemingly playing a key role in the diet of harp seals and minke whales. In periods of low capelin abundance, minke whales increased the predation on cod and krill whereas harp seals switched to amphipods. In recent years, the capelin stock has been of medium or large size, and zooplankton has not played any role in cod feeding. There is a negative relationship between the amount of capelin and macrozooplankton (Dalpadado and Skjoldal, 1996) explained as a direct effect of variable grazing pressure from capelin. This mechanism may also affect the competition among cod, profiting on a large capelin stock and the sea mammals, profiting on a high abundance of zooplankton. This may partly explain the negative relationship between seal condition and amount of capelin referred to above.

The general retraction of the ice edge northwards during the last decade may have opened up new areas both for primary and secondary producers, and there are indications from the ecosystem surveys (Michalsen et al., 2013) that macrozooplankton is much more abundant in the marginal northern areas than centrally in the Barents Sea. It is difficult to infer from these observations how that would affect the feeding situations for the predatory stocks. The lack of zooplankton in central areas may be caused by down grazing since the capelin stock has moved through this area on the feeding migration northwards. Whether the sea mammals may benefit from increased plankton stocks in the north, depends on whether the capelin halt the northward migration before they reach the northern limit of zooplankton distribution, that is, whether there are rich feeding areas for the mammals north of the capelin feeding area. Observations from the ecosystem surveys (Michalsen et al., 2013) suggest that the minke whales may have found such areas to feed in Skern-Mauritzen et al. (2011). However, few seal observations have been made during these surveys, probably because the seals are dependent on ice and have moved north of the area observed during these surveys. If the zooplankton rich areas do not extend to the ice edge, the harp seal may suffer food shortages more than the whales do, that can feed where the food is available, disregarding the distance to the ice edge. The fact that blubber thickness has decreased more among seals than among minke whales (**Figure 14**) indicates that such mechanisms may have been present in recent years.

What is Likely to Happen—Short Term and Longer term?

Short Term

Given the recent average recruitment we expect that the cod stock will decline from the high level presently observed and this may result in improved individual growth, as the growth rate of a cod cohort is dependent on the abundance of the cohort itself as well as adjacent cohorts (Kovalev and Yaragina, 2009). The harp seal stock is also likely to continue to decrease due to recent poor recruitment, and the available *per capita* food may increase and improve the conditions for the seals. The Norwegian spring spawning herring stock has suffered from low recruitment for several years, and historically, such periods of poor recruitment have alternated with single or a few very strong year classes (ICES, 2013b). New strong herring year classes may occur any time, and this could have a significant negative effect on capelin recruitment and thus possible cascading effects on the ecosystem (see e.g., Hjermann et al., 2010). A decreasing capelin stock will probably (but not necessarily—see Gjøsæter et al., 2009) affect the cod growth and condition negatively. Krill is observed to be a major component in the diets of both harp seals (Lindstrøm et al., 2013) and minke whales (Haug et al., 1996, 2002), particularly during summer. Increased krill biomass, as a result of relaxed top-down control by capelin, is therefore likely to be more beneficial to the sea mammals than the cod. However, if juvenile herring does not replace capelin it is possible that minke whales may experience the same conditions as in 1995–1996 when they had to switch to krill and gadoids.

Longer Term

Increasing water temperatures and reduction or loss of sea ice may have major effects on the energy flux in the system (e.g., Wassmann et al., 2006; Post et al., 2013). Model simulations suggests that reduced sea ice weakens the stratification and hence the phenology of the lower trophic levels. Weaker and more variable water stratification is assumed to result in a higher pelagic production and a weaker benthic-pelagic coupling (Wassmann et al., 2008). If these simulations are correct, we might expect a lower benthic production which is likely to affect cod more than the mammal predators since cod feed on the benthic community (Johannesen et al., 2012). On the other hand earlier and prolonged seasonal ice-melt may cause increased mismatches between phytoplankton blooms and zooplankton production (e.g., Søreide et al., 2010) and as a result lower pelagic production. The ecological consequence of more light and ocean freshening, which have antagonistic effects on phytoplankton production, is poorly understood (Wassmann et al., 2011). A more recent study (Ardyna et al., 2014) suggests that loss of sea ice triggers late autumn phytoplankton blooms but which of the predators that will benefit most from this is difficult to say, however, changes in the distribution and length of the production period is likely to affect the migration patterns of both cod and the marine mammal species.

In case of a continued warming, predator and prey stocks are likely to move further north—but cod is not likely to move into deep Polar Ocean. Although minke whales are shelf feeders they do feed in deep sea areas and as such they will have no problem of feeding successfully in the polar ocean and, to a lesser extent, the same applies for harp seals. However, if the ice conditions in the White Sea, the main breeding area for Barents Sea harp seals, deteriorate, the seals may have to change to other breeding areas and this could affect their migration pattern considerably. Cod migration patterns could also change considerably if new spawning areas such as the Bear Island area or the Novaya Zemlya coast appear. A radical shift of breeding/spawning areas represents a profound change to the whole life history of a stock, since this will affect the drift pattern of larvae (fish) and feeding area of the young (seals) in an unpredictable way.

A gradual shift in species composition toward more Atlantic dominated zooplankton species which has been observed the past decade (Dalpadado et al., 2012) implies that fatty arctic ice-associated prey such as amphipods is being replaced by less fatty Atlantic species (Wassmann et al., 2006; Falk-Petersen et al., 2007). The outcome of this change is difficult to predict but, in general, less energy-rich food will allow the predators to build up less energy during the feeding season which, in turn, will affect their ability to undertake long migrations to spawning/breeding areas and to develop gonads or suckle their young. Increased water temperature will speed up all the processes in the ecosystem due to increased metabolism with the exception of sea mammals that will use less energy because they are thermoregulated animals. As a result the energy turnover will increase and this will most likely result in a more variable ecosystem.

There have been several modeling attempts using dynamics multispecies models (e. g., Bogstad et al., 1997; Schweder et al., 2000; Lindstrøm et al., 2009); "what-if" scenarios (20–100 years into the future) has been run with respect to harp seal, minke whale, cod, capelin and herring. Model comparisons are difficult to make and conclusions are difficult to draw due to differences in model structure and assumptions. For example, in Gadget and MULTSPEC, a larger whale population resulted in higher stock levels of capelin and slightly reduced cod and herring stocks; the rise in predation on capelin as a result of a larger whale stock was more than compensated for by reduced predation pressure on capelin from cod and herring (Bogstad et al., 1997; Lindstrøm et al., 2009). In contrast, increased whale numbers in the Scenario Barents Sea model (Schweder et al., 1998) resulted in a reduced capelin stock. Thus the indirect effect of whales on capelin through the food web was dominant in the MULTSPEC and Gadget models, while in the Scenario Barents Sea model the direct effect of whales preying on capelin were dominant. The difference may be due both to the functional forms as well as to parameter values used in the models. Of these three models, only the Gadget model for the Barents Sea is still operative.

The multispecies models mentioned above have all focused on top-down effects (predation mortalities induced by the top predators). Less attention has been given to modeling bottom-up effects (effects of varying food abundance on predator population dynamics), but our present study indicates that such effects also are important. The same model frameworks could still be used.

The results from such studies should in any case be treated with great caution. One reason is that in those models migration and thus geographical overlap is at present not affected by climatic conditions or stock size. That kind of effects could, however, be included in such models (see Howell and Filin, 2014 for an example with a cod-capelin model), and could possibly improve the ability of such models to give realistic future scenarios. Appropriate modeling of the direct and indirect impact of marine mammals on commercial species is also very important, as seen from the difference between results from different models described above.

Conclusions

There are a variety of factors influencing the competition between cod, harp seals and minke whales in the Barents Sea. Their performance is affected both by their food consumption in the main feeding season in summer-autumn, when they compete for food, as well as their feeding during the rest of the year. The main advantages for cod are likely: (1) Larger availability of food (mainly capelin) during winter-spring than for marine mammals. This particularly affects immature cod, which has being doing better than mature cod, and (2) A wider range of prey species available to cod than to marine mammals, due to the cod's larger vertical range. This may more than outweigh the wider size range of prey available to marine mammals. Harp seals are more dependent on prey items found close to the ice edge than the other two predator stocks are, and thus it makes sense that the performance of harp seals is worse than that of the two other top predators in the area.

Data on Barents Sea cod diets and condition are collected routinely every year, while collection of similar data from harp seals and minke whales are done much more fragmentarily. For a more proper and quantitative comparison of the relation between cod and the mammals in the Barents Sea, diet and condition data from the mammals must be collected in such a way that a time series similar to the one on cod becomes available.

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Recent changes in distribution and relative abundance of cetaceans in the Norwegian Sea and their relationship with potential prey

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This study aimed to assess possible shifts in distributional patterns of cetaceans residing in the Norwegian Sea, and to relate the distribution to their feeding ecology during the summer seasons of 2009, 2010, and 2012. During this same period, historically large abundances in the order of 15 million tonnes pelagic planktivorous fish such as Norwegian spring-spawning herring (*Clupea harengus*), northeast Atlantic mackerel (*Scomber scombrus*) and blue whiting (*Micromesistius poutassou*), have been reported feeding in the Norwegian Sea during the summer. There is also observed elevated average surface temperatures and a reduction in zooplankton biomass during the last two decades. Such changes might influence species composition, distribution patterns and feeding preferences of cetaceans residing the region. Our results show higher densities of toothed whales, killer whales (*Orcinus orca*) and pilot whales (*Globicephala melas*), than the previous norm for these waters. Baleen whales, such as minke whales (*Balaenoptera acutorostrata*) and fin whales (*Balaenoptera physalus*), which are often associated with macro-zooplankton, displayed a distribution overlap with pelagic fish abundances. Humpback whales (*Megaptera novaeangliae*) were observed in low numbers, indicating a shift in habitat preference, compared to sighting data collected only few years earlier. Our study illustrate that both small and large cetaceans that reside in the Norwegian Sea have the capability to rapidly perform shifts in distribution and abundance patterns strongly associated with adaptive search behavior in relation to both changing levels of abundance in their prey and elevated sea-surface temperatures. This study provides new evidence on high ecological plasticity in response to changing predator-prey trophic relationships and elevated sea-surface temperatures.

Keywords: whales, dolphins, spatial distribution, shift, feeding, pelagic fish, climate change

INTRODUCTION

Marine mammal distributional shifts as a consequence of a warming climate are reported worldwide (Würsig et al., 2002; Moore and Huntington, 2008; Ferguson, 2009; Simmonds and Elliot, 2009; Smith and Reeves, 2010; Kovacs et al., 2011). Certain freshwater systems and Arctic related regions, currently undergoing the most rapid climatic changes, experience the most profound effects particularly with the small and especially niche dependent cetaceans (IPCC, 2007, 2014; Burek et al., 2008; Moore and Huntington, 2008; NAMMCO, 2013). A number of recent reviews concerning the possible impact of climate change upon marine mammals predict that their distribution, prey preference and long term recruitment will be affected (IWC, 1997, 2009; Learmonth et al., 2006; Burek et al., 2008; Laidre et al., 2008; Moore and Huntington, 2008; MacLeod, 2009; Evans et al., 2010).

Since the initiation in 1978 of systematic collections of hydrological data from the Norwegian Sea, the annual average temperature and salinity has increased 1°C and 0.1 PSU, respectively (Skjoldal et al., 2004). Large variations are also reported in distribution and abundances of pelagic planktivorous fish, which are important as prey for many of the large cetacean species, but there are still uncertainties about the causal mechanisms behind these fluctuations (Holst et al., 2004). Little information on whale feeding ecology exists from this ecosystem but it is regarded, especially during the summer seasons, as an important foraging ground and transit route to and from higher latitudes (Jonsgård, 1966, 1968; Øien, 1988, 2003, 2013; Christensen et al., 1992; Nøttestad and Olsen, 2004; Pike et al., 2005). Despite ascertainable changes in the whale prey communities in the Norwegian Sea, no clear changes in fin- (*Balaenoptera physalus*) or humpback whale (*Megaptera novaengliae*) distribution patterns were detected in a study investigating sighting data collected during 2006 and 2007 (Nøttestad et al., 2014a), compared to distributional trends reported 10–15 years earlier (Skjoldal et al., 2004;

Vikingsson et al., 2009). A recent study on offshore-feeding killer whales (*Orcinus orca*) in this system found that they mainly targeted northeast Atlantic mackerel (*Scomber scombrus*) (Nøttestad et al., 2014b). This was in contrast to the earlier perception that their main prey was the Norwegian spring-spawning (NSS) herring (*Clupea harengus*) (Sigurjónsson et al., 1988; Similä et al., 1996; Simon et al., 2006). This has been the case at least for the more coastal areas, but no such focused large scale study prior to Nøttestad et al. (2014b) had given attention to the offshore areas of this highly productive marine ecosystem. Furthermore, the collective behavior of killer whales have been found fine-tuned to prey schooling size and behavior (Nøttestad et al., 2002, 2014b).

However, over the last few years even more striking changes in prey species composition are reported from this system; the northeast Atlantic mackerel stock has showed a dramatic estimated increase in abundance from 1.6 million tonnes (Mt) in 2007 to 9.0 Mt in 2014 (ICES, 2013b, 2014; Nøttestad et al., 2014c). The NSS herring biomass has recently decreased from >12 Mt in 2009 to <5 Mt in 2014 (ICES, 2013b, 2014), and the Atlantic blue whiting (*Micromersitius poutassou*) biomass decreased from a spawning stock biomass of nearly 8 Mt in 2002 to 2.9 and 5.5 Mt in 2010 and 2014 respectively (ICES, 2013b, 2014).

In light of the updated knowledge on the shifts in important cetacean prey-changes in distribution, biomass and species composition, we aim to better determine and assess how temporal changes in distributional patterns can be distinguished and possibly how the role of phenotypic plasticity (the ability of an organism to change its phenotype in response to changes in the environment) acts for different cetacean species residing the Norwegian Sea. We will investigate the most recent cetacean sighting data from this area, conducted during three synoptic summer surveys in 2009, 2010, and 2012, by studying its possible relationships to measurements of prey distribution and by including other key environmental variables.

MATERIALS AND METHODS

Three transect surveys were undertaken in the Norwegian Sea from the 15th of July to the 6th of August in 2009 and 2010, and from the 1st to the 28th of July in 2012. In total four different Norwegian vessels were chartered for the purpose of this study: M/V "Libas" (2009 and 2010), M/V "Eros" (2009), M/V "Brennholm" (2010 and 2012), and the research vessel R/V "G.O. Sars" (2012). The geographical coverage and data collection in 2011 were too limited in the northern part of the Norwegian Sea to be included in the time series. Only one Norwegian vessel, compared to two vessels participating the other years and no dedicated marine mammal observers were present onboard in 2011. The geographical area covered by the survey was very similar the two first seasons, while the most northern part was not covered during the survey in 2012 (**Figures 1–3**).

Marine mammal sightings were made by two trained and experienced whale observers on each vessel along the survey tracks during daylight hours (about 10–12 h per day). Furthermore, opportunistic sightings were also performed between stations from the bridge during nighttime, when applicable, since the light regime was dominated by midnight sun. It was therefore sufficient sunlight for reliable visual sightings of marine mammals up to 24 h per day when the surveys were conducted in high latitudes from July to August. Thus, most of the track lines were surveyed either by dedicated or opportunistic effort and the effort was comparable between the years 2009, 2010, and 2012 as well as to the previous sighting surveys. Sightings were made mostly from a platform at the wheelhouse rooftop (11–15 m height depending on vessel) whenever weather permitted (Beaufort < 4 and no or moderate rain). The sightings were otherwise made from the bridge (9–13 m height). The marine mammal sightings were done along transects and during transit between transects, however no recordings were made while trawling or when performing other station work. Observations were made using the observation regime adopted by Palka and Hammond (2001) and Lawson and Gosselin (2009). A sighting was noted on the basis of direct observation with the naked eye and binoculars, and was documented with digital video-recordings and photographs. This procedure ensured valid estimates and verification of marine mammal group size related to each sighting. Both passing and closing mode were applied during sightings of marine mammals. In a passing mode, the ship moves continuously along a transect line, whereas in a closing mode, the ship stops normal searching procedures once a group of cetaceans is sighted (goes "off-effort"), leaves the transect line and approaches the sighted group to identify the species and stock composition of the group and make reliable estimates of group size (Schwartz et al., 2010). The survey design had predominantly east-west transects with 35–60 nautical miles distance between survey lines. Combined with high survey speed of 10–12 knots for all vessels in all years, this ensured that the risk of double counting for both pelagic fish and marine mammals was absent or extremely low. The sighting data were not corrected for surface-sighting probability. Very good wind and weather conditions with optimal sighting conditions dominated during these summer surveys. Nevertheless, the aim of these surveys was not to perform quantitative abundance estimation of marine mammals, rather studying distribution, relative abundance and ecological aspects of a wide range of marine mammals present in the Norwegian Sea ecosystem.

In total, 334 CTD (Conductivity Temperature Depth) casts ($n = 93$ in 2009, $n = 152$ in 2010 and $n = 89$ in 2012) were performed using SAIV and SEABIRD sensors. The CTDs were deployed from surface to 500 m depth and the stations were spaced approximately ∼110 km (60 nmi) apart along the transect lines, although less distance (35–50 nmi) between transect lines and stations were done in the northernmost regions.

Meso- and macro-zooplankton were sampled at each pelagic trawl station using a WP2 net with a diameter of 56 cm and mesh size of 180 μm. A total of 333 WP2 vertical hauls were carried out from 200-0 m ($n = 93$ in 2009, $n = 152$ in 2010 and $n = 88$ in 2012). Zooplankton biomass was calculated to total dry weight in g m^{-2} using the methods described in Gjøseter et al. (2000).

A total of 348 trawl hauls ($n = 93$ in 2009 and $n = 148$ in 2010 and $n = 107$ in 2012) were made at pre-defined positions, using a commercial blue whiting pelagic trawl net (Egersund trawl in 2010), Atlantic salmon adapted pelagic trawl (2009) and a pelagic sampling trawl (Multpelt 832 in 2012). Trawl depths

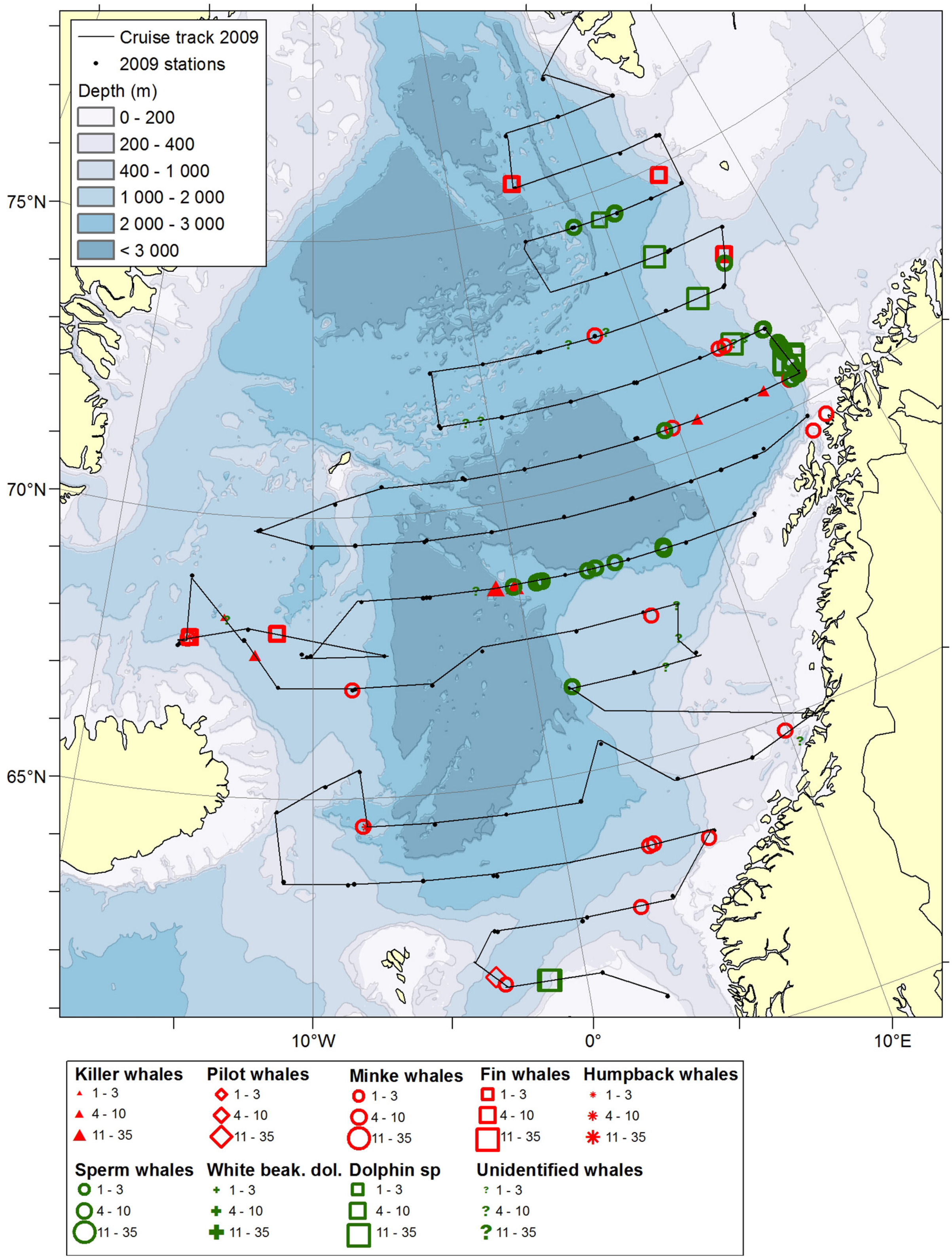

FIGURE 1 | Distribution of cetaceans sighted in the Norwegian Sea during the summer season of year 2009. Black lines illustrate cruise tracks from two vessels, whereas black dots represent stations for pelagic trawl sampling of pelagic fish, plankton nets (0–200 m) and physical oceanography from CTD (0–500 m).

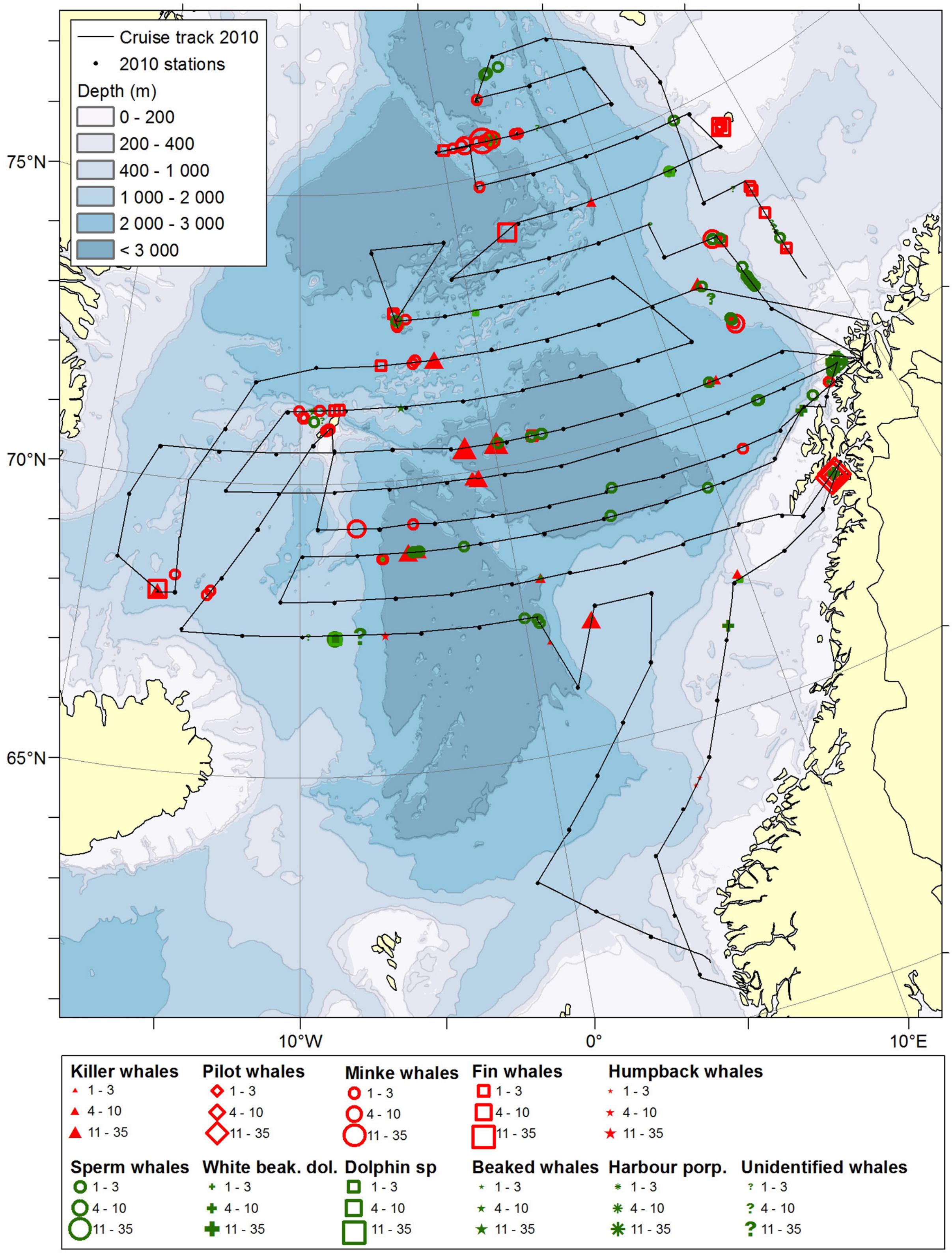

FIGURE 2 | Distribution of cetaceans sighted in the Norwegian Sea during the summer season of year 2010. Black lines illustrate cruise tracks from two vessels, whereas black dots represent stations for pelagic trawl sampling of pelagic fish, plankton nets (0–200 m) and physical oceanography from CTD (0–500 m).

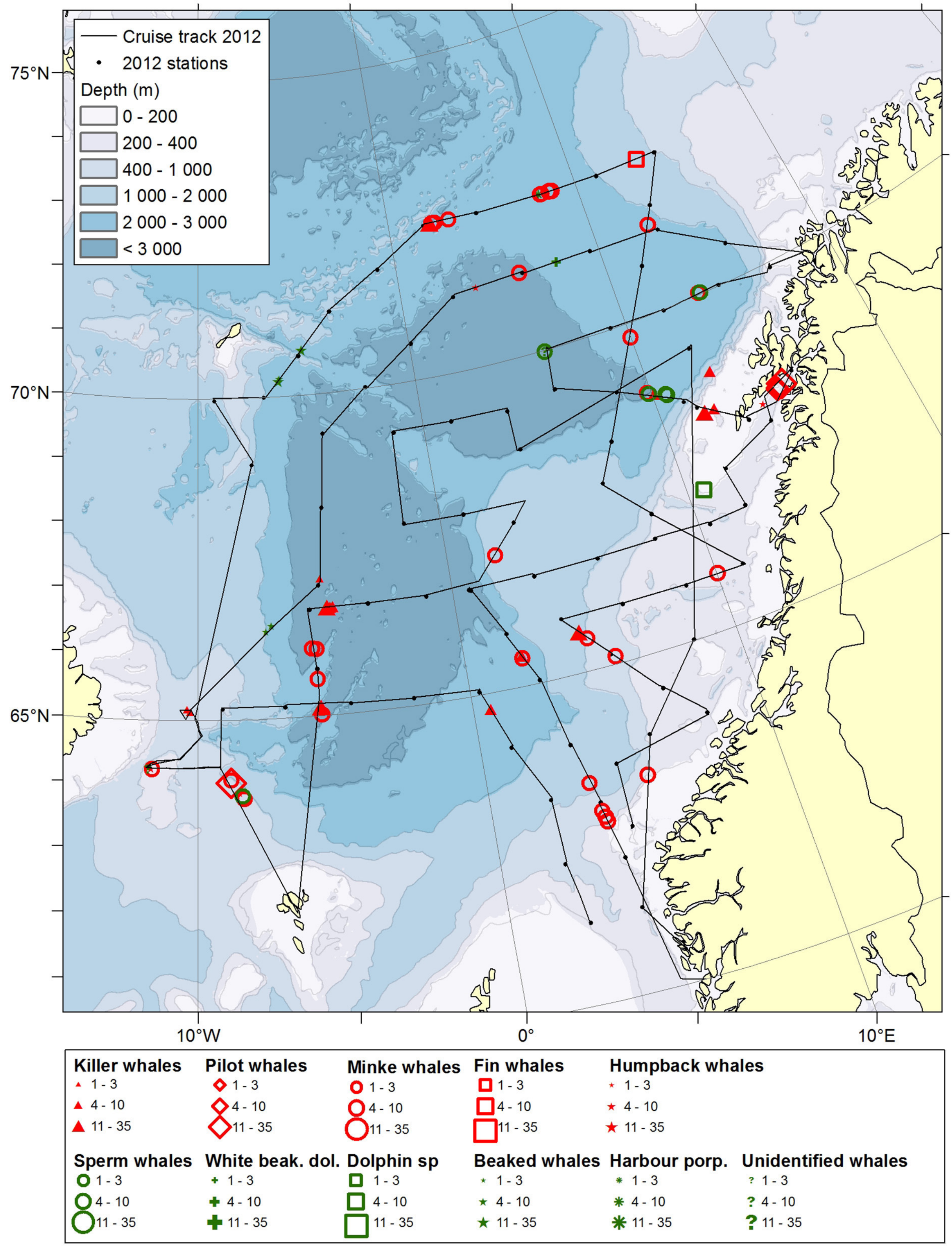

FIGURE 3 | Distribution of cetaceans sighted in the Norwegian Sea during the summer season of year 2012. Black lines illustrate cruise tracks from two vessels, whereas black dots represent stations for pelagic trawl sampling of pelagic fish, plankton nets and physical oceanography from CTD (0–500 m).

ranged from 0–60 m, towing speed was 4.0–5.3 knots and towing duration was set to ~30 min. Towing distance during trawling varied between 3.7 and 4.9 km, corresponding to 4.0 and 5.3 knots respectively, depending on currents and weather conditions. The catches were sorted, identified to species and weighed. The accuracy on the total fish catches from pelagic trawling was around ±10 kg, whereas individual sorted fish samples had an accuracy of ±1 g.

Complete stations conducted by combining CTD sampling, plankton nets and standardized pelagic trawl hauls were included as predictor variables in a Generalized Additive Model (GAM) nonparametric regression analysis, using the Gaussian distributional fit (SAS Institute Inc., Box 8000 Cary, N.C., U.S.A). The most common prey species in the study area were included (#kg in catch) [NEA mackerel, NSS herring, Atlantic blue whiting, capelin (*Mallotus villosus*), krill and gonatus (*Gonatus fabricii*) (**Tables 3A,B**)] and environmental variables (sub-surface temperature (°C) and bottom depth (m) as close as possible to the actual position of a sighting. Bottom depth was extracted from the General Bathymetric Chart of the Ocean (GEBCO: www.gebco.net). Response variables included number of individuals of a cetacean species or absence of marine mammals observed during the entire study, within 20–30 nmi distance from each station depending on northern latitude. Since the sightings of marine mammals are continuous data and the oceanographic and biological data originates from station data spaced 20–30 nmi apart, we need to make assumptions on overlap based on different spatial resolution of the different sources of information. The 0.05 level of probability was accepted as indicating statistical significance and all mean values are shown ± standard deviations.

RESULTS

TOOTHED WHALES

Killer whale was the most common cetacean species observed during all three study years, followed by pilot whales (**Table 1**). Killer whales had $N = 48$ individuals in 2009, $N = 136$ in 2010 and $N = 182$ in 2012. Pilot whales had $N = 6$ individuals in 2009, $N = 31$ in 2010 and $N = 114$ in 2012. Killer whales and pilot whales had also the highest observed group sizes among the marine mammals (**Table 2**). Killer whale group size varied from an average 5.1–9.2 animals whereas pilot whale group size varied from an average of 5.2–17.0 animals between years.

Killer and pilot whales increased significantly in appearance in the Norwegian Sea during the consecutive study years, whereas the sperm whale numbers decreased (**Table 1**).

Killer whales were positively correlated with distribution and concentrations of Northeast Atlantic mackerel ($p < 0.0001$, $n = 402$) (**Table 3A**) and shallow bottom depths ($p < 0.0072$, $n = 402$) when pooling the data for all years. They were positively correlated with high concentrations of mackerel for the years 2010 ($t = 3.73$, $df = 179$, $p < 0.001$) and 2012 ($t = 3.04$, $df = 116$, $p < 0.005$).

Pilot whales were significantly correlated with high concentrations of NSS herring ($p = 0.0002$, $n = 380$) (**Table 3A**), and shallow bottom depths ($p = 0.0002$, $n = 380$). Pilot whales were solely observed in shallower waters than 300 m depth.

Table 1 | Overview of number of individuals from different cetacean species sighted in 2009, 2010, and 2012.

Species/Year	2009	2010	2012
	Numbers		
Killer whales	48	136	182
Pilot whales	6	31	114
Minke whales	26	60	31
Fin whales	7	20	2
Humpback whales	4	8	8
Sperm whales	36	49	8
White beaked dolphin	0	20	4
Dolphin sp	67	22	1
Beaked whales	0	11	20
Unidentified whales	34	33	2
Harbor porpoises	0	4	1

Table 2 | Overview of average group size (±SD) from cetacean species sighted in 2009, 2010, and 2012.

Species/Year	2009	2010	2012
	Group size (±SD)		
Killer whales	6.0 (5.9)	5.1 (5.7)	9.2 (6.1)
Pilot whales	6.0 (0.0)	5.2 (3.3)	17.0 (11.9)
Minke whales	1.1 (0.3)	1.2 (0.6)	1.0 (0.0)
Fin whales	1.3 (0.5)	1.3 (0.6)	2.0 (0.0)
Humpback whales	2.0 (1.4)	1.6 (0.9)	1.1 (0.4)
Sperm whales	1.1 (0.3)	1.0 (0.1)	1.3 (0.8)
White beaked dolphin	0.0 (0.0)	4.7 (4.7)	1.0 (0.0)
Dolphin sp	9.6 (7.6)	2.8 (1.3)	1.0 (0.0)
Beaked whales	0.0 (0.0)	3.0 (4.0)	3.3 (1.0)
Unidentied whales	1.4 (0.8)	2.4 (0.8)	1.0 (0.0)
Harbor porpoises	0.0 (0.0)	1.0 (0.0)	1.0 (0.0)

Harbor porpoises were only found significantly associated with shallow waters ($p = 0.0167$, $n = 373$).

Beaked whales were found associated with NSS herring ($p < 0.0001$, $n = 380$) and deep bottom depths ($p = 0.0354$, $n = 380$).

White beaked dolphins were significantly correlated with shallow water ($p = 0.0073$, $n = 372$) and were predominantly observed along the shelf break. The unidentified dolphin species were significantly correlated with biomasses of zooplankton ($p = 0.0195$, $n = 377$) and low temperatures ($p = 0.0142$, $n = 377$).

Total numbers of sperm whales sighted were $N = 36$ in 2009, $N = 49$ in 2010, and $N = 8$ in 2012, respectively (**Table 1**). These sightings were not found significantly correlated with the distribution or concentrations of any of the prey species, nor environmental variables included in the regression model.

BALEEN WHALES

Minke whale was the most sighted baleen whale in 2009 ($N = 26$), 2010 ($N = 60$), and 2012 ($N = 31$). Minke whales were significantly correlated with the occurrence of NSS herring ($t = 5.71$, $df = 416$, $p < 0.0001$), but no such relationship were

Table 3A | Regression model components (most common available prey), and results from the GAM procedure analyzing their relationship to toothed whale species densities.

Toothed whales	**Prey species**	**Parameter estimate**	***SE***	***t*-Value**	***Pr* > *t***
Killer whale	Mackerel	0.00104	0.00016619	6.23	<0.0001
	Herring	0.00011562	0.00036200	0.32	0.7496
	Blue whiting	−0.00063017	0.00288	−0.22	0.8269
	Capelin	−0.00229	0.01404	−0.16	0.8703
	Krill	0.00168	0.02188	0.08	0.9389
	Gonatus	−0.03691	0.11126	−0.33	0.7403
Pilot whale	Mackerel	0.0000.2177	0.00016033	0.14	0.8920
	Herring	0.00126	0.00033252	3.78	0.0002
	Blue whiting	−0.00167	0.00248	−0.67	0.5017
	Capelin	−0.00175	0.01211	−0.14	0.8853
	Krill	−0.00408	0.01888	−0.22	0.8289
	Gonatus	0.01911	0.09604	0.20	0.8424
Harbor porpoise	Mackerel	0.00000360	0.00000789	0.46	0.6482
	Herring	0.00001312	0.00001640	0.80	0.4243
	Blue whiting	−0.00006128	0.00012227	−0.50	0.6165
	Capelin	−0.00013314	0.00059617	−0.22	0.8234
	Krill	−0.00027587	0.00092705	−0.30	0.7662
	Gonatus	0.00137	0.00472	0.29	0.7720
	Krill	−0.00256	0.00329	−0.78	0.4366
	Gonatus	0.00278	0.01676	0.17	0.8681
Beaked whale	Mackerel	−0.00000738	0.00002956	−0.25	0.8030
	Herring	0.00029929	0.00005795	5.16	<0.0001
	Blue whiting	−0.00016116	0.00045785	−0.35	0.7250
	Capelin	−0.00011599	0.00223	−0.05	0.9586
	Krill	0.00037641	0.00347	0.11	0.9137
	Gonatus	−0.00630	0.01767	−0.36	0.7215
White beaked dolphin	Mackerel	0.00003873	0.00004892	0.79	0.4291
	Herring	−0.00004111	0.00010159	−0.40	0.6860
	Blue whiting	−0.00031637	0.00075750	−0.42	0.6765
	Capelin	−0.00072686	0.00369	−0.20	0.8441
	Krill	−0.00171	0.00574	−0.30	0.7659
	Gonatus	0.00845	0.02923	0.29	0.7727
Unidentified dolphin	Mackerel	0.00005546	0.00010491	−0.53	0.5974
	Herring	−0.00014165	0.00020531	−0.69	0.4907
	Blue whiting	−0.00044792	0.00163	−0.28	0.7830
	Capelin	−0.00060183	0.00792	−0.08	0.9395
	Krill	−0.00146	0.01232	−0.12	0.9057
	Gonatus	−0.01935	0.06269	−0.31	0.7577
Sperm whale	Mackerel	−0.00003582	0.00002684	−1.33	0.1828
	Herring	−0.00001064	0.00005601	−0.19	0.8494
	Blue whiting	−0.00013608	0.00043126	−0.32	0.7525
	Capelin	−0.00152	0.00212	−0.72	0.4748
	Krill	−0.00256	0.00329	−0.78	0.4366
	Gonatus	0.00278	0.01676	0.17	0.8681

found for zooplankton ($t = 1.67$, $df = 416$, $p < 0.095$) when combining all years (**Table 3B**).

Fin whales and humpback whales were observed with lower numbers and smaller group sizes in the study area between 2009 and 2012 (**Tables 1**, **2**). Fin whales were significantly correlated with distribution and high concentrations of capelin ($p = 0.0017$, $n = 376$), low temperatures ($p = 0.0026$, $n = 376$) and shallow bottom depths ($p < 0.05$, $n = 376$) (**Table 3B**).

Table 3B | Regression model components (most common available prey), and results from the GAM procedure analyzing their relationship to baleen whale species densities.

Baleen whales	Prey species	Parameter Estimate	*SE*	*t*-Value	*Pr* > *t*
Minke whale	Mackerel	0.00001202	0.00002928	0.41	0.6815
	Herring	0.00026727	0.00004682	5.71	<0.0001
	Blue whiting	−0.00020912	0.00046775	−0.45	0.6551
	Capelin	0.00033474	0.00229	0.15	0.8837
	Krill	−0.00181	0.00356	−0.51	0.6113
	Gonatus	−0.00065228	0.01808	−0.04	0.9712
Fin whale	Mackerel	−0.00000165	0.00002002	−0.08	0.9343
	Herring	−0.00006462	0.00004134	−1.56	0.1189
	Blue whiting	−0.00012213	0.00030993	−0.39	0.6938
	Capelin	0.00435	0.00138	3.16	0.0017
	Krill	0.00134	0.00233	0.58	0.5653
	Gonatus	−0.00967	0.01189	−0.81	0.4166
Humpback whale	Mackerel	0.000000364	0.00001910	0.19	0.8492
	Herring	0.00005772	0.00003771	1.53	0.1267
	Blue whiting	−0.00011707	0.00029623	−0.40	0.6929
	Capelin	−0.00018162	0.00144	−0.13	0.9000
	Krill	0.00135	0.00224	0.60	0.5486
	Gonatus	−0.00694	0.01141	−0.61	0.5434

Humpback whales were not significantly correlated with distribution and concentrations of any of the selected regression model components such as pelagic fish and macro-zooplankton (**Table 3B**).

ZOOPLANKTON

Zooplankton concentrations including *C. finmarchicus*, krill and amphipods were generally low with an average weight of 4.8 g/m^2, 4.0 g/m^2, 6.0 g/m^2 for the years 2009, 2010 and 2012. In general, the plankton concentrations were lowest in the central Norwegian Sea and highest in the south western part and east of Iceland in the frontal area between the warm Atlantic water and the colder Arctic water. *C. finmarchicus* was generally found in small concentrations in the western survey area, while *C. hyperboreus* was collected in the northern and northwestern part of the Norwegian Sea. Krill and amphipods were not found or in very small quantities in most areas except in the westernmost areas.

DISCUSSION

A compelling result from this study is the more frequent toothed whale sightings, in particular of killer- and pilot whales, in the Norwegian Sea compared to previous historic sighting surveys (Hammond and Lockyer, 1988; Buckland et al., 1993; Abend and Smith, 1999; Nøttestad and Olsen, 2004; Øien, 2013). Fin whales seemed to have switched toward a fish prey vs. a diet consisting of krill and amphipods only few years earlier (Nøttestad et al., 2014a). There have been a change in distribution and reduction in biomass of krill and amphipods in the Norwegian Sea during the last 10–15 years (Dalpadado et al., 1998; Melle et al., 2004). Quantifying macro-zooplankton such as krill and amphipods using vertical hauls with WP2 nets is difficult since these nets with such small opening and mesh size are generally not regarded as efficient sampling gear for macro-zooplankton including krill (except the sub-adult stages). Nevertheless, we also used more qualitative data from our extensive numbers of trawl hauls stations to document presence or absence of krill and amphipods caught during pelagic trawling close to the surface in relation to marine mammal sightings. Humpback whales were found in very low numbers and no overlap was detected between their distribution and potential prey species. Findings from 2006 to 2007 showed a different picture with much higher sighting numbers and a distribution toward the northernmost waters of the Norwegian Sea associated with NSS herring (Nøttestad et al., 2014a).

The high numbers of killer whales and pilot whales sighted increased substantially from year to year during our study. Killer whales were associated with NEA mackerel, which is in line with results also found in the same area during 2006/2007 (Nøttestad et al., 2014b). Mean group size of killer whales was between 5.1 and 9.2 animals from 2009 to 2012, which is comparable with mean group size = 8.2 animals found in the Norwegian Sea in summers 2006 and 2007 (Nøttestad et al., 2014b). The collective behavior of killer whales thus seems to be fine-tuned to the schooling behavior and aggregation level of their dominant mackerel prey (Nøttestad et al., 2002, 2014b). Pilot whales are opportunistic feeders that may exploit locally abundant prey, but they are traditionally regarded as consumers of squid (Nøttestad and Olsen, 2004; Olson, 2009). Pilot whales prey on some commercially important fish such as NEA mackerel and NSS herring, and appear to be able to adjust their diet in response to changes in prey abundance (Desportes and Mouritsen, 1993). In our study, pilot whales were to a large degree found associated with NSS herring and were found in groups of variable average size ranging from 5.2 to 17.0 animals, probably adjusted to their schooling prey species, but they were also found to be associated with high zooplankton concentrations, as the only cetacean species in our study. This species was also associated with shallow bottom regions (<300 m) which is not particularly associated with their traditionally dominant prey as squid are predominantly found on much deeper waters. The influence of warm Atlantic water has been very strong in the Norwegian Sea during the period from 2009 to 2012 (Beszczynska-Möller and Dye, 2013). The warm surface waters combined with low concentrations of meso- and macro zooplankton such as copepods, krill (*Meganyctiphanes norvegica*, *Thysonoessa inermis,* and *Thysonoessa longicaudata*) and amphipods (*Themisto libellula*) and a large mackerel stock feeding in the Norwegian Sea during summer, has expanded their spatial distribution to new and previously unknown territories far to the north and west. Nevertheless, the decrease in zooplankton biomass including *Calanus finmarchicus* in the Norwegian Sea may have stabilized after 2009, and in recent years there has been a tendency of increase (Huse et al., 2012; Broms, 2014), which may have affected the distribution and aggregation of pelagic fish and furthermore presence and distribution of marine mammal species. NSS herring has also responded to the warmer waters by feeding further north and northwest in summer than earlier years (ICES, 2013a). Since presence of mackerel and NSS herring has steadily increased in northern waters from 2009 to 2012, including along the Polar Front between Atlantic and Arctic water masses, this has led to increased availability of pelagic fish for the cetaceans (Nøttestad and Olsen, 2004; ICES, 2014; Nøttestad et al., 2014c). It seems clear that the high abundance of pelagic fish species estimated to be around 15 Mt have attracted more feeding toothed whales such as killer and pilot whales to the Norwegian Sea ecosystem.

Sperm whales were sighted in modest numbers and mainly occurring as solitary individuals during our sighting surveys. There is little scientific knowledge available on the status of abundance and distribution of their main cephalopod prey species (*G. fabricii*) (Roper et al., 2010). However, there are indications of decreasing cephalopods abundance including *G. fabricii* over the past decades (Wiborg et al., 1982; Gardiner and Dick, 2010).

Historically, the Norwegian Sea ecosystem has been important for baleen whale feeding during summer (Jonsgård, 1966, 1968). The baleen whales observed during this study are found to be more associated with pelagic fish compared to meso- and macro zooplankton (see Nøttestad et al., 2014a), suggesting a temporal shift in prey distribution. Elevated sub-surface temperatures documented in the Norwegian Sea during the last few years compared to 10–20 years ago (Skagseth and Mork, 2012; Beszczynska-Möller and Dye, 2013; ICES, 2013c), may have influenced distribution and aggregation of potential prey species for marine mammals feeding within this ecosystem. We found that both fin whale and minke whale, among the most abundant baleen whales in our study, were significantly associated with NSS herring as also found along the Barents Sea shelf edge (Skern-Mauritzen et al., 2009) and not correlated with macro-zooplankton such as krill as dominant prey species in earlier periods based on direct stomach samples (Jonsgård, 1966, 1968). This is partly in contrast to a study performed in the Norwegian Sea during summers 2006–2007 where fin- and humpback whales were found correlated with the presence of macro-zooplankton in cold Arctic water (Nøttestad et al., 2014a). This change suggests that macro-zooplankton is becoming less available and pelagic fish is becoming more available as dominant prey in the Norwegian Sea during the active feeding period in summer. Higher temperatures combined with less abundance of meso- and macro zooplankton found in our study from 2009 to 2012 compared to earlier studies (Dalpadado et al., 1998; Melle et al., 2004), suggest sub-optimal conditions for species such as *C. finmarchicus*, krill and amphipods in the Norwegian Sea. Cetaceans preying on these species will then follow and shift their distribution to obtain more optimal feeding on these species. Low group sizes of both fin- and humpback whales observed from 2009 to 2012 coincide with similar findings from 2006 and 2007, suggesting that these baleen whale species mainly hunt solitary or in small groups within the Norwegian Sea ecosystem in summer (Nøttestad et al., 2014a).

The Norwegian Sea has traditionally been an important migration corridor for baleen whales toward northern feeding grounds and to a lesser extent vital as feeding grounds for minke-, humpback- and fin whales (see Nøttestad and Olsen, 2004; Clapham, 2009; Øien, 2013; Nøttestad et al., 2014a). A reduction in, e.g., minke whale abundance is observed in the Norwegian Sea during the last decade (Øien, 2013). Prey species such as krill and amphipods may have shifted their spatial distribution to more northern latitudes (Buchholtz et al., 2010; Kraft et al., 2013), which probably influences the minke whales main migration patterns. The minke and fin whales are regarded as opportunistic in their prey choice, leading us to believe that a preference toward NSS herring and not zooplankton for the animals residing in our study area is probably not an unusual finding. Vikingsson et al. (2014) found that minke whales in Icelandic waters have shifted their distribution and diet composition during the last years from a diet dominated by sandeel and macro-zooplankton to a fish diet dominated of herring and gadoids. Cold water species such as krill and capelin were less present in the minke whale diet, coinciding with our results on spatial overlap, where herring, in both studies, were found to be the most important prey species for minke whales in recent years. Despite large abundance of available prey species such as NSS herring and blue whiting in the study area, the fin whales sighted were predominantly swimming far to the north, and were found associated with the cold water species capelin. The sighted humpback whales in our study were not found to be associated with any registered prey species. This might indicate low feeding activities for this species within this region; however, the statistical data was represented with few humpback whale observations.

Toothed whales in general and group living dolphins in particular, apply coordinated hunting strategies, which is suited to capture smaller and less dense concentrations of pelagic fish. Killer whales and pilot whales can also circumvent and manipulate the anti-predator behavior of mackerel and NSS herring to their own benefit by packing looser shoals and aggregations to become denser schools, as well as adjust their group size to prevailing patchiness and school size of pelagic fish (Nøttestad et al., 2014b). This might be important factors influencing the success of these species in this region. Due to low concentrations and densities of meso- and macro-zooplankton during summer, pelagic fish are forced to spread out in smaller and looser shoals and concentrations in order to optimize their own feeding for dominant and easily accessible prey species (Fernö et al., 1998). When pelagic fish are more evenly distributed in small aggregations, they become less available for solitary baleen whales, which dominated in our sighting data. Their hunting technique is much less cost-efficient when schooling fish and swarms of krill and amphipods do not to appear in dense patches.

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Distribution, abundance, and feeding ecology of baleen whales in Icelandic waters: have recent environmental changes had an effect?

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The location of Iceland at the junction of submarine ridges in the North-East Atlantic where warm and cold water masses meet south of the Arctic Circle contributes to high productivity of the waters around the island. During the last two decades, substantial increases in sea temperature and salinity have been reported. Concurrently, pronounced changes have occurred in the distribution of several fish species and euphausiids. The distribution and abundance of cetaceans in the Central and Eastern North Atlantic have been monitored regularly since 1987. Significant changes in the distribution and abundance of several cetacean species have occurred in this time period. The abundance of Central North Atlantic (CNA) humpback and fin whales has increased from 1800 to 11,600 and 15,200 to 20,600, respectively, in the period 1987–2007. In contrast, the abundance of minke whales on the Icelandic continental shelf decreased from around 44,000 in 2001 to 20,000 in 2007 and 10,000 in 2009. The increase in fin whale abundance was accompanied by expansion of distribution into the deep waters of the Irminger Sea. The distribution of the endangered blue whale has shifted northwards in this period. The habitat selection of fin whales was analyzed with respect to physical variables (temperature, depth, salinity) using a generalized additive model, and the results suggest that abundance was influenced by an interaction between the physical variables depth and distance to the 2000 m isobaths, but also by sea surface temperature (SST) and sea surface height (SSH), However, environmental data generally act as proxies of other variables, to which the whales respond directly. Overall, these changes in cetacean distribution and abundance may be a functional feeding response of the cetacean species to physical and biological changes in the marine environment, including decreased abundance of euphausiids, a northward shift in summer distribution of capelin and a crash in the abundance of sand eel.

Keywords: climate change, fin whale, common minke whale, whale abundance, feeding ecology, humpback whale, oceanic warming, habitat modeling

INTRODUCTION

Cetaceans are important top predators in Icelandic waters with a total of 23 species recorded (Hersteinsson, 2004) of which 12–14 species are considered regular inhabitants. In terms of biomass and consumption, cetaceans play an important role in the Icelandic ecosystem. Sigurjónsson and Víkingsson (1997) estimated the total annual consumption by 12 cetacean species as 6 million tons corresponding to around four times the total Icelandic fishery landings. The diet composition of these cetaceans is poorly known except for common minke whales (*Balaenoptera acutorostrata*), fin whales (*Balaenoptera physalus*) and harbor porpoises (*Phocoena phocoena*). Fin whales feed almost exclusively on euphausiids, mostly *Meganyctiphanes norvegica*, on the traditional whaling grounds in the Irminger Sea (Víkingsson, 1997). Fluctuations in environmental conditions affecting *per capita* prey availability have been shown to affect body condition and pregnancy rate in North Atlantic fin whales (Williams et al., 2013). Common minke whales have a much more varied diet ranging from euphausiids to large gadoid fish. Sand eel (*Ammodytes* sp.), herring (*Clupea harengus*) and capelin appear to be the most preferred prey (Víkingsson et al., 2014). The feeding ecology of blue (*Balaenoptera musculus*) and humpback whales (*Megaptera novaeangliae*) in Icelandic waters is not known. However, blue whales are known to feed exclusively on krill in the North Atlantic (Sears and Perrin, 2009) whereas humpback whales are reported to feed on both krill and pelagic schooling fish such as capelin and herring (Clapham, 2009).

Substantial warming and salinification has been observed in Icelandic and adjacent waters in the past two decades (Mortensen and Valdimarsson, 1999; Bersch, 2002; Malmberg and Valdimarsson, 2003; Hátún et al., 2005). Concurrently, pronounced changes have been reported in the distribution and abundance of several animal species in Icelandic waters. Some of these changes appear to be related to increased flow of Atlantic water masses into North Icelandic waters, including a northward expansion of the distribution of haddock (*Melanogrammus aeglefinus*), monkfish (*Lophius piscatorius*), and capelin (*Mallotus villosus*) (Astthorsson et al., 2007; Solmundsson et al., 2010). Sand eel abundance in southern and western Icelandic waters was apparently drastically reduced around 2005, with severe consequences for some seabird populations (Lilliendahl et al., 2013; Vigfusdottir et al., 2013). In terms of biomass, the most influential change is probably the recent invasion of Northeast Atlantic mackerel (*Scomber scombrus*) into Icelandic waters (Astthorsson et al., 2012). There are limited data available on temporal trends in meso- and macro zooplankton in Icelandic waters. Silva et al. (2014) found a decrease in euphausiid abundance in the oceanic (offshore) waters south and west of Iceland during 1958–2007, while in south Icelandic shelf waters they reported an increase in euphausiid larvae during 1990–2011. Recent and ongoing changes in the Icelandic marine environment affect several species that are important as prey for cetaceans. Depending on the ecological flexibility of the different species, these changes could be expected to affect the distribution and abundance of cetaceans in the area.

Large scale surveys, aimed at estimating and monitoring the distribution and abundance of cetaceans in the Central North Atlantic (CNA), have been conducted regularly since 1987 (Sigurjónsson, 1992; Lockyer and Pike, 2009; Víkingsson et al., 2009). Major changes in the distribution and abundance of several cetacean species have been observed over the past 20 years, particularly around the turn of the century. However, the potential effects on habitat use of cetaceans are poorly documented. Within the context of a changing environment, it is important to understand the link between baleen whales and their environment at various temporal and spatial scales in order to assess potential ecosystem-level effects, mediated by changing environmental conditions (Hátún et al., 2009). For future conservation and management it is of utmost importance to gain better understanding of these effects and the interactions among key species in the ecosystem.

In this paper we describe these changes in cetacean distribution and abundance and investigate to what extent they can be explained by recent biological (prey) and physical (oceanography) changes in the marine environment in this area. As part of this investigation, we present a first attempt at modeling the habitat use of fin whales in the Northeast Atlantic over a 20-year period, as a function of both physiographic and remotely sensed environmental variables. Fin whales were chosen for this exercise because of their wide distribution within the survey area and their spatial and temporal overlap with readily available environmental parameters.

MATERIALS AND METHODS

HYDROGRAPHY

Iceland is located at the intersection between large submarine ridges along the Mid Atlantic Ridge in the northern North Atlantic resulting in complex circulation in Icelandic waters (**Figure 1**). In combination with energetic atmospheric circulation this leads to a highly variable environment on the boundary between colder and warmer waters. The East Greenland Current and East Icelandic Current bring colder water from the north while the North Atlantic Current and the Irminger Current carry warmer waters from the south. With the polar front lying through the Denmark Strait area and the Irminger Sea, this climatic boundary fluctuates with various proportions of Polar, Arctic and Atlantic water, especially north of Iceland but also in the Irminger Sea.

Oceanographic data to describe decadal changes in hydrographic conditions in Icelandic waters are based on long-term sampling conducted by the Marine Research Institute (MRI), Reykjavík Iceland (Malmberg and Valdimarsson, 2003; Valdimarsson et al., 2012). Temperature and salinity data used here were obtained with a CTD after 1990, mainly within the context of seasonal monitoring at stations around Iceland. Some data in the Irminger Sea were from an international redfish monitoring project coordinated through ICES. CTD data were processed according to internationally recommended standards. Data from before 1990 were obtained with Nansen bottles and reversing thermometers and then interpolated on 1 dbar intervals before being depth averaged in the same manner as CTD data.

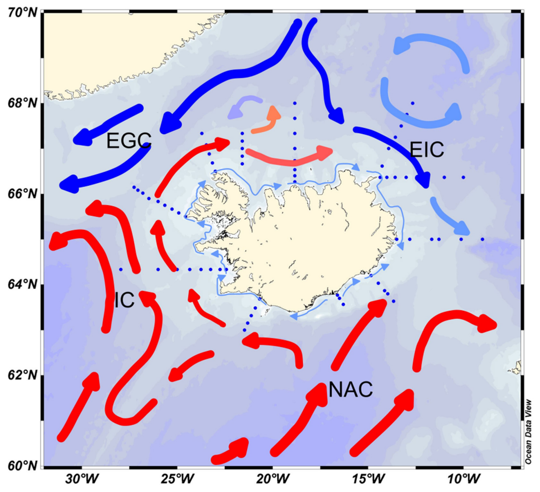

FIGURE 1 | Oceanography of the Icelandic area. EGC, East Greenland Current; EIC, East Iceland Current; IC, Irminger Current; NAC, North Atlantic Current. The dotted lines represent sampling stations.

DISTRIBUTION AND ABUNDANCE OF CETACEANS

The North Atlantic Sightings Surveys (NASS and TNASS) constitute the largest series of cetacean surveys conducted to date in both spatial and temporal extent (Pike, 2009). These multinational surveys have covered large parts of the summer distributions of North Atlantic baleen whales. To date, the series includes five large-scale surveys (1987, 1989, 1995, 2001, and 2007), the most recent one (TNASS 2007, CODA, SNESSA) extending across the whole North Atlantic from the east coast of North America to the European west coast (NAMMCO, 2009). In all these surveys, the CNA (Donovan, 1991) has been covered by Icelandic, Faroese and Norwegian research effort. The Icelandic continental shelf area was surveyed by air using cue-counting methods for abundance estimation (Donovan and Gunnlaugsson, 1989; Hiby and Hammond, 1989; Borchers et al., 2009; Pike et al., 2011a). Offshore waters of the CNA were covered by vessel surveys using conventional line transect methods (Sigurjónsson et al., 1989, 1991; Pike et al., 2009a, 2010b; Víkingsson et al., 2009). In addition to the above, full scale aerial surveys were conducted in Icelandic waters in 1986 and 2009 (Gunnlaugsson et al., 1988; Pike et al., 2011b).

The common minke whale was the primary target species of the aerial surveys covering Icelandic continental shelf waters, while the fin whales was the primary target species in the shipboard component covering Icelandic and adjacent offshore waters. The timing of the surveys was roughly the month of July, corresponding to the assumed peak abundance of the main target species, fin and common minke whales. The sei whale (*Balaenoptera borealis*) was a target species of the 1989 survey that had no aerial component and took place around 2 weeks later and extended further south than the other surveys (Sigurjónsson et al., 1991). The analysis presented here was largely confined to the CNA, an area that received a fairly systematic coverage by Iceland and the Faroes. To account for variable coverage within this area, post-stratification was applied for analysis of trends (Víkingsson et al., 2009). For comparisons within the shelf area, southern Icelandic waters were represented by aerial survey blocks 1, 2, 8, and 9 and northern Icelandic waters by blocks 4–7 (for delineation of aerial survey blocks **Figure 6**). **Table 1** summarizes the aerial and shipboard surveys on which the analyses presented here are based.

Data on the catch distribution of fin whales were retrieved from the official databases of the MRI and the Icelandic Fisheries Directorate. Prior to the pause in fin whaling 1990–2005, positions were reported in squares (0.5° latitude × 1° longitude) used in the fisheries sector (Sigurjónsson, 1988) but, since 2006, more precise positions (to the nearest minute of latitude and longitude) have been reported.

Modeling of fin whale distribution

The large-scale link between fin whale distribution and its habitat in the Northeastern Atlantic was investigated by modeling the relationship between whale abundance and environmental covariates. Data on fin whale abundance were derived from the five Faroese and Icelandic line transect cetacean sighting surveys conducted from 1987 to 2007 (Lockyer and Pike, 2009). Transects were divided into effort segments, each of which ended when there was a change in survey conditions (sea conditions, weather) or a sighting. Data on cetaceans sighted included species, group size, and radial distance and angle to the group (Víkingsson et al., 2009).

In a first step, the detection probabilities, $\widehat{p}$, of fin whales in each effort segment were estimated using the DISTANCE 6.2 software package (Thomas et al., 2010). Covariates available to improve precision and reduce bias in estimating detection probability included: sea conditions (Beaufort scale), weather index, visibility, vessel identity (nine vessels or three categories according to platform height), number of observers and group size. The weather index reflected the cloud cover as well as the amount of precipitation or fog and occasionally included wind direction. The final detection function was chosen by minimizing Akaike's Information Criterion (AIC) and by comparing the Cramér-von Mises goodness of fit test statistics (Thomas et al., 2010) and, all other things being equal, the precision of estimated average detection probability. Perpendicular distances were right truncated at 4000 m to improve detection function model fit; beyond this distance sightings were sporadic (Thomas et al., 2010). Only sightings with species identification of high and medium certainty were included in this analysis. Searching effort and sightings made in sea conditions greater than Beaufort scale 5 were excluded.

Abundance of fin whales, $\widehat{N}$, in each effort segment, *i*, was estimated using the Horvitz-Thompson estimator:

$$\widehat{N}_i = \sum_{j=1}^{n_i} \frac{1}{\widehat{p}_{ij}}$$

where n_i is the number of fin whales observed in the i^{th} effort segment and $\widehat{p}_{ij}$ is the estimated probability of detection of the j^{th} detected group in segment *i*.

Covariate data available to model the influence of environmental features on fin whale abundance included physiographic, remotely sensed and reconstructed data (**Table 2**). Some covariates of interest, especially salinity and chlorophyll a, could not be included because some survey years pre-dated the use of certain satellite sensors (e.g., SeaWIFS operated only since 1997). Satellite altimetry data date back only to 1993; however, a sea surface height (SSH) data set from 1950 to 2009, reconstructed based on *in situ* tide-gauge records, was made available by Meyssignac et al. (2012). This dataset had global coverage up to 70°N, which led to the exclusion of a minimal number of effort segments further north. Depth, slope, seabed aspect and distance covariates were linked to effort segment midpoints in Manifold 8.0. Sea surface temperature (SST) and SSH values were assigned to effort segment midpoints by interpolating the value from four surrounding cells based on coordinates and time using R 3.0.1 (R Core Team, 2013).

Multi-panel scatterplots and Pearson correlation coefficients were used to assess collinearity between pairs of covariates (Zuur et al., 2009). Collinearity between two covariates was considered significant when the Pearson correlation coefficient exceeded 0.6. During the model fitting process, only the covariate that explained most of the deviance was retained in the model for covariates identified as collinear.

Table 1 | Survey data used in the analyses of cetacean abundance.

Species	Survey years	Area	Platform	Method	Figure	Source
Common minke whale	1986, 1987, 2001, 2007, 2009	Icelandic continental shelf	Aircraft	Cue counting (A)	5	Borchers et al., 2009; Pike et al., 2009b, 2011a
Common minke whale	1986, 1987, 1995, 2001, 2007, 2009	Icelandic continental shelf	Aircraft	Line transect densities (R)	6 and 7	Pike et al., 2009b, 2011b
Fin whale	1987, 1989, 1995, 2001, 2007	Central North Atlantic	Vessels	Line transect (A)	8	Sigurjónsson et al., 1989, 1991; Víkingsson et al., 2009; Pike et al., 2008
Fin whale	1987, 1989, 1995, 2001, 2007	Central North Atlantic	Vessels	Habitat modeling (R)	9	MRI database
Humpback whale	1986, 1987, 1995, 2001, 2007, 2009	Icelandic continental shelf	Aircraft	Sighting rates (whales/nm) (R)	12	Pike et al., 2009b, 2011b
Humpback whale	1987, 1995, 2001, 2007	Central North Atlantic	Vessels	Line transect (A)	12	Pike et al., 2010c

A, Estimated absolute abundance; R, Relative abundance; Figure, Figure numbers in this article. Source: References to reports giving details of data and methods.

Table 2 | List of physiographic and environmental covariates considered for inclusion in the model as explanatory variables.

Name	Description	Source
PHYSIOGRAPHIC VARIABLES		
Depth	Sea bed depth (m)	ETOPO1 1 arc-minute gridded global relief data. NOAA National Geophysical Data Center. http://www.ngdc.noaa.gov/
Slope	Slope(°) of the sea floor	Derived from ETOPO1 bathymetric data using transform surface dialog in Manifold 8.0
Aspect	Aspect (−180, 180) of the sea floor	Derived from ETOPO1 bathymetric data using transform surface dialog in Manifold 8.0
Distance to isobaths (Dist0, Dist200, Dist2000)	Distance of the effort segment midpoint to the coast, the 200 m deep isobath and the 2000 m deep isobath	Calculated in Manifold 8.0 using SQL queries
REMOTELY SENSED VARIABLES		
Monthly Sea surface temperature (SST)	Night-time monthly averages of SST (°C) from March to August	4 km Advanced Very High Resolution Radiometer (AVHRR) Pathfinder Version 5. Distributed by PO.DAAC and NODC http://podaac.jpl.nasa.gov/
Current Sea Surface temperature	Night-time current monthly average SST (°C) at the time of the cetacean survey	4 km Advanced Very High Resolution Radiometer (AVHRR) Pathfinder Version 5. Distributed by PO.DAAC and NODC http://podaac.jpl.nasa.gov/
RECONSTRUCTED VARIABLES		
Sea surface height (SSH)	1° × 1° annually averaged sea surface height (m)	Meyssignac et al., 2012

The relationship between estimated abundance of fin whales and environmental covariates was modeled using Generalized Additive Models (GAMs) (Hastie and Tibshirani, 1990). GAMs are commonly used to relate distribution or abundance of animals to environmental characteristics due to their greater flexibility compared to Generalized Linear Models (GLMs) (Wood, 2001).

A GAM for abundance data with log link function was used with the general structure:

$$\widehat{N}_i = exp[\theta_0 + \sum_k f_k (X_{ik})]$$

where θ_0 is the intercept term, f_k are the smoothed functions of the explanatory covariates, and X_{ik} is the value of the k^{th} explanatory covariate in the i^{th} segment.

As is common with such data, the response variable, $\widehat{N}$, was overdispersed with a higher proportion of zeroes and of relatively large values than expected if the data were Poisson distributed. Models have been developed to deal with zero-inflated data (Barry and Welsh, 2002; Warton, 2005); however, a quasi-Poisson or negative binomial error distribution are appropriate when fitting models to overdispersed count data (Ver Hoef and Boveng, 2007). The Tweedie distribution has also been proposed because it has an additional parameter offering higher flexibility (Miller et al., 2013). These three error distributions, quasi-Poisson, negative binomial and Tweedie, were investigated when fitting the GAMs; quantile-quantile (QQ) plots, plots of Pearson residuals and response vs. fitted values plots were visually assessed to determine the most appropriate error distribution to use.

In models of count data, effort segments of variable length are typically accounted for by using an offset term, which assumes that the effort variable is a linear predictor with coefficient equal to 1 (Wood, 2006). However, in these data the relationship between the response variable and effort segment length did not meet this assumption and the latter was instead included as a smoothed covariate.

Data from surveys may be spatially auto-correlated and, if model covariates do not account for this, residuals may also be correlated leading to underestimated SEs of coefficients and possibly to unwarranted retention of covariates in model selection. A semi-variogram of model residuals from the final GAM plotted against distance between observations was inspected to assess whether there was spatial correlation in the model residuals (Zuur et al., 2009).

Smooth terms were modeled using penalized cubic regression splines with a shrinkage term, which allows smoothers to reduce to 0 degrees of freedom and to be dropped from the model (Wood, 2006). Interaction terms were fitted using tensor product interactions when the main effects were also included in the model. The package mgcv v. 1.8-1 for R was used to fit models (Wood, 2001).

Model selection used a forward stepwise procedure based on three evaluation criteria: (1) model GCV (Generalized Cross Validation) score, which is an approximation to AIC; (2) percentage of deviance explained; and (3) probability that a covariate was included in the model by chance using analysis of deviance tests (Wood, 2001).

For the predictive maps, a grid of 0.5° × 0.5° resolution populated with covariate values was generated in Manifold 8.0 for each survey year over the extent of survey coverage. Predictions of relative fin whale abundance in each grid cell for each survey year were generated in R based on the final GAM model. The point estimates of predicted relative abundance in each grid cell were smoothed into density surfaces using kriging with Gaussian distribution, implemented in Manifold 8.0, for presentation.

CETACEAN PREY SPECIES

Capelin

Capelin is among the most important commercially exploited pelagic fish species in Icelandic waters. The fishery for this species was initiated in the 1960s and continues to date. Acoustic monitoring of capelin distribution and abundance has been conducted by the MRI since 1980 by surveys in autumn and winter and has been reported annually in stock status reports (Marine Research Institute, 2014).

Sand eel

Sand eel have not been subject to commercial harvesting in Icelandic waters. However, they are important as a food source for other fish species, seabirds and marine mammals (Víkingsson et al., 2003, 2014; Lilliendahl and Solmundsson, 2006; Bogason and Lilliendahl, 2009; Vigfusdottir et al., 2013). Attempts to monitor sand eel abundance were not initiated until 2006, in relation to poor breeding success of seabirds in south Iceland. However, auxiliary information can be obtained from stomach content data from haddock sampled during MRI's annual groundfish surveys (Bogason and Lilliendahl, 2009; MRI, unpublished data).

Euphausiids (krill)

Data on euphausiid abundance were obtained from Sir Alistair Hardy Foundation for Ocean Science (SAHFOS) from their Continuous Plankton Recorder (CPR) program (Silva et al., 2014). The CPR collects plankton from vessels of opportunity crossing the North Atlantic along standard routes. The samples are processed, including species identification at SAFHOS (Batten et al., 2003). The northernmost routes of the CPR surveys cover the areas south and southwest of Iceland.

RESULTS

HYDROGRAPHY

Changes in temperature and salinity in the waters south and west of Iceland in recent decades have been characterized by observations from the deepest station in the Faxaflói section west of Iceland (**Figure 2A**). This station is located in the core of the Atlantic water as it flows northwards along the shelf break in the Irminger Current. After the basin wide changes before the mid-1990s, temperature and salinity in the mixed layer started to increase rapidly, demonstrating the increase of water of Atlantic character in this part of the Sub Polar Gyre. Similar changes were observed in temperature further north on the Latrabjarg section (station Lb4 Northwest Iceland) in the northward flow of the branch of the Irminger Current which feeds the inflow of Atlantic water to the area north of Iceland, i.e., the North Icelandic Irminger Current (**Figure 2B**). The rise in temperature was particularly steep between 1995 and 2000 (**Figure 2**). In the following years, these changes are also apparent in the shelf area to the north of Iceland and most markedly as higher winter temperatures (**Figure 3**). Since 1998, winter temperature and salinity were higher than the average for the measurement period (1970–2014) in all years except 2002. In general, a similar but more variable rise in temperature was observed in other seasons. **Figure 4** shows changes in summer temperatures at 200 m depth in the Irminger Sea between 1994 and 2003. Appreciable warming occurred in this period, particularly in the deep water area between the continental shelves of Iceland and Greenland.

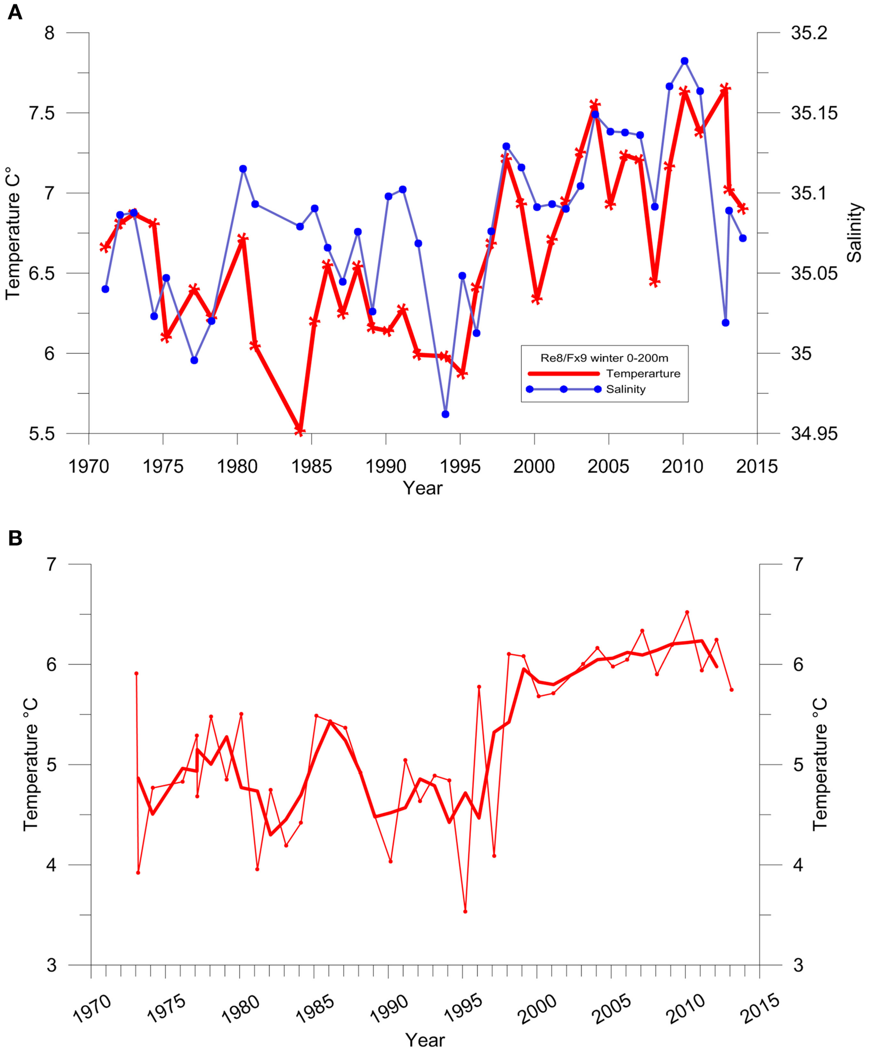

FIGURE 2 | (A) Temperature (red) and salinity (blue) at a repeated hydrographic station, Fx9, in winter at the shelf slope west of Iceland. Dept average over 0–200 m depth. **(B)** Temperature at a repeated hydrographic station, Lb4, in winter at Latragrunn. Depth average over 80–180 m depth. Thick line shows 3-year running mean.

DISTRIBUTION AND ABUNDANCE OF CETACEANS

Common minke whale

Abundance estimates of common minke whales from aerial surveys conducted during 1987–2009 over the Icelandic continental shelf varied widely (**Figure 5**). Point estimates of abundance increased appreciably between 1987 and 2001 although the difference was only marginally significant (Borchers et al., 2009; Pike et al., 2009b). The survey in 2007 revealed a reduction in minke whale abundance to less than half that of 2001 and an extra aerial survey conducted in 2009 showed even further decline in numbers (**Figure 5**).

Figure 6 shows concurrent changes in relative densities (number of whales/nm^2 at the surface) of common minke whales on the Icelandic continental shelf according to the aerial surveys conducted during 1986–2009. As for the estimated abundance, the estimates for the whole survey area show a slightly increasing, but non-significant trend within the range of 0.04 and 0.06 animals/nm^2 between 1986 and 2001. In the next survey (2007), the densities had decreased sharply to less than 0.02 animals/nm^2 and this drop in density was confirmed in the survey conducted in 2009 (**Figure 6**).

The decreased densities after 2001 were evident in most subareas of the aerial survey. However, the degree of the decline was highly variable within the continental shelf stratum with the steepest declines in southern and western coastal waters (**Figure 6**). **Figure 7** compares the mean densities of the southern (blocks 1, 2, 8, and 9) and northern (blocks 4–7) survey blocks for the periods 1986–2001 and 2007–2009. In the earlier period, mean density in the southern/western area was more than double that of the northern area. In the later period, density in both areas declined to about the same level; thus the decline was much steeper in the southern area (79%) than in the northern area (46%).

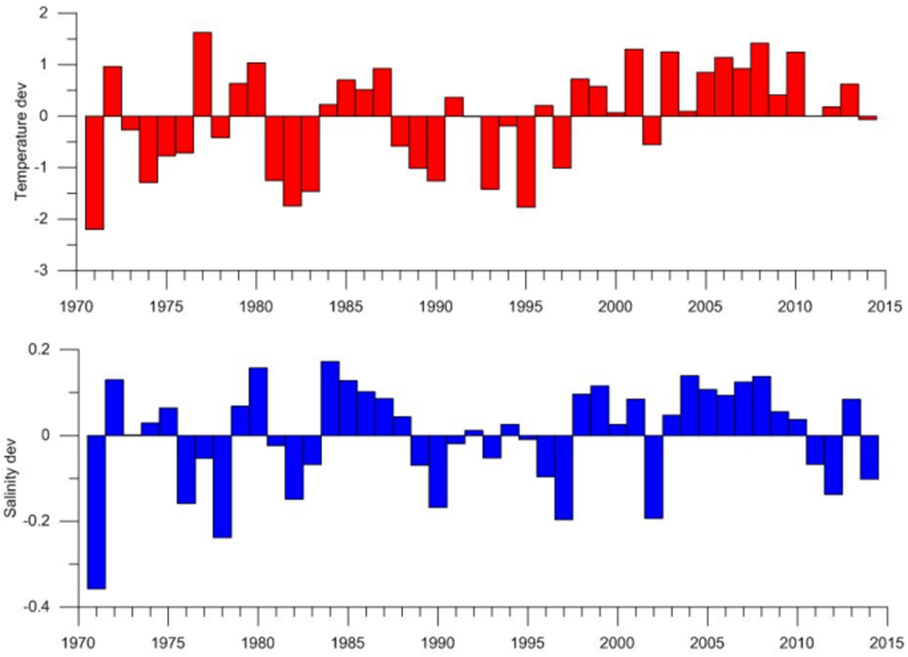

FIGURE 3 | Temperature and salinity deviations from Siglunes section north of Iceland 1970–2013. Deviations are from depth average and mean from stations Si2–Si4.

Fin whale

The estimated abundance of fin whales increased during the survey period from 15,200 in 1987 to 20,600 in 2007 (**Figure 8**). During 1987–2001 the annual increase in the total CNA was estimated as 4%, while the annual growth rate was estimated as 10% in the Irminger Sea between Iceland and Greenland (Víkingsson et al., 2009).

In the habitat modeling, the covariates retained in the final GAM included smooth functions for SST, SSH and survey effort segment length, and an interaction term between depth and distance to the 2000 m isobath. A negative binomial error distribution with log link function was identified as the best description of the data. Pearson correlation coefficients showed high collinearity between all monthly SST covariates ($r = 1$, $p < 0.0001$), and between all combinations of Depth, Dist0, and Dist200 ($r > 0.7$, $p < 0.0001$). Accordingly, only one SST covariate and one of Dist0, Dist200, or Depth were included in the final model. The semi-variogram indicated that there was no spatial correlation in the model residuals (**Supplementary Figure 1**).

The results of the final model, which explained 15.7% of the deviance, are given in Supplementary Table 1. **Figure 9** shows the fitted smooth function for each covariate included in the final model. The probability of sighting fin whales decreased with increasing segment length, supporting the decision to include effort as a smoothed covariate rather than an offset term (**Figure 9F**). SST in the study area at the time of the surveys ranged from 2.5°C to 15.7°C and the highest probability of encountering fin whales was predicted to be in waters with surface temperatures between 5 and 11°C peaking around 6–7°C (**Figure 9D**). Fin whales were less likely to be observed at greater distances from the 2000 m isobath and in shallower waters (**Figures 9B,C**). This pattern was also reflected in the interaction between these two covariates (**Figure 9A**). Sightings were mainly made at intermediate SSH of 0.02–0.04 m elevation as well as in waters with SSH depressions greater than 0.05 m (**Figure 9E**).

The Irminger Sea and the area northeast of Iceland were predicted to hold the highest abundance of fin whales in all years (**Figures 10A–E**), except in 1989 when the area north of Iceland was not surveyed (**Figure 10B**). Within the Irminger Sea, fin whales were predicted to be mostly concentrated along the 2000 m isobath. Predicted relative abundance was high along the East Greenland shelf particularly in 2001 and 2007. The area west of the British Isles had consistent low predicted abundance of fin whales. These predictions were overall in agreement with the observations of fin whales.

As noted previously (Pike et al., 2008; Víkingsson et al., 2009), the distribution of fin whales has changed in the Irminger Sea. Whales aggregated over the continental slope in 1987, 1989, and 1995, but were dispersed throughout the Irminger Sea in 2001 and 2007. The model failed to explain the high number of sightings south of Iceland in 1989 (**Figure 10B**).

Since the resumption of fin whaling in 1948 the operation has been limited to a single land station in Hvalfjörður, West Iceland (Sigurjónsson, 1988). Because of factory regulations concerning freshness of products, catches have been limited to approximately 24 h cruising distance from the station. The distribution pattern of the fin whale catches has been rather stable and largely confined to areas close to the continental slopes of the Irminger Sea west of

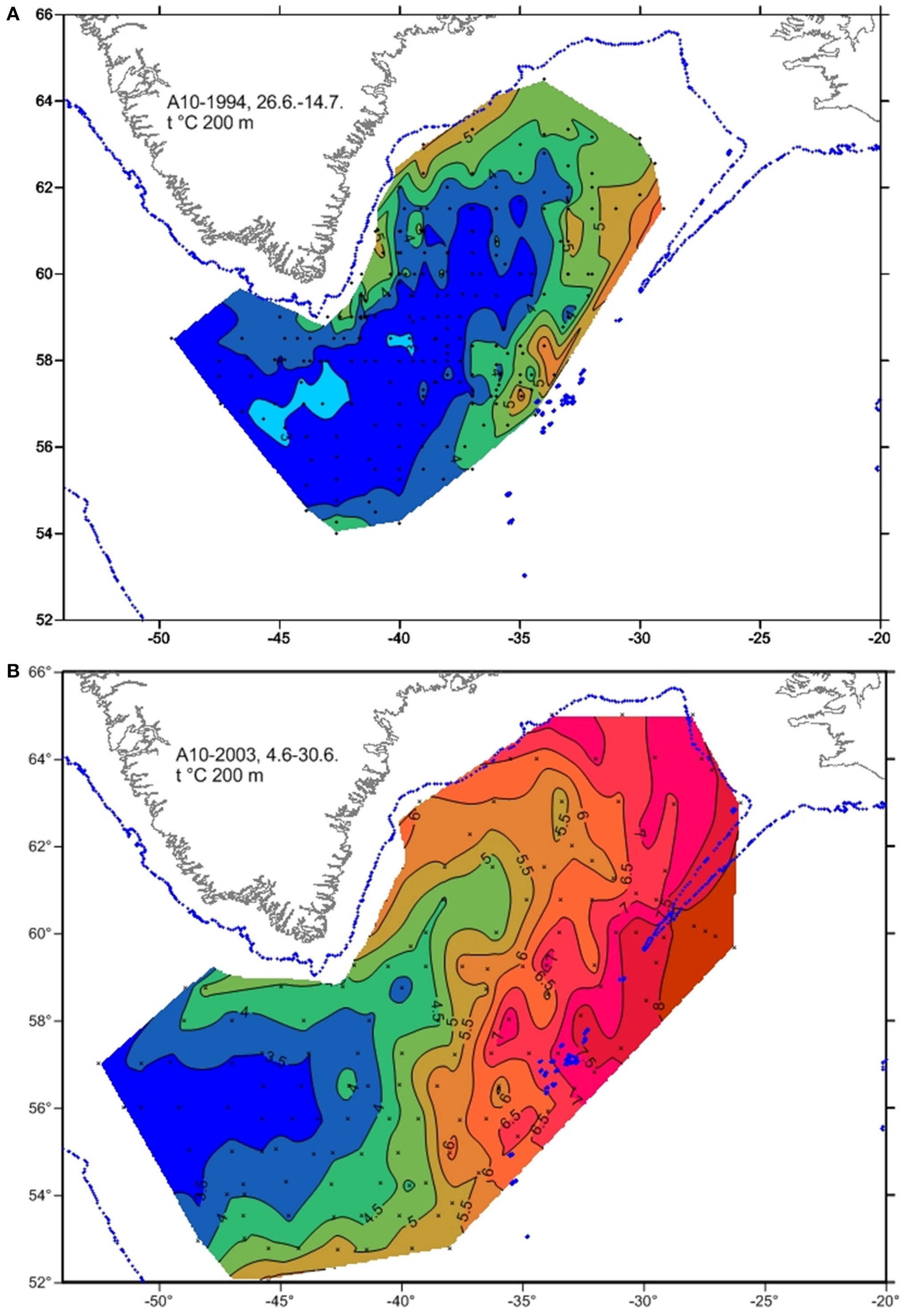

FIGURE 4 | Sea temperatures at 200 m depth in the Irminger Sea in June 1994 (A) and 2003 (B).

Iceland (**Figure 11**). The catch distribution of sei whales has been somewhat wider including areas further east along the southern coast of Iceland. The catch distribution of fin whales in 2014 differed appreciably from all the previous seasons since 1948. During 16–26 June, 26 fin whales were caught within the traditional fin whaling grounds west and southwest of Iceland. In the following 2 weeks only two fin whales were caught in this area despite considerable search effort. After widening the search area fin whales were found in high densities in offshore south Icelandic waters. During the rest of the season, 13 July-23 September 2014, 104 fin whales were taken in these "new" fin whaling grounds and four in the traditional grounds (**Figure 11**).

Humpback whale

Figure 12 shows the estimated relative abundance of humpback whales from the 1986–2009 aerial surveys and estimated absolute abundance from the 1987–2007 shipboard surveys. Both indices show an increase in the point estimates from 1986/1987 to 2001 with a slight decrease thereafter. However, confidence intervals are wide and the estimates since 1995 are not significantly different from each other.

CETACEAN PREY SPECIES

Sand eel

Figure 12 shows the average number of sand eel in haddock stomachs sampled during the annual Icelandic groundfish surveys

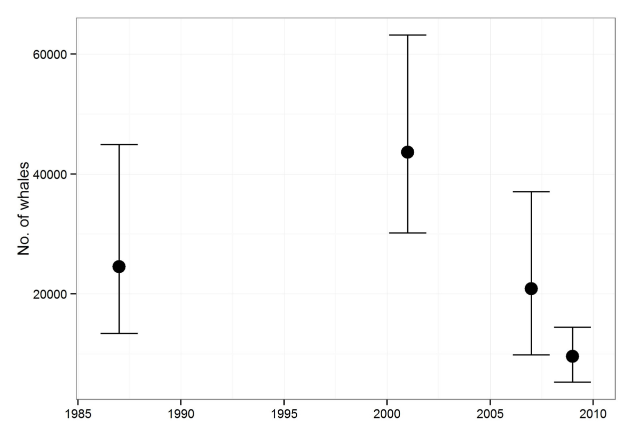

FIGURE 5 | Abundance estimates (with 95% confidence intervals) of common minke whales in the Icelandic continental shelf area derived from aerial surveys conducted during 1987–2009.

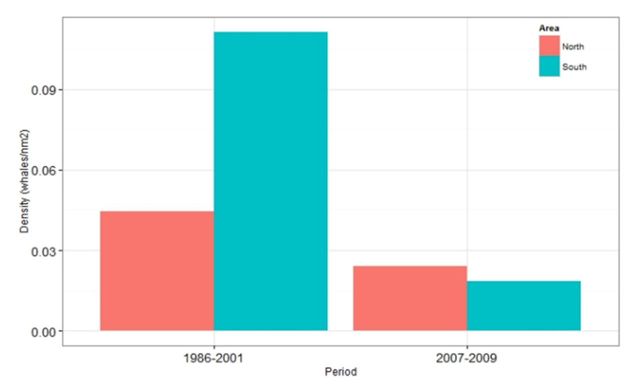

FIGURE 7 | Comparison of changes in densities (Number of animals/nm^2) of common minke whales in northern (blocks 4–7) and southern (blocks 1, 2, 8, and 9) coastal Icelandic waters. For delineation of aerial survey blocks see **Figure 6**.

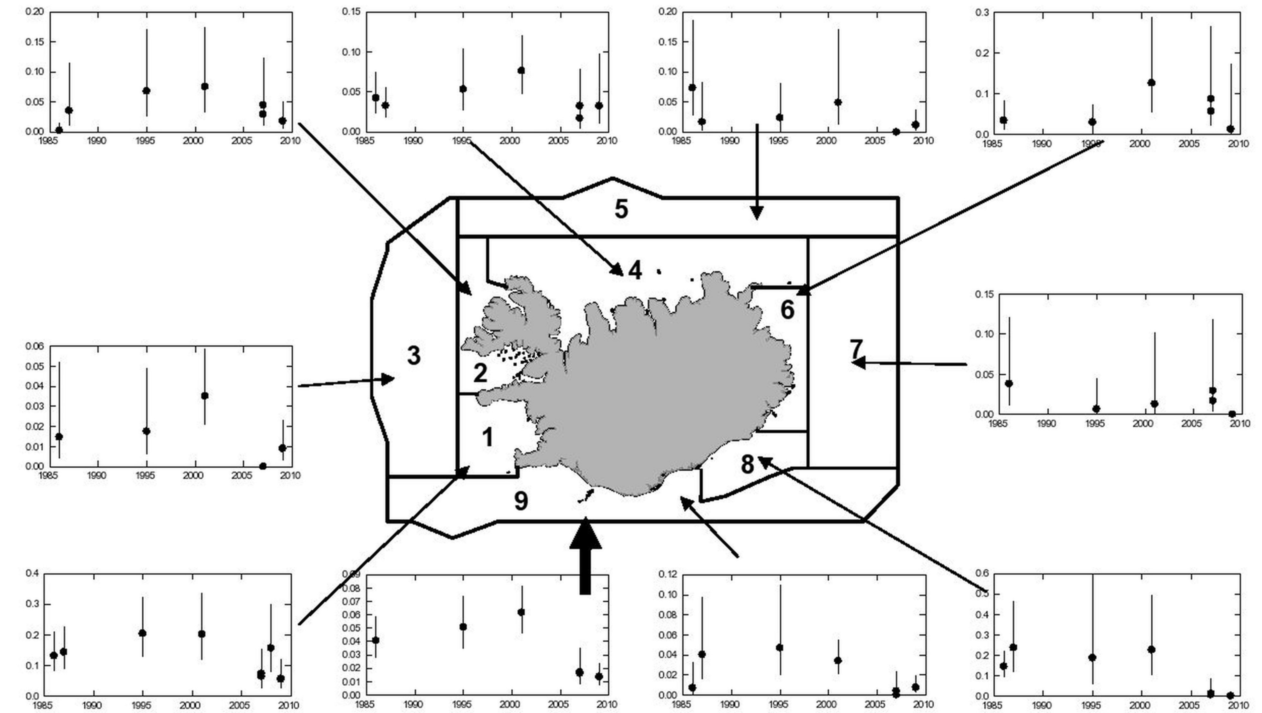

FIGURE 6 | Trend in relative abundance (number of whales/nm^2 at the surface with 95% confidence intervals) of common minke whales, 1986–2009, as indicated by line transect density in the Icelandic aerial survey area. Two estimates, using both primary observers, and a single primary observer, are shown for 2007 and 2009. The thick arrow refers to the total survey area.

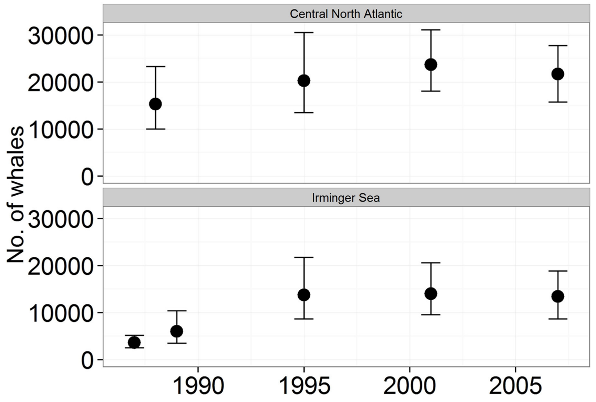

FIGURE 8 | Abundance (with 95% confidence intervals) of fin whales according to the North Atlantic Sightings Surveys 1987–2001 in the total Central North Atlantic stock area (upper) and in the Irminger Sea west of Iceland (lower). For area delineations see Víkingsson et al. (2009).

1997–2010. Sand eel numbers decreased sharply from around 3/stomach in 1997 to 0 in 2004. In all subsequent years except 2007, the mean number of sand eel per stomach was less than 0.25 (**Figure 13**).

Capelin

A major shift in distribution and migration pattern of capelin appears to have taken place around the turn of the century (**Figure 14**). A northward shift in distribution of 0-group capelin away from the Icelandic continental shelf waters north off Iceland was first observed in 2003, coinciding with the onset of a greatly reduced recruitment to the capelin stock (Pálsson et al., 2012a,b, 2014). This situation seems to have prevailed ever since (Marine Research Institute, 2014). The distribution of adult capelin has also shifted westwards toward the coast of Greenland (**Figure 14**).

Euphausiids

Figure 15 shows total abundance of euphausiids in South Icelandic waters (area A6 in Silva et al., 2014) during 1958–2007 as recorded by the CPR. A significant decreasing trend was observed in this period (simple linear regression $r^2 = 0.25$, $p < 0.001$).

DISCUSSION

During the past two decades, pronounced changes have occurred in the marine environment around Iceland. Following 1995, an increase in temperature and salinity was observed in the waters south and west of Iceland (**Figure 2**), which prevailed for almost two decades and has been reflected in the biota (see below). Generally, salinity and temperature have also been higher in the waters north of Iceland since the late 1990s (**Figure 3**). These changes have been linked with the changed distribution and recruitment of capelin north of Iceland (Pálsson et al., 2012a,b, 2014). Concurrent with increasing temperatures and salinity and a northward shift of fronts following increased flow of Atlantic water to the areas north of Iceland, marked changes have occurred in the distribution of several fish species, including a northward shift in haddock and monkfish (Astthorsson et al., 2007; Solmundsson et al., 2010; Valdimarsson et al., 2012). At the same time an expansion in mackerel distribution westwards and northwards into Icelandic waters took place (Astthorsson et al., 2012). Due to the large size of the stock, this "mackerel invasion" into Icelandic waters represents a substantial change in the ecosystem of the Icelandic continental shelf. In addition, 0-group fish of the cold-water species capelin retreated northwards on the Icelandic shelf while the mature component has progressively spread along the shelf break off East Greenland (Vilhjalmsson, 2007; Pálsson et al., 2012a). The sand eel population off southern and western Iceland has been in decline and was drastically reduced around 2005 because of recruitment failure (Bogason and Lilliendahl, 2009). The oceanographic and ecological changes are both likely to have contributed to the changes observed in distribution and abundance of several cetacean populations.

COMMON MINKE WHALES

Densities of common minke whales in the Icelandic continental shelf area decreased markedly between 2001 and 2007 and the estimated abundance in 2009 was less than a quarter of that in 2001 (**Figure 5**). The shipboard component of the 2007 survey failed to detect a corresponding increase in abundance of minke whales in the offshore regions of the CNA stock area, although large areas north of Iceland and along the coast of East Greenland received no or poor coverage due to unfavorable weather and ice conditions (Pike et al., 2010a). Therefore, the details of a potential shift in distribution are unknown.

Investigations of stomach contents of minke whales have shown pronounced changes in diet composition in recent decades. During 1977–1997, sand eel was the predominant prey in southern and western Iceland while capelin occurred in 42% and euphausiids in 58% of the stomachs in the northern areas (Sigurjónsson et al., 2000). During 2003–2007 a significant change had occurred in the minke whales' diet composition with the contribution of euphausiids and capelin decreasing from 45 to 17% and 36 to 22%, respectively in comparable areas (Víkingsson et al., 2014). The proportions of large gadoids [mainly haddock and cod (*Gadus morhua*)] and herring increased coincidently between these two periods. The overall percentage of sand eel in minke whale stomachs was still high in the latter period, but decreased appreciably within the period from 90% in 2003 to 20% in 2007 in the southern areas (Víkingsson et al., 2014).

These dietary changes coincide well with the documented changes in the local abundance of the prey species sand eel, capelin and euphausiids (Astthorsson et al., 2007; Marine Research Institute, 2014). The massive decrease in sand eel abundance during 1997–2003 indicated by the analyses of haddock stomachs is supported by decreased breeding success of sand eel-dependent seabirds in southern Iceland (Lilliendahl et al., 2013; Vigfusdottir et al., 2013). The subsequent low levels of sand eels in minke whale stomachs are in agreement with data from a sand eel monitoring program initiated in 2006 (Bogason and Lilliendahl, 2009). The decreased proportion of capelin in the minke whale diet is also consistent with lower availability of capelin in north Icelandic waters during summer (**Figure 14**) and the increased contribution of haddock and herring reflects growth in these stocks (Marine Research Institute, 2014). These diet studies, together with the series of abundance estimates, suggest that

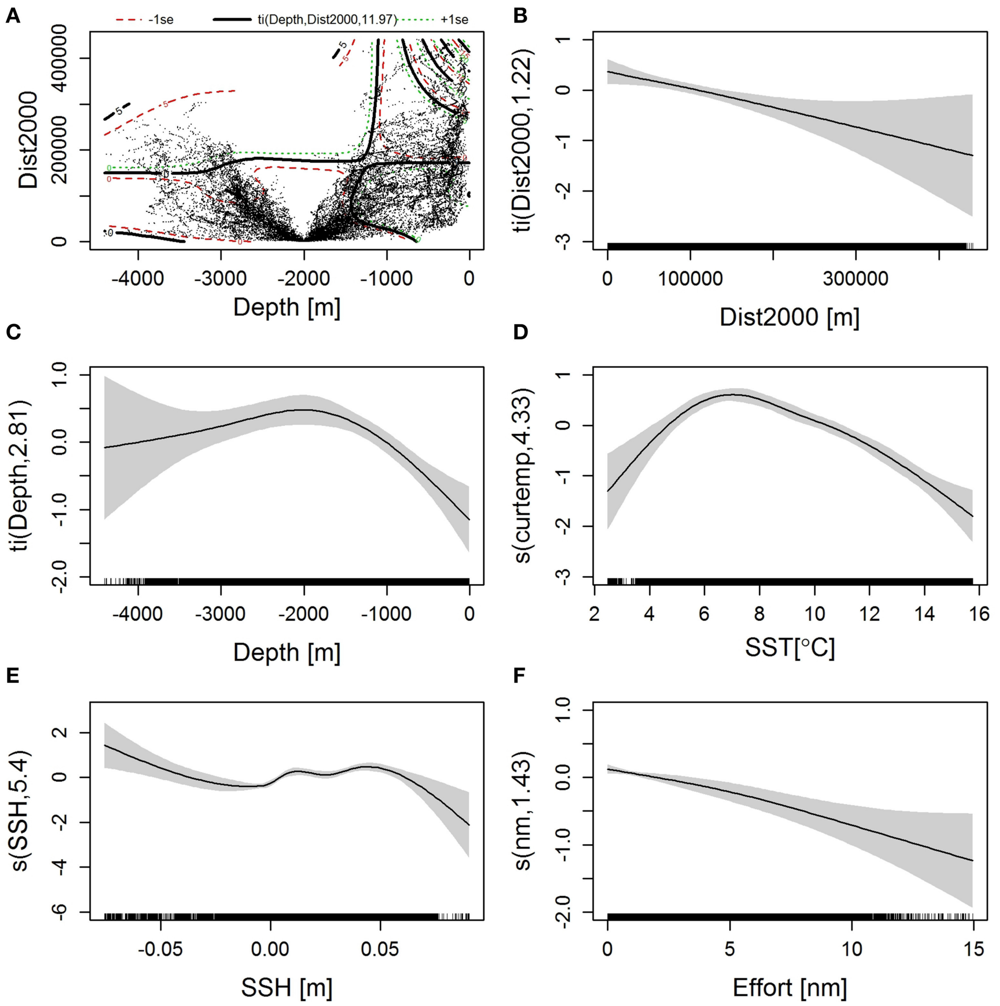

FIGURE 9 | Smooth functions fitted in the final GAM for (A) 2-D interaction between Depth and Distance from the 2000 m isobath, (B) Distance from the 2000 m isobath, (C) Depth, (D) Sea surface temperature, (E) Sea surface height, and (F) survey effort. Positive values of the smoothed function indicate a positive effect on the response variable. In **(A)**, the dots represent values of the response variable, and the black, green and red lines are contours of the fitted function ±1 SE. Given above the plot is the smoother term and the estimated degrees of freedom (see Supplementary Table 1). In **(B–F)**, shaded areas represent the 95% confidence interval. Tick marks on the horizontal axis show the distribution of observations. The vertical axes describe the smoother term and estimated degrees of freedom (see Supplementary Table 1).

minke whales appear to have responded to the environmental changes both by changes in diet and by leaving the Icelandic continental shelf area. While it seems likely that some of the whales followed the capelin to the coast of East Greenland, this cannot be verified because of the lack of coverage of that area by the 2007 survey.

FIN WHALES

The habitat use modeling indicated that fin whale summer feeding areas are characterized by water depth, distance to the 2000 m isobath, SST and SSH (**Table 2**, **Figure 9**). Inter-annual variations in the predicted distribution of fin whales showed that increased use of the Irminger Sea in 2001 and 2007 (**Figures 10D,E**) coincided with an increase in SSH in the area. Sea-level changes are often related to ocean heat-content changes, as water expands with increasing temperatures (Church et al., 2013). The observed changes in SST and SSH over the years have previously been reported to have ecosystem consequences (Ottersen et al., 2001; Häkkinen and Rhines, 2004; Hátún et al., 2009).

While recovery following the pause in whaling in 1990 could be part of the explanation of the increase of fin whale abundance in Icelandic waters, the catch history of the 20th Century and stock assessments suggest that the stock had recovered to a large extent before the period being considered here (Víkingsson et al., 2009). The increase in fin whale abundance in the Irminger Sea between 1989 and 2001 coincided with a marked increase in sea temperature in the area (**Figures 4**, **10**). In particular, the expansion of fin whale distribution into deeper waters (>1000 m) of the Irminger Sea seems to be related to appreciable warming of this area between 1994 and 2003 (**Figure 4**) as noted by Víkingsson

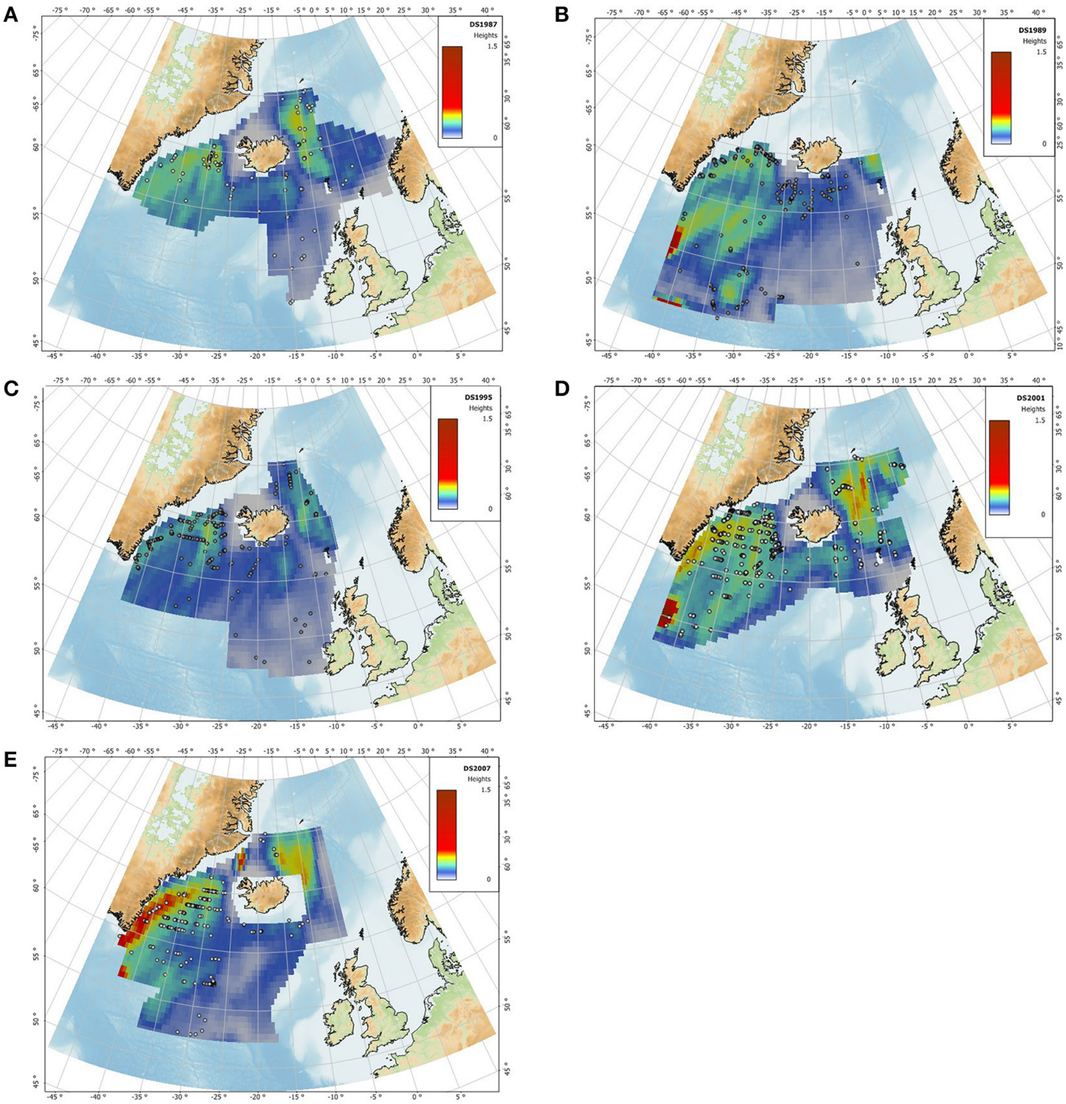

FIGURE 10 | Predicted density surface maps derived from the final GAM with an average segment length of 1.75 nm and SST from July for the survey years 1987 (A), 1989 (B), 1995 (C), 2001 (D), and 2007 (E). Warmer colors indicate higher predicted relative abundance. Dots represent observations of fin whale groups during the surveys. Predicted relative abundance in each grid cell was smoothed using kriging.

and Valdimarsson (2006). Assuming that the diet of fin whales in this area consists overwhelmingly (> 90%) of euphausiids, mainly *Meganyctiphanes norvegica* (Víkingsson, 1997), it is tempting to conclude that the increased temperatures have facilitated growth in euphausiid abundance and thereby increased carrying capacity for fin whales (Víkingsson et al., 2009). However, there has been a decrease in euphausiids in shelf and oceanic habitats southwest, south and southeast of Iceland from 1958 to 2007 with the lowest numbers in each region in 2007 (**Figure 14**), despite increasing primary production in terms of phytoplankton in those areas (Silva et al., 2014).

Results from the habitat modeling presented here support a link between environmental conditions and fin whale abundance. However, environmental data generally act as proxies of other variables, to which the whales respond directly (Pershing et al., 2009). Prey availability often forms the missing link between oceanographic variables and higher-trophic level predators (Croll et al., 2005; Friedlaender et al., 2006; Anderwald et al., 2012). The key to understanding this link is to understand how fin whales respond to changes in prey availability, as well as how prey itself is affected by changing environmental conditions. For instance, the predicted highest abundance of fin whales around the 2000 m isobaths and virtual absence from shallow coastal waters is in accordance with the preference of the fin whale's main prey *M. norvegica* for deeper waters. The observed decrease in *M. norvegica* after 1995 could be an indication of a change in fin whale diet in recent years, similar to the diet shift in minke whales (Víkingsson et al., 2014). Such a shift would explain a less concentrated distribution along the shelf edge and higher observed and predicted numbers of fin whales throughout the Irminger

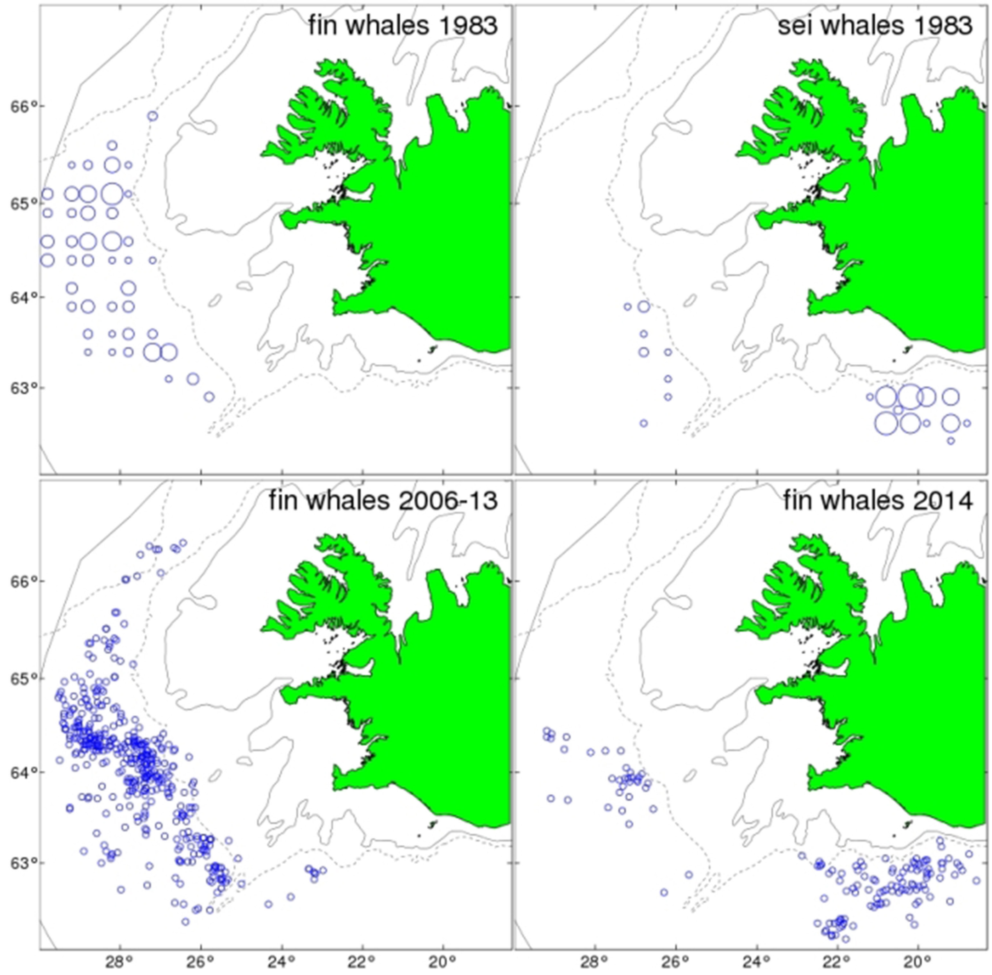

FIGURE 11 | Catch positions of fin whales 1983, 2006–2013, and 2014, and sei whales 1983. Circles for individual whales 2006–2014, but in 1983 whales were reported by squares. Circle area is in proportion to catch numbers in square.

Sea. Increased predation from the growing fin whale population might also have contributed to the decrease in euphausiid abundance.

Unfortunately, euphausiid monitoring by the extensive long-term Continuous Plankton Recorder (CPR, SAHFOS) series only reaches as far north as the waters south and southwest of Iceland and recent Icelandic research has mostly been confined to continental shelf waters where different euphausiid species prevail (Astthorsson and Gislason, 1997). Therefore, these studies are not necessarily representative of the main fin whale feeding grounds west of Iceland. It is noteworthy that while the CPR data show a decrease in adult euphausiid abundance during 1960–2007 (**Figure 14**), there was an increase in the density of euphausiid larvae during 1990–2010 in southwestern Icelandic waters (Silva et al., 2014). While this apparent discrepancy might possibly be explained by the different time frames of these two data series or by a weakened temporal synchrony between the development of young euphausiids and the phytoplankton bloom it would also be consistent with increased predation pressure on adult euphausiids, e.g., by mackerel and fin whales. The warming of the deep waters of the Irminger Sea might also have facilitated growth of other potential prey for fin whales. Updated studies on diet composition of fin whales might clarify this.

Overall, the habitat modeling results suggest that the weakening of the Subpolar Gyre, with associated changes in SST and salinity, had bottom-up effects on primary and secondary production. The poor spatial and temporal overlap between the CPR data and NASS cetacean data precluded the inclusion of krill abundance as a covariate. The explanatory power of the GAM might have been improved if data on prey biomass or primary production had been available because baleen whale distribution has been reported to be tightly coupled with zooplankton density (Friedlaender et al., 2006). However, the dynamic nature of krill requires close spatio-temporal proximity in whale sightings and measurements of krill to detect this trophic link; temporal lags as a result of independently collected prey and cetacean data can weaken the association (Laidre et al., 2010). Further work is therefore required to clarify possible changes in prey availability and diet composition of fin whales.

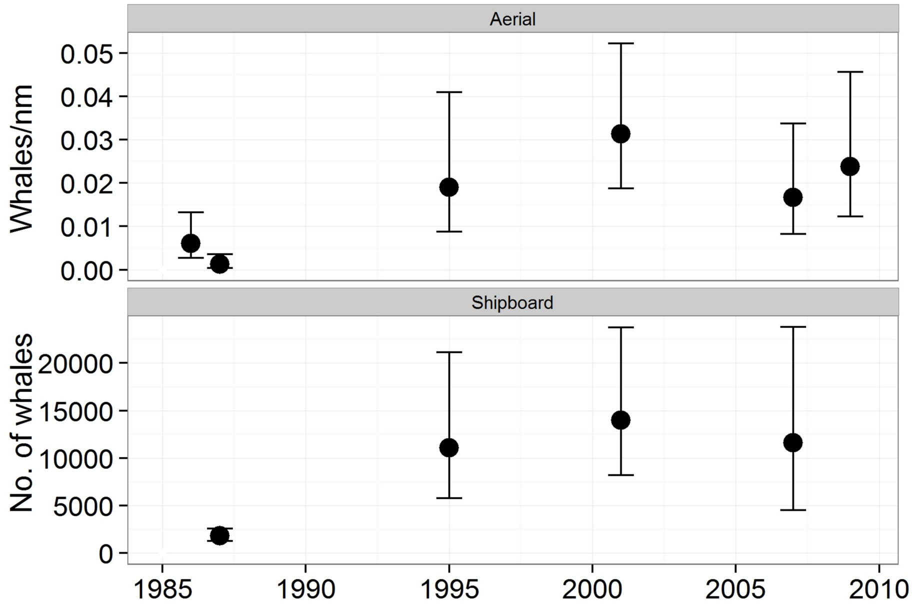

FIGURE 12 | Humpback whale abundance 1986–2009. Sightings rates (animals/nm) in the Icelandic continental shelf area (upper) Estimated total abundance in the Central North Atlantic (lower). Ninety five percent confidence intervals are shown.

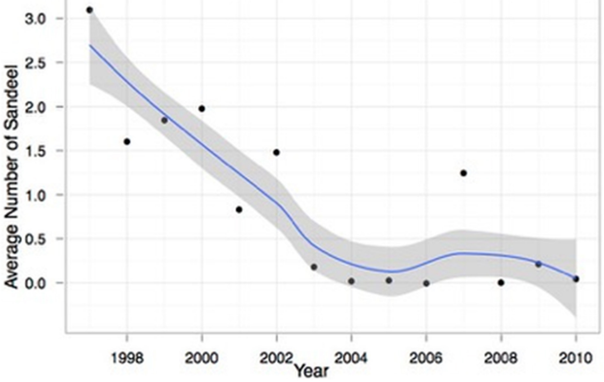

FIGURE 13 | Mean number of sand eel in haddock stomachs analyzed in the Icelandic groundfish survey 1997–2010. A loess smoother has been fitted to the time series, shown with 95% confidence intervals.

The fin whale catch distribution in 2014 was highly unusual with an unprecedented pattern relative to the history of the whaling operation dating back to 1948. Historically, sei whales have been caught in considerable numbers in this area, and these catches would certainly have included fin whales had they been encountered. Therefore, the unusual catch distribution in 2014 seems to indicate a sudden shift in distribution of fin whales between 2013 and 2014. According to the whalers, the traditional western area looked lifeless with no visible krill patches at the sea surface and unusually few seabirds. A notable exception to this was the widespread presence in the area of large schools of mackerel that were clearly visible at the surface. These observations from the whalers have been confirmed by a 2014 ecosystem survey that recorded high abundance of mackerel in the Irminger Sea (Nøttestad et al., 2014).

HUMPBACK WHALES

Catch statistics from the first period of modern whaling in Icelandic waters, the so-called Norwegian whaling period 1883–1915, indicate that humpback whales were hunted down to very low levels. Only six humpback whales were caught after whaling was resumed in 1948 until they received total protection again in 1955. Sigurjónsson and Gunnlaugsson (1990) reported an annual increase in relative abundance of 14.8% during 1979–1988 west of Iceland. This growth rate, coupled with the small absolute abundance estimate of around 2000 humpback whales in 1987 (Gunnlaugsson and Sigurjónsson, 1990) indicates that the number of animals in the area must still have been very small prior to 1970. Pike et al. (2009b) reported annual rates of increase in abundance of 12% for the period 1987–2001.

The most recent data presented here suggest that this rapid growth may have leveled off around the turn of the century (after the 1995 survey). Feeding habits of humpback whales in Icelandic waters are not well corroborated by stomach contents data. However, visual observations have indicated that capelin and euphausiids likely constitute important parts of the diet (MRI unpublished information). In particular numerous reports from capelin fishermen and capelin research cruises have documented substantial numbers of humpback whales following the migration of capelin in Icelandic waters during winter (Gunnlaugsson and Víkingsson, 2014). In recent years, humpback whale songs associated with mating behavior have been recorded in North Icelandic waters (Magnúsdóttir et al., 2014). Although this acoustic activity does not demonstrate that breeding actually takes place in Icelandic waters, an establishment of a new breeding area, in

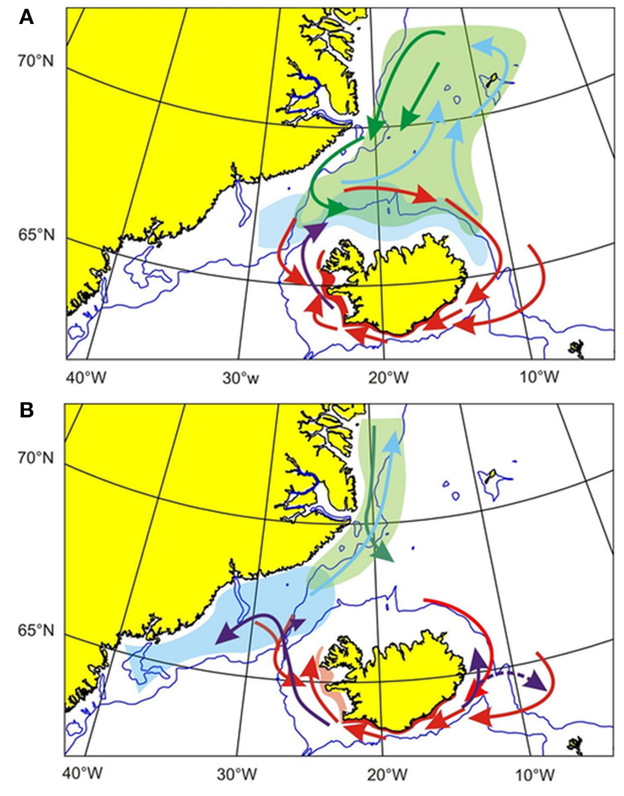

FIGURE 14 | (A) Main patterns in distribution and migration of capelin until the turn of the last century. Light blue, Nursery area; Green, Feeding grounds of adult capelin. Blue arrows indicate feeding migrations and green arrows autumn return migrations toward Iceland waters. Red, Spawning migrations and areas; Violet arrows, 0-group drift (Modified after Vilhjalmsson, 2007). **(B)** A hypothesis for changed patterns of distribution and migration of capelin in recent years. Blue: Nursery area. Green: Feeding grounds of adult capelin, Spring and summer feeding migrations are indicated by blue arrows, but autumn return migrations by green arrows. Red: Spawning migrations (arrows) and main spawning areas. Violet arrows: 0-group drift. (After Pálsson et al., 2012b).

addition to the two known southern breeding areas, could help explain the large population increase in Icelandic waters and the apparent contradiction between abundance estimates at feeding and breeding grounds of the North Atlantic, as discussed by Smith and Pike (2009).

The increase in humpback whale abundance in Icelandic waters, leveling off around the year 2000, follows a pattern similar to the rise in temperature (**Figure 2**). However, it is hard to relate this growth to any known biological changes in the marine environment because the presumed most important prey species (capelin, euphausiids, and possibly sand eel) have not followed the same trends in abundance. In recent decades, high rates of increase have also been documented for humpback whales in several other areas without a clear explanation (Bannister, 1994; Stevick et al., 2003; Findlay et al., 2011; Heide-Jørgensen et al., 2012).

BLUE WHALES

Blue whale populations have not recovered to the same extent as the closely related fin whales or humpback whales, with estimated abundance in the CNA of around 1000 animals (Pike et al., 2009c). However, a significant increase in abundance has been reported for the period 1969–2001 (Sigurjónsson and Gunnlaugsson, 1990; Pike et al., 2009c). During 1987–2001 the increase rate was higher in Northeastern Icelandic waters than west of Iceland (Pike et al., 2009c) indicating a northward shift in relative distribution. Such a shift is consistent with anecdotal evidence from whale watching operations in Icelandic waters. A whale watching company specializing on blue whales was operated from the Snæfellsnes peninsula, West Iceland during 1996–2004. From around 2000, the number of encounters with blue whales decreased appreciably leading the company to give up their blue whale tours in 2004 due to scarcity of blue whales (Pétur Ágústsson, pers. comm). During this period of decline in West Iceland, blue whale sightings increased in the whale watching area Skjálfandi Bay in Northeast Iceland. Photo-identification matches have shown that at least some of the whales previously frequenting West Icelandic waters now occur in Northeastern Icelandic waters during midsummer (MRI, unpublished data).

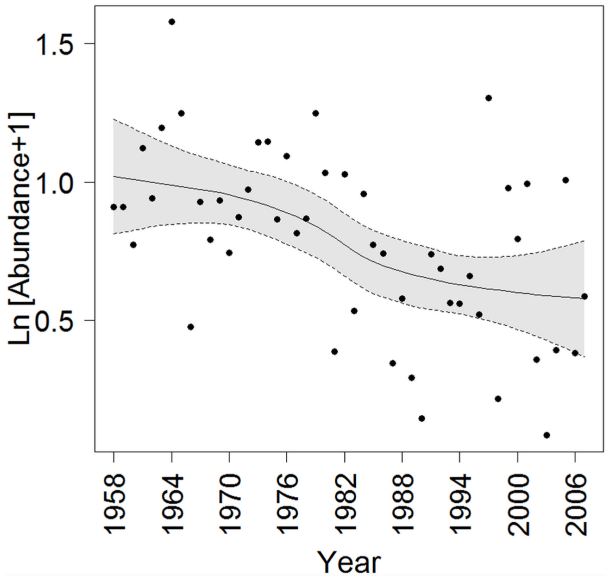

FIGURE 15 | Total euphausiid abundance (Ind m^{-3}) in area A6 from 1958 to 2007 as recorded by the Continuous Plankton recorder (CPR). Abundance values indicate annual averages and a loess curve (span = 0.71) with 95% confidence intervals (shaded gray area) is fitted to the data. Refer to Figure 1 in Silva et al. (2014) for location of CPR area.

CONCLUSIONS

Pronounced oceanographic changes have occurred in Icelandic waters since the mid-1990s, including a rise in sea water temperature and increased flow of warm Atlantic water into the waters north of Iceland. Although the exact mechanisms remain unclear, these changes appear to have caused a northward shift in the distribution of several fish species, a decrease in krill abundance and a collapse in the sand eel population off southern and western Iceland. Considerable changes in distribution and abundance of several cetacean species are apparent from the series of cetacean surveys dating back to 1986. Some of these changes appear to be related to these oceanographic and biological changes while others are harder to explain. Thus, the decrease in common minke whale abundance in the Icelandic continental shelf area seems to be related to the decrease in the abundance of the preferred prey species, sand eel in the southern part and capelin in the northern part. The apparent shift of blue whales from southwestern to northeastern Icelandic waters may be related to the decrease in euphausiid abundance in the waters south and southwest of Iceland.

Concurrently with increasing sea temperature in the deep waters of the Irminger Sea, the distribution of fin whales expanded into this area and the total abundance of fin whales in the Irminger Sea increased. However, the relationship between the rise in temperature and fin whale abundance is unclear. A potential increase in euphausiids, the fin whale's dominant prey species in this area, is not supported by CPR data and could instead indicate that fin whales have switched prey. However, data from the main fin whale feeding grounds are lacking because the CPR data series covers only the southernmost part of that area.

Humpback whales were rare in Icelandic waters throughout most of the 20th century but a significant increase occurred between 1970 and 2001 in the CNA. From 1995, abundance has been rather stable at around 10–15,000 whales. Feeding ecology of humpback whales in Icelandic waters is poorly documented but capelin and euphausiids are known to be among their prey species. It is hard to relate the increased abundance of humpback whales since the 1970s to any known biological changes in the marine environment.

Continued monitoring of the distribution and abundance of cetaceans as well as further studies into their feeding ecology are essential for better understanding of the recent and ongoing changes documented here.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fevo.2015.00006/abstract

Supplementary Figure 1 | Semi-variogram of model residuals from the final GAM plotted against distance between observations in km. Spatial independence shows itself as a horizontal band of points (Zuur et al., 2009)

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