THEME SECTION

Seabirds and climate change

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INTRODUCTION

Seabirds and climate change: roadmap for the future

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ABSTRACT: Based in part on a symposium held at the first World Seabird Conference in September, 2010 in Victoria, BC, Canada, we present a Theme Section (TS) on the topic of seabirds and climate change. We introduce this TS with a meta-analysis of key attributes of the current seabird–climate literature, based on 108 publications representing almost 3000 seabird–climate associations (mostly correlations) published up to 2011. Using the papers in this TS and our meta-analysis, a brief roadmap for the future of seabird–climate change research is presented. Seabird studies have contributed substantially to the literature on marine climate effects. To improve our understanding of climate change effects on seabirds at the global scale, however, additional low-latitude, mechanistic, and 'end-to-end' modeling studies, including integration of climatic, oceanographic, food web, and population dynamics models, should be conducted. This approach will enhance our understanding of the relationship between climate and population dynamics, and facilitate seabird conservation in a changing world.

KEY WORDS: Conference proceedings · Climate effects · Marine birds · Meta-analysis

INTRODUCTION

It is now widely accepted that climate variability and change have strong, persistent effects on marine ecosystems (Stenseth et al. 2002, Harley et al. 2006, Hoegh-Guldberg & Bruno 2010). The Intergovernmental Panel on Climate Change (IPCC) projects mean increases in air temperature of 1.1°C by the 2020s, 1.8°C by the 2040s, and 3.0°C by the 2080s as a result of rising greenhouse gas concentrations (Solomon et al. 2007). Much of this heat will be absorbed by the world's oceans. Already, as a result of past changes in air temperature, heat content of the ocean has increased dramatically (Belkin 2009, Levitus et al. 2009, Burrows et al. 2011). Given ocean warming, coupled with other predicted physical changes including sea level rise and declines in sea ice, effects on marine life are expected to intensify in the coming century. Consequently, the need to improve our understanding of the effects of climate change on various marine organisms has become urgent to facilitate effective species and ecosystem conservation as well as protection of the various ecosystem services that marine environments provide for society (Richardson & Poloczanska 2008, Doney et al. 2012).

Seabirds exist at the ecotone of the atmosphere and the ocean, use both marine and terrestrial habitats, and therefore may be particularly sensitive to multiple and potentially synergistic climate variations. It has been suggested that seabirds are reliable indicators of ecosystem change associated with climatic as well as other anthropogenic and natural factors (Cairns 1987, MEPS 2007, 2009, reviewed by Durant et al. 2009). Seabirds are the most threatened marine taxonomic group in the world, with ~25% of species currently listed as threatened or considered of special concern (IUCN 2011, Croxall et al. 2012). In addi-

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tion to climate change, threats to seabird populations include habitat loss and degradation due to invasive species, coastal development, physiological stressors due to food shortages and pollution, and mortality due to by-catch in certain types of fishing (i.e. Lewison et al. 2012). In relation to climatic factors, effects on seabirds appear to be mostly indirect, operating through changes in local to regional food webs and the pelagic habitat. Seabirds mainly rely on micronekton (forage fish and squids) and mesozooplankton (copepods and krill) for successful foraging. Owing to their lower trophic positioning, micronekton and particularly mesozooplankton are likely more sensitive to climatic variations than upper trophic level species such as seabirds (Richardson 2008). However, changes in the distribution and abundance of prey would have direct effects on seabirds through changes in bottom-up food web dynamics (Ware & Thomson 2005) and predator–prey interactions. At breeding colonies, seabirds could be affected by warming of air temperature and in some cases changes in the timing or intensity of precipitation, which may inhibit access to nesting colonies or, in severe cases, cause mortality due to overheating and physiological stress. How different seabird species will respond to coupled climate and ecosystem change is undoubtedly related to many factors, including life history characteristics, food habits, range, and abundance (e.g. Furness & Tasker 2000). Furthermore, some seabirds may fare well in a warming ocean, whereas others may become locally, regionally, or perhaps even globally extinct (e.g. Kitaysky & Golubova 2000, Jenouvrier et al. 2009, Wolf et al. 2010, Lewison et al. 2012). Fortunately, many demographically comprehensive, long-term studies of seabirds (e.g. Barbraud & Weimerskirch 2001) provide a rich information base for assessments of ongoing and future climatic effects on seabird populations, species, and communities. These studies often include information on food habits, seasonality, and species interactions, so that mechanisms of demographic or distributional change may be properly inferred (Cury et al. 2011).

In anticipation of the next IPCC report, Assessment Report 5, currently scheduled for release in 2014, the purpose of this Theme Section (TS) is to provide a series of up-to-date studies which investigate and evaluate how climate variability and change have affected and may affect seabirds in the future. This TS is based mainly on a symposium held in conjunction with the first World Seabird Conference (WSC) from 7 to 11 September 2010 in Victoria, British Columbia, Canada. The WSC was hosted by the Pacific Seabird Group (PSG) in cooperation with almost 2 dozen other organizations and societies from across the globe (www.worldseabirdconference.com/main.cfm?cid=1813). The papers in this TS investigated how climate variability and change might affect phenology (timing of breeding, migration), breeding or roosting habitat, range, demographic traits (breeding success, survival, recruitment), at-sea distribution, nutritional stress, food habits (diet composition), and community structure of seabirds, covering 10 ecosystems from both the northern and southern hemispheres (Table 1). These variables have been identified as key response types from previous ecological investigations (Sydeman et al. 2009, Weimerskirch et al. 2012). From the onset, we solicited studies that provided quantitative links between trends in the physical environment variables hypothesized to be affected by climate change (i.e. water temperature and stratification, winds and currents, sea level, ocean acidification, and pH), and trends in seabird parameters (see Brown et al. 2011). Most papers in this TS met this goal.

ROADMAP TO THE FUTURE

Meta-analysis

To place the papers of this TS in perspective, we conducted a literature review and provide an initial meta-analysis (cf. Parmesan & Yohe 2003, Rosenzweig et al. 2008) of data gleaned from 108 seabird–climate studies published in primary journals (see the Supplement at www.int-res.com/articles/suppl/m454p107_supp.pdf). We conducted this literature review using the ISI Web of Knowledge based on the following search terms: (1) seabirds climate change, (2) seabirds climate variability, (3) seabird climate trends, (4) seabird climate food availability, (5) seabird climate variation, and (6) seabirds climate. We mined the literature cited sections of prominent authors to find more papers about seabirds and climate change. Inclusion requirements were that each study had to be longer than 2 yr in duration, and authors had to state explicitly that one of their objectives was to explore the effects of climatic factors on a seabird-dependent variable. From these 108 papers, a total of 2877 records of seabird–climate associations (mostly correlations and regression results) were compiled, irrespective of reported statistical significance (though significance was noted). A record is defined as a statistical test between a seabird response (dependent) variable against a climate

Table 1. Scope of papers in this Theme Section, showing spatial and temporal coverage, no. of bird species studied, and the climatic and seabird-related factors that were assessed. GoA: Gulf of Alaska, NAO: North Atlantic Oscillation, SOI: Southern Oscillation Index, PDO: Pacific Decadal Oscillation, AO: Arctic Oscillation, SST: sea surface temperature, NA: not available, (–): not considered

Authors	Ecosystem (latitude)	Time period (no. of years of data)	Spatial variation considered	No. of spp.	Climate factors			Seabird responses					
					Climate index	Regional temperature	Other	Phenology	Diet	Condition/ stress	Breeding	Survival/ mortality	Abundance
Burthe et al.	North Sea (55–58°N)	1983–2006 (24)	No	5	NAO	SST	–	x	x	–	x	–	–
Lynch et al.	Southern Ocean (62–64°S)	1991–2007 (15)	Yes	3	SOI	Air, SST	Sea ice	x	–	–	–	–	–
Surman et al.	Eastern Indian Ocean (28°S)	1991–2010 (2)	No	4	SOI	SST	Sea level	x	–	–	x	–	–
Thompson et al.	Gulf of Alaska (49–50°N)	1996–2009 (11)	Yes	15	–	At depth	Salinity	x	–	–	–	–	x
Provencher et al.	Canadian Arctic (60–74°N)	1976–2009 (10)	Yes	1	–	–	Sea ice	–	x	–	–	–	–
Watanuki & Ito	Japan Sea (44°N)	1984–2009 (21)	No	3	PDO, AO	Air, SST	Wind, currents	x	x	–	x	–	–
Grémillet et al.	Arctic Ocean (70–79°N)	2005–2007 (3)	Yes	1	–	SST	–	–	x	x	x	x	–
Dorresteijn et al.	Bering Sea (56–57°N)	2003–2009 (5)	Yes	1	PDO, AO	–	Sea ice	–	x	x	–	–	–
Satterthwaite et al.	Bering Sea, GoA (52–57°N)	1996–2009 (11)	Yes	1	PDO	SST	Sea ice	–	–	x	x	x	x
Smith & Gaston	Canadian Arctic (63°N)	1988–2007 (21)	No	1	NAO, AO	Air, SST	Sea ice, precipitation	–	x	–	x	x	x
Hass et al.	Western Atlantic (NA)	1893–2003 (NA)	NA	1	–	–	Hurricanes	–	–	–	–	x	x
Sidhu et al.	Southern Ocean (38°S)	1968–2008 (41)	No	1	–	SST	Temperature gradients	–	–	–	–	x	–
Sandvik et al.	Eastern Atlantic (28–79°N)	Variable (12–75)	Yes	29	NAO	NA	Life histories	–	–	–	x	x	x
Barbraud et al.	Southern Ocean (~40–80°S)	Variable (variable)	Yes	Review	Various	NA	Sea ice, wind, currents	x	x	x	x	x	x

(independent) variable. On average, we tabulated ~27 tests per paper, and found that few authors adjusted for multiple tests in their analyses, nor did many authors test or adjust for autocorrelation in climatic or seabird time series. Our search and initial meta-analysis of the seabird–climate literature should not be considered comprehensive; new papers published after 2011 are not included, and literature from certain key regions (e.g. Southern Ocean) is somewhat incomplete due to limitations in our search criteria. However, our review and analysis can be considered representative of the literature on seabird–climate interactions up to 2011. As such, it provides a benchmark with which to evaluate the papers published in this TS as well as a key part of defining a roadmap for the future of seabird–climate research.

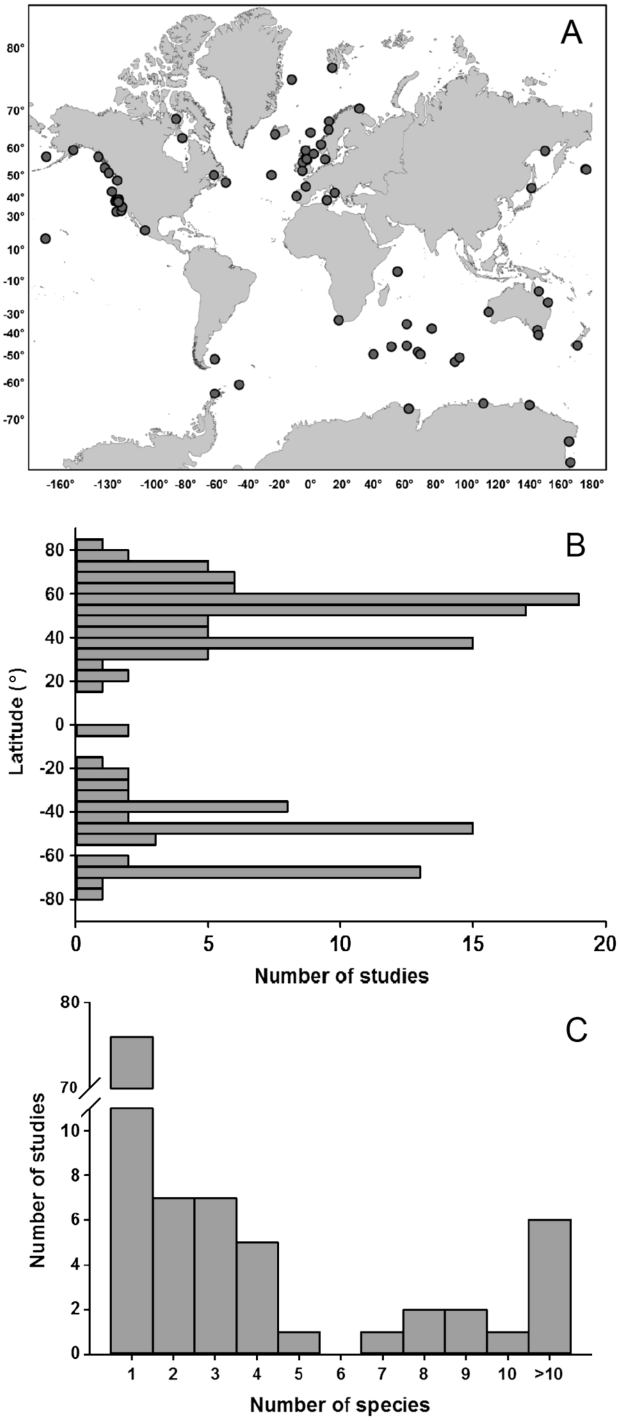

Fig. 1. (A) Study locations, (B) latitudinal distribution and (C) number of species per study in 108 publications on seabirds and climate change

Climate variability versus climate change

We summarized previous studies with respect to the author's objectives and found that 49% of the papers were focused on 'climate variability' whereas 28% emphasized 'climate change', and 23% referred to both climate change and climate variability as objectives. These statistics suggest that about half of the previous studies were intended as studies of climate change effects on seabirds. Note that in this TS, all of the papers were intended to be about climate change, though in some cases, authors explored climate variability as a means to explore potential climate change effects in the future.

Global coverage

With respect to climatic effects, seabirds are a well-known taxonomic group, with study sites distributed around the world (Fig. 1A). Previous studies of seabird–climate interactions are concentrated in the NE Atlantic (North Sea, Norwegian Sea) and off the west coast of North America (California Current to Gulf of Alaska). While studies are widely distributed, there are many regional oceans with little or no information. There are few studies in the large oligotrophic or equatorial upwelling regions of the central Atlantic and Pacific Oceans. In the sub-tropical central Indian Ocean, however, there have been several seabird–climate studies. A summary of latitudinal variation in study location demonstrates that tropical and sub-tropical regions, in particular, are under-represented in the seabird–climate literature (Fig. 1B). Some of the contributions to this TS help to fill some of these gaps in the global coverage of seabird–climate investigations, e.g. for the sub-arctic Bering Sea (Dorresteijn et al. 2012, Satterthwaite et al. 2012), the sub-tropical western Atlantic (Hass et al. 2012), and the sub-tropical eastern Indian Ocean (Surman et al. 2012). More studies in various regions of the world are clearly needed for a global assessment of climate change on seabirds. To that end, some time series of seabird parameters in low-latitude systems have been developed, but have not been analyzed in relation to climate (e.g. Young et al. 2012); we encourage researchers to use or share these data so that key questions pertaining to the effects of climatic factors on seabirds can be addressed for under-studied regions of the world.

Number of species per study

In our review of the literature, we found data on a total of 98 species with an average of 3 species per study, but most studies (53.7%) were conducted on single species at single sites (Fig. 1C). A concern with using single-species studies in meta-analyses is that they may be publication biased, as only data sets demonstrating change might be deemed suitable for publication by journal reviewers and editors. While clearly important for syntheses of climate change effects on seabirds and other taxa, negative (no change) data could be difficult to publish unless combined with positive (change) data for other species. Notably, in previous global-scale meta-analyses on the biological effects of climate change, Parmesan & Yohe (2003) and Parmesan (2007) only used multi-species studies. For a global synthesis of seabird–climate interactions, the number of species per study is a constraint. In this TS, only 2 of 12 original data papers (Sidhu et al. 2012, Smith & Gaston 2012) are based on a single species studied at a single location (Table 1). About half of the papers presented here are based on multiple species, for which both positive ‘change’ and negative ‘no change’ results are reported. The other papers, which focus on single species, all include multiple study sites that allow for tests of spatial variability. The addition of spatial components (e.g. multiple colonies in a meta-population context) greatly enhances the information content (and degrees of freedom) of seabird responses and climatic factors, strengthening inferences regarding detection of change and attribution of observed variability to climatic factors.

Temporal characteristics of previous studies

Somewhat remarkably, 85% of seabird–climate studies reported on continuous (i.e. annual) seabird time series data sets. A total of 10% of previous studies reported on time series which were irregular (i.e. missing some years in an otherwise regular research program) and 4% compared seabird parameters in 2 different time periods. The mean period covered in the 108 papers was ~23 yr, with an average of ~20 years of data per study. In this TS, the longest study covers 41 yr (Sidhu et al. 2012). Statistically speaking, long-term, preferably continuous, studies are required to both detect and attribute change in taxa to climate change. Most methods of robust attribution, including multi-step meta-analysis (e.g. Rosenzweig et al. 2008, Hegerl et al. 2009), are based on multi-decadal time series which facilitate detection of change using statistical trend analyses, as well as integration of physical environmental and biological data that can be used to attribute change to natural and anthropogenic climate signals.

Seabird parameters studied

In previous studies, approximately 88% of the seabird–climate associations involved any of 5 seabird response (dependent) variables: reproduction (e.g. breeding success and other measures of reproductive performance), abundance, survival (of both adults and juveniles), phenology (timing measurements), and adult condition (Fig. 2A). Other measurements, which were more rarely investigated, included chick growth, community change, behavior, and distribution. Notably, distributional change is a key variable often reported for studies of climate change effects on plankton and fish (e.g. Beaugrand et al. 2002, Perry et al. 2005), yet distribution has not been a focus in previous seabird–climate research. In this TS, 8 papers considered change in reproduction, 6 investigated aspects of abundance, 7 considered survival/mortality parameters, 6 involved phenological measurements, 7 considered food habits, 2 included data on body condition, and 2 focused on nutritional stress (Table 1). Thus, we present a balanced set of seabird parameters, and notably a higher percentage than is typical in the literature on diet, a variable that provides direct linkages between changes in the physical and biological environments and seabird populations. However, as found in our meta-analysis, studies of seabird distribution and range shifts in relation to climate change were under-emphasized. Thompson et al. (2012b), however, report on a related topic, namely seasonal variation in distribution and abundance of seabirds in the southeast Gulf of Alaska.

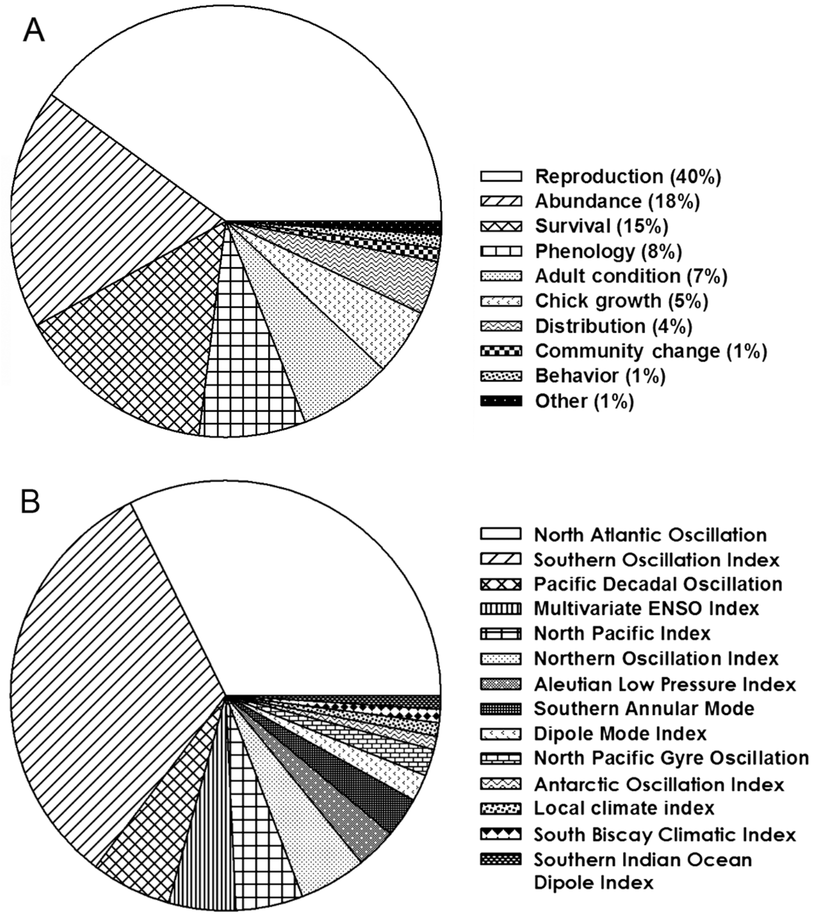

Fig. 2. (A) Seabird responses and (B) climatic indices studied in 108 publications on seabirds and climate change

Climate parameters studied

Based on our meta-analysis, the large-scale climate indices previously studied were dominated by the Southern Oscillation Index (SOI) and North Atlantic Oscillation (NAO); these 2 variables accounted for roughly 2/3 of all seabird–climate records (Fig. 2B). In this TS, the SOI, NAO, Pacific Decadal Oscillation (PDO), and Arctic Oscillation (AO) were all studied in about equal proportions (Table 1); in addition, local and regional air and sea temperature, ice cover and other variables (especially winds and currents) were well-represented. Meta-analysis also revealed that no study to date has considered the effects of ocean acidification (pCO_2 or pH) or de-oxygenation on seabird food resources, despite the fact that these physical variables have garnished significant attention, especially in the past decade (Doney et al. 2012). While basin-scale climate indices often provide strong correlations with seabird variables, understanding mechanisms of change in seabird populations and communities will be facilitated by matching variation in local to regional-scale marine climate with global climate models (GCMs). However, the fact that GCMs provide output on relatively large spatial scales whereas seabirds respond to environmental factors operating at local and regional scales remains a challenge. Moreover, for the oceans, GCMs demonstrate ubiquitous warming, whereas some regions of the oceans, notably eastern boundary current upwelling ecosystems are cooling (Burrows et al. 2011). Therefore, down-scaling and correcting the models to account for regional cooling trends are required before seabird data can be integrated with results from GCMs. Without such inputs from the climate modeling community, attribution of changes in seabird parameters to climate change will remain limited in geographic scope and may lead to biased and erroneous conclusions.

Significance of effects by biome

From our literature review, we categorized previous studies by Longhurst biome (tropical/sub-tropical, transitional, sub-polar/polar; Longhurst 2007) and examined the significance of all climatic factors combined by biome with respect to their effects on seabird variables. Overall, about 31 % of the seabird–climate records obtained in tropical biomes were significant (defined as a statistical test with $p < 0.05$). This declined to about 20 % being significant in the transitional biomes, and 17 % significant in the sub-polar/polar biome (Fig. 3A); these differences were significantly different (logistic regression, $p < 0.05$). As noted in ‘Global coverage’ above, previous studies in tropical/sub-tropical systems were relatively rare, but despite the limited sample size of seabird–climate records in this biome, our analysis suggests that tropical seabird species and populations may be at least as sensitive to climate change as mid- or high-latitude ones. Further research is needed to ascertain whether this observation is robust. In this TS, only Surman et al. (2012) provide new information to enhance the number of tropical/sub-tropical studies worldwide.

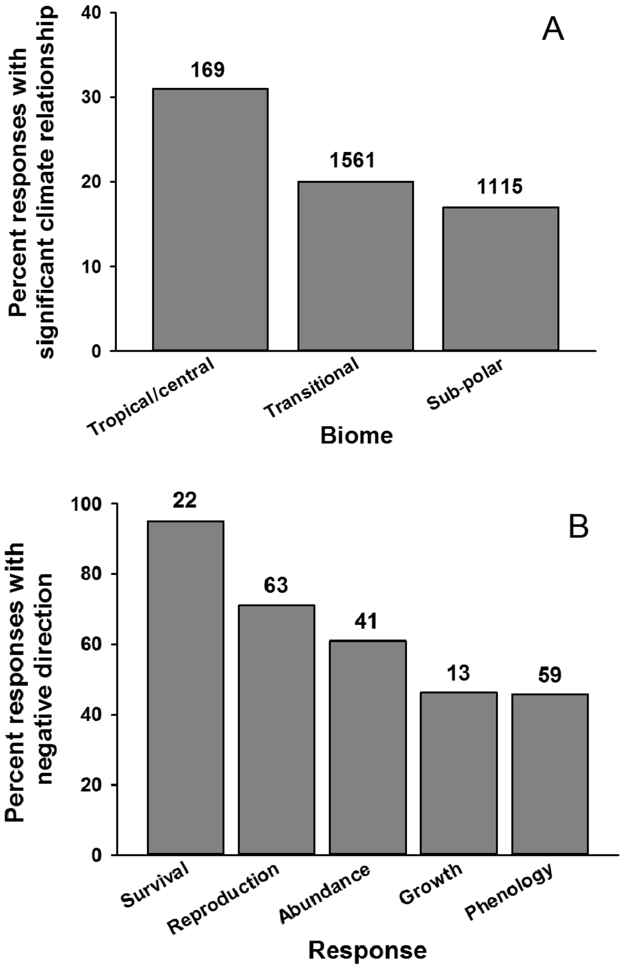

Fig. 3. (A) Percentage of statistically significant ($p < 0.05$) seabird responses to climatic factors by Longhurst biome (Longhurst 2007). (B) Percentage of seabird responses that had a negative relationship with sea surface temperature in the transitional biome by response type. Reproduction: reproductive success. Numbers above bars: sample size (n)

Variation in temperature effects

Within the transitional biome, there were sufficient data to assess the effects of sea surface temperature on a suite of different seabird parameters (Fig. 3B). Survival was almost always (>90% of records) negatively related to increasing temperature, and about 70% of the time reproductive success was also negatively related. In contrast, relationships with temperature were equally positive and negative for relative abundance, growth and condition, and phenology. This variation suggests that general hypotheses concerning climate warming and its effects on marine life (e.g. earlier phenology, poorer reproduction, and pole-ward shifts in distribution; Doney et al. 2012) may not always be applicable to seabirds, or may be associated with multiple mechanisms operating simultaneously (e.g. immigration and shifts in range), with opposing signs in relation to temperature or other climatic factors. Instead, this variation highlights the need to consider regional and local mechanisms to elucidate both positive and negative relationships between climate and seabird parameters.

DISPARATE MECHANISMS OF RESPONSE

Since seabirds are heterotrophic, nektonic marine organisms, it is not surprising that most previous studies of climate variability effects on seabirds suggest indirect mechanisms, operating through variation in water column characteristics (Ainley & Hyrenbach 2010) or food webs and prey availability (Barbraud et al. 2012, Dorresteijn et al. 2012, Thompson et al. 2012a). Direct effects, however, are possible, though these have been under-studied. For example, sea level rise may inundate low-lying breeding colonies, but most low-lying breeding sites are located in the tropics where seabird–climate studies are comparatively rare. Physiological stress due to overheating on colonies is also possible (Gaston et al. 2002, Oswald et al. 2008), but has not been adequately addressed to date, with most authors focusing on water instead of air temperature (but see Lynch et al. 2012, Smith & Gaston 2012, Watanuki & Ito 2012). Climate change-induced increases in wind fields could affect foraging success; in the case of procellarid seabirds which rely on wind for flight capacity, this change may improve foraging success with positive demographic consequences (Weimerskirch et al. 2012). In this TS, the direct negative impacts of wind are demonstrated by Hass et al. (2012), who alert us to the effect of hurricanes on the extinction risk of an endangered species (Table 2). Future studies on direct mechanisms of response in seabirds are warranted.

Indirect effects and food-related mechanisms of response, however, dominate the studies in this TS (Table 2), as they do in the literature. Briefly, the amount of energy available to seabirds in the environment plays a significant role in many, if not most, seabird–climate relationships. Underlying this concept is the assumption of bottom-up food web interactions, i.e. that climate variability and change affect primary productivity with amplified effects to mid- (zooplankton and forage fish) and upper (seabird) trophic levels. In this TS, Burthe et al. (2012), Pro-

Table 2. Major findings of articles in this Theme Section

Authors	Scale	Primary mechanism(s) of response
Burthe et al.	Regional	Temporal mismatch in abundance between trophic levels limits bottom-up energy transfer
Lynch et al.	Local	Change in timing can result in greater interspecific competition for nesting space on colonies
Surman et al.	Regional	Changes in large-scale currents and eddy kinetic energy limit prey availability to breeding birds
Thompson et al.	Mesoscale	Ocean warming and lengthened growing season allow delay of migration
Provencher et al.	Regional	Loss of sea ice alters forage fish community due to reduction in primary productivity
Watanuki & Ito	Local, regional	(1) Arctic winds cause freezing of nesting habitat, restricting access (2) Currents and advection alter forage fish community and prey availability
Grémillet et al.	Regional	Plasticity in foraging behavior buffers response to climate variability and prey availability
Dorresteijn et al.	Regional	Ocean warming causes a change in diet and nutritional stress of planktivorous seabirds
Satterthwaite et al.	Basin	Warming drives nutritional stress-induced mortality of piscivores to the benefit of northern but not southern sites
Smith & Gaston	Regional	Lagged effects of climate variation affect different demographic attributes
Hass et al.	Basin	High wind events cause habitat displacement and mortality
Sidhu et al.	Regional	Increased spatial temperature gradients between water masses affect survival
Sandvik et al.	Basin	Life history trade-offs between survival and reproduction or recruitment predict population response
Barbraud et al.	Basin	Interaction of long-line fisheries bycatch and climate influences populations

vencher et al. (2012), Watanuki et al. (2012), Grémillet et al. (2012), and Dorresteijn et al. (2012) show how seabird food webs are changing in different regions. The changes in food webs, exemplified by changes in seabird diet, sometimes (Burthe et al. 2012) but not always (Dorresteijn et al. 2012, Grémillet et al. 2012, Provencher et al. 2012, Watanuki & Ito 2012) reflect changes in diet quality; often the food web change is driven by species abundance or availability (Dorresteijn et al. 2012). In some cases, these changes affect breeding success or other demographic attributes. Comparison of seabirds operating on different trophic levels may be particularly relevant in this regard. For example, at the Pribilof Islands, Alaska, opposite responses are observed between sympatric planktivorous (Dorresteijn et al. 2012) and piscivorous (Satterthwaite et al. 2012) seabird species to the same changes in the physical environment.

CONCLUSIONS

Based on the literature and supported by this TS, it is clear that seabirds are responding to climate change on a global scale and can contribute to our understanding of climate change effects on marine ecosystems. Yet, our interpretations are limited because despite having some of the best (long-term and comprehensive) biological time series in the marine realm, seabird data sets are still of insufficient duration to separate natural inter-decadal variability from human-induced climate change effects (i.e. Sidhu et al. 2012). Therefore, one of our key recommendations is the need to maintain and possibly enhance existing long-term research and monitoring programs, even in times of financial limitations. These programs are necessary to develop the time series required to provide strong inference concerning seabirds and anthropogenic global warming.

A second key part of our roadmap for the future involves developing better mechanistic hypothesis and testing seabird–climate relationships in a predictive context. As noted in this TS, some mechanisms are apparently stronger than others. In particular, many climate-related effects appear to operate indirectly, with changes to seabird trophic ecology most often proposed as an explanatory mechanism (Table 2). Rarely, however, is concurrent information on prey abundance available to link climate, oceanographic conditions, food resources, and seabird responses. Moreover, for a global assessment of climatic effects on seabirds, we need to investigate and demonstrate such mechanisms across sites and ecosystems. While it is not practical to monitor food resources for many colonies or ecosystems, new physiological tools which directly relate nutritional stress to population processes (Kitaysky et al. 2007, 2010) can be applied on relatively large geographical scales at reasonable expense (Satterthwaite et al. 2012, Dorrensteijn et al. 2012); measurements of the stress hormone corticosterone might be particularly useful in this regard (Barbraud et al. 2012). Also needed, however, is better information about the demography, structure (genetics), and connectivity (dispersal statistics) of seabird populations. As shown by Sandvik et al. (2012), to understand the 'fitness landscape', fecundity and survival need to be measured simultaneously with concurrent measurements of changes in the physical environment. Seabirds may be buffered sufficiently to overcome nutritional deficits and reproduce successfully (Grémillet et al. 2012), but this could come at the cost of their survival.

Third, given the need for a global assessment and greater understanding of mechanisms involving primary productivity and food webs, both physical oceanography and ecosystem science will be a backbone for seabird climate change ecology. We see integration of numerical oceanographic (e.g. Regional Ocean Modeling System [ROMS]), ecosystem (e.g. Nutrient-Phytoplankton-Zooplankton [NPZ] models) and individual-based population dynamics models of seabirds as a fruitful approach. For example, ROMS models could be forced by output from the next generation of GCMs to provide key information about the likelihood of change in pelagic, and perhaps coastal, habitats. NPZ models coupled with ROMS could provide information on key changes in seabird food webs and prey abundance. Finally, population dynamics models could integrate changes in habitat characteristics and food resources in the predictive demographic framework advocated above (this section). In this manner, mechanisms of change (pathways of response) could be articulated and tested mathematically, and subsequently compared and verified using empirical data (Jenouvrier et al. 2009, Wolf et al. 2010). The road map to the future, thus, includes more 'end-to-end' modeling and long-term empirical studies with an emphasis on interdisciplinary research. Only through such an integrative approach will accurate predictions of change in seabird populations be possible, thereby facilitating seabird conservation in a changing world.

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Contribution to the Theme Section 'Seabirds and climate change'

Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web

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ABSTRACT: Differential phenological responses to climate among species are predicted to disrupt trophic interactions, but datasets to evaluate this are scarce. We compared phenological trends for species from 4 levels of a North Sea food web over 24 yr when sea surface temperature (SST) increased significantly. We found little consistency in phenological trends between adjacent trophic levels, no significant relationships with SST, and no significant pairwise correlations between predator and prey phenologies, suggesting that trophic mismatching is occurring. Finer resolution data on timing of peak energy demand (mid-chick-rearing) for 5 seabird species at a major North Sea colony were compared to modelled daily changes in length of 0-group (young of the year) lesser sandeels *Ammodytes marinus*. The date at which sandeels reached a given threshold length became significantly later during the study. Although the phenology of all the species except shags also became later, these changes were insufficient to keep pace with sandeel length, and thus mean length (and energy value) of 0-group sandeels at mid-chick-rearing showed net declines. The magnitude of declines in energy value varied among the seabirds, being more marked in species showing no phenological response (shag, 4.80 kJ) and in later breeding species feeding on larger sandeels (kittiwake, 2.46 kJ) where, due to the relationship between sandeel length and energy value being non-linear, small reductions in length result in relatively large reductions in energy. However, despite the decline in energy value of 0-group sandeels during chick-rearing, there was no evidence of any adverse effect on breeding success for any of the seabird species. Trophic mismatch appears to be prevalent within the North Sea pelagic food web, suggesting that ecosystem functioning may be disrupted.

KEY WORDS: Timing of breeding · Climate change · Prey size · *Ammodytes marinus* · Winter NAO · Long-term studies · Zooplankton · Phytoplankton

INTRODUCTION

Phenology (the timing of seasonally recurring biological events) plays a crucial role in linking organisms to their biotic and abiotic environments (Forrest & Miller-Rushing 2010). Recent climate warming has significantly altered the phenology of a wide range of taxa across ecosystems (Thackeray et al. 2010), but responses frequently vary among species, potentially disrupting the synchronisation of key ecological interactions (Visser & Both 2005). In particular, failure of a predator to overlap the period of peak resource de-

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mand (typically breeding) with peak prey availability may lead to 'trophic mismatch,' and such decoupling may alter food web structure and ecosystems (Cushing 1990, Edwards & Richardson 2004). A recent review found that trophic mismatch was widespread, with predator phenology shifting too little or too much in response to that of prey (Visser & Both 2005).

Marine systems are vulnerable to trophic mismatch because they exhibit highly seasonal pulses of primary productivity upon which the fitness of higher trophic levels depends (Cushing 1990). Studies across multiple trophic levels are rare, mainly because phenological data at the appropriate temporal and spatial resolution are lacking. Most studies have investigated single species responses and are unable to explicitly test for mismatch (Leggett & DeBlois 1994). Studies have also compared phenology of a focal consumer with climate data such as sea-surface temperature (SST; e.g. Durant et al. 2003, Frederiksen et al. 2004a, Shultz et al. 2009) that may indicate variation in prey availability, including phenology, or be used as a cue by predators to predict key phenological events in their prey (Frederiksen et al. 2004a, Moe et al. 2009). Several studies have suggested that mismatch may be an important determinant of fitness in seabirds (e.g. Durant et al. 2006, Hipfner 2008, Watanuki et al. 2009).

Here we examine phenological changes across 4 trophic levels of a pelagic food web in the north-western North Sea from 1983 through 2006. This system has a 'wasp-waist' structure (Cury et al. 2000), with high species richness at upper and lower trophic levels but markedly lower richness at the mid-trophic position linking secondary producers (zooplankton) and top predators (mammals, fish and birds). Lesser sandeel *Ammodytes marinus* occupies this key mid-trophic position (Daan et al. 1990). Over the study period there have been significant hydro-biological changes and increased sea temperatures in this area (Edwards et al. 2002). A major ecosystem regime shift occurred in the late 1980s (Beaugrand 2004), and there have been profound changes in plankton communities (Edwards et al. 2002) and fish distributions (Perry et al. 2005). Previous studies in this area have investigated phenological changes in species from primary producers to top predators and found contrasting patterns suggestive of trophic mismatch (Edwards & Richardson 2004, Wanless et al. 2009, Frederiksen et al. 2011). However, none have adopted an integrated approach and compared multiple trophic levels within the same area over the same time period. A major aim of our study was to use a standardised approach to quantify changes in the timing of key events for species or taxonomic groups across all 4 trophic levels (Fig. 1a). Disparity in phenological trends would be indicative of trophic mismatch in the system. We also assessed whether phenology was related to climate variables (SST and winter North Atlantic Oscillation, wNAO) and if climate responses

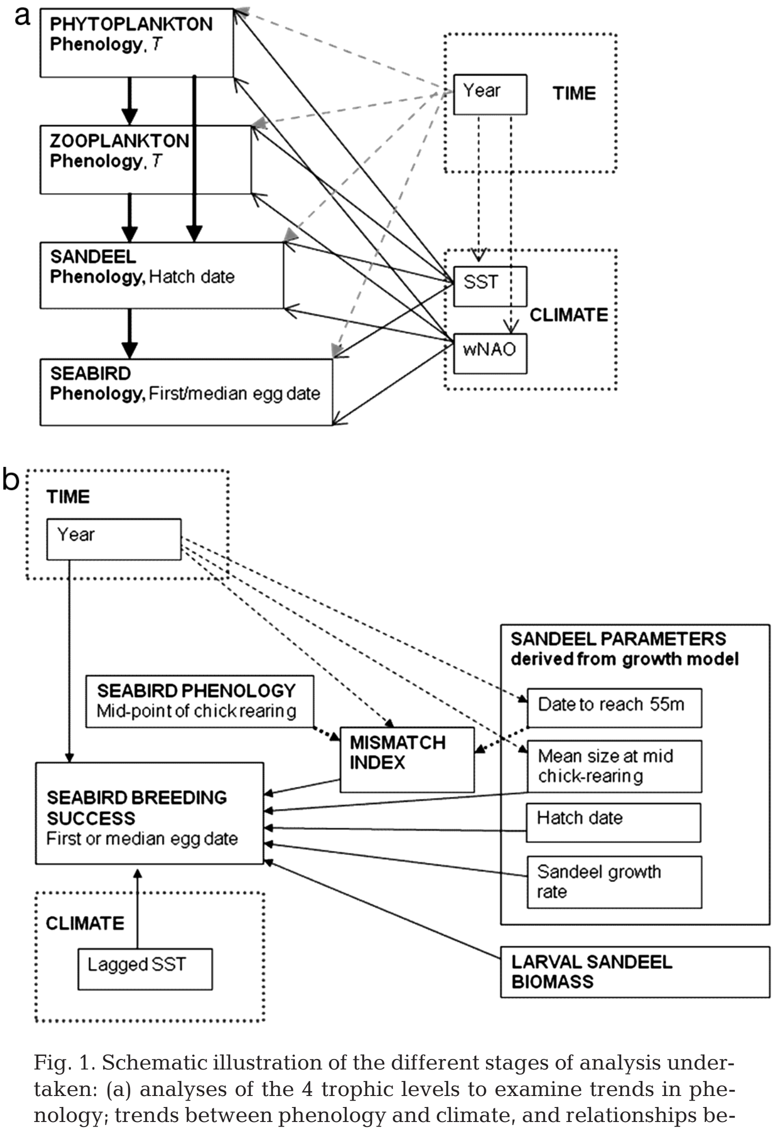

Fig. 1. Schematic illustration of the different stages of analysis undertaken: (a) analyses of the 4 trophic levels to examine trends in phenology; trends between phenology and climate, and relationships between phenologies of adjacent trophic levels; (b) detailed analyses of the seabird and sandeel data to examine phenological trends and the impact of mismatch on breeding success. SST: sea surface temperature; wNAO: winter North Atlantic Oscillation; *T*: month (day of year) of central tendency

were similar in terms of their magnitude and direction across the different trophic levels.

To investigate in more detail how the relative timing of trophically linked events have changed over time, we focussed on 5 seabird species and their major sandeel prey (Furness & Tasker 2000, Daunt et al. 2008). Although trophic mismatch theory is most often applied to the timing of peak prey abundance, prey size is a key component and is known to be important for seabirds in our study area (Wanless et al. 2005). We therefore compared modelled annual length-at-date of 0-group sandeels (Frederiksen et al. 2011; sandeel hatched in the current year) with the timing of peak energy demand in each seabird species, which we assumed corresponded to the mid-chick-rearing period (Drent & Daan 1980) (Fig. 1b). Under this modified version of the mismatch hypothesis our prediction was that mid-chick-rearing should coincide with sandeels having attained a threshold size, since individuals are expected to balance increasing prey quality through the season with the fitness advantages of breeding as early as possible (Daunt et al. 2007, Harris et al. 2007). We assessed whether the timing of chick-rearing had become decoupled from seasonal changes in sandeel length, and estimated mean size of fish at mid-chick-rearing to quantify the consequences of mismatch on prey energy value. Finally, we used the mismatch index to explore the fitness consequences of mismatching on seabird breeding success.

MATERIALS AND METHODS

Climate

Monthly average SST data were obtained from NOAA Pathfinder Version 5.0 (Kilpatrick et al. 2001) for an area of the North Sea (55 to 58°N, 3°W to 0°E) between 1983 and 2006. Since spring events were our main interest for comparison across the trophic levels we focussed SST analysis on February and March values (hereafter winter/spring SST). June and July (hereafter summer SST) values were also modelled with seabird breeding phenology as this period overlapped with mid-chick-rearing. As large-scale seasonal measures of climate have been found to be useful predictors of ecological processes (Hallett et al. 2004) and as 4 of the 5 seabird species being considered may be distributed outside the western North Sea during winter, we also considered wNAO indices (www.cgd.ucar.edu/cas/jhurrell/indices.html) for the winter prior to spring phenology events.

Phenology data

Phenology data were available across all trophic levels between 1983 and 2006, and analyses were thus restricted to this period.

Phytoplankton (primary producers) and zooplankton (primary consumers)

The continuous plankton recorder (CPR) survey is an upper layer plankton monitoring programme (Richardson et al. 2006). We analysed a subset of plankton data that are important in the diet of sandeels *Ammodytes marinus*. Phytoplankton and copepod nauplii are the main prey of larval sandeels (Monteleone & Peterson 1986), while older stages of calanoid copepods (particularly *Temora* spp. and *Calanus* spp.) are important for postlarval stages, <10 cm in length (Macer 1966). Accordingly, we focussed on spring-peaking copepod species (sandeel hatch date occurred mainly in February to March) and analysed data for *C. helgolandicus*, *C. finmarchicus*, *T. longicornis*, *Calanus* spp. Stages I to IV, and copepod nauplii. *Calanus* spp. nauplii feed preferentially on diatoms (Soreide et al. 2008). As there was no evidence that particular diatom species were important for copepods, we analysed the total summed monthly abundances of the 10 most abundant diatoms in spring (individual species data are presented in Table S1 of the supplement at www.int-res.com/articles/suppl/m454p119_supp.pdf) and a colour index of phytoplankton. Data were obtained from an area of the North Sea (55 to 58° N, 3° W to 0° E; Johns 2009) that provided a balance between sampling resolution and proximity to the Isle of May, Scotland (56° 11′ N, 2° 33′ W), the focal point of seabird observations.

For plankton, the phenology measure was the month of central tendency, *T*, (see Edwards & Richardson 2004) converted to day of year for comparison with other taxa. The average monthly abundances over the 24 yr period for each species were used to determine whether the seasonal pattern was unimodal or bimodal (spring and autumn). For unimodal taxa, *T* was calculated using data from the entire year, whereas, for bimodal taxa, it was calculated using data from the first 6 mo of the year (see Edwards & Richardson 2004). Due to missing monthly values for all species of plankton in 1995, this year was omitted from plankton phenology analyses.

Sandeels (secondary consumers)

Estimates of sandeel phenology (hatch dates) were obtained from a statistical model implemented using Markov Chain Monte Carlo procedures that combined 2 time series of sandeel size at date data, i.e. from larval fish captured during CPR surveys and 0-group fish obtained from foraging puffins (see Frederiksen et al. 2011 for full details).

Seabird predators

Analysis focussed on 5 species of seabirds for which 0-group sandeels are an important dietary component for adults and/or chicks on the Isle of May (Daunt et al. 2008): common guillemot *Uria aalge* (hereafter guillemot), razorbill *Alca torda*, European shag *Phalacrocorax aristotelis* (hereafter shag), black-legged kittiwake *Rissa tridactyla* (hereafter kittiwake) and Atlantic puffin *Fratercula arctica* (hereafter puffin). Median egg dates were recorded in guillemots and razorbills from daily checks of monitoring plots (mean of ca. 800 and ca. 100 breeding sites, respectively). For shags, annual median ringing dates of chicks were analysed (mean ca. 800 chicks ringed mid-way through the chick-rearing period at a mean age of 20 to 25 d) since median laying dates (estimated from weekly checks of ca. 100 pairs) were only available for a subset of years and were strongly correlated with median egg date ($r = 0.94$, $df = 20$, $p < 0.001$). Kittiwake first egg dates were analysed (from daily checks of the whole colony of >3000 pairs) as median egg dates were only recorded in a subset of years (from 5 d checks of ca. 200 pairs; correlation between first and median: $r = 0.90$, $df = 8$, $p < 0.001$). First egg dates were also analysed for puffins, back-calculated from daily checks of the entire colony for adults bringing fish back to chicks (>10 000 pairs; see Wanless et al. 2009 for details) since median egg dates (based on back-calculation from wing and bill measurements of chicks from a mean of ca. 30 individuals; see Harris & Wanless 2011 for details) were only available for a subset of years (correlation between first and median: $r = 0.61$, $df = 13$, $p = 0.015$). Even though first egg dates are likely to be subject to a higher level of stochastic variation than median egg dates (Wanless et al. 2009), they were assumed to be reliable indicators of the timing of breeding for kittiwakes and puffins because of the correlation with median egg dates in the subset of years where both were recorded.

Phenological regressions

Standard linear regressions with year were used to investigate temporal trends in SST, wNAO and phenology of trophic levels. In order to avoid false detection of significant correlations due to multiple testing, we applied the Benjamini & Hochberg (1995) correction factor to this set of models. In all cases we report the uncorrected p-values. Phenology data for sandeel hatch date showed evidence of a break-point (Frederiksen et al. 2011), and were therefore analysed using a piecewise regression model employing the segmented package in R (Muggeo 2008). In order to assess whether the phenologies of consumers and their prey covaried over time, we examined whether there were pairwise correlations between phenologies of taxa across successive trophic levels. We investigated whether phenology was correlated with climate by regressing the phenology of each species against SST or wNAO. We analysed trends using simple linear regression, without taking temporal autocorrelation into account, and thus assume that consecutive years are independent. Autocorrelation plots of model residuals were examined and, in general, showed no apparent evidence of autocorrelation, suggesting that the assumption of independence was reasonable. There was only 1 case (linear regression of kittiwake first egg phenology and wNAO) in which the regression coefficient was significant and the model residuals showed evidence of autocorrelation.

Trophic mismatch in seabirds and sandeels

To evaluate phenological mismatch in greater detail we focussed on interactions between seabirds and 0-group sandeels, since, not only was the temporal resolution of these data markedly better than for lower trophic levels, but information on other aspects of performance such as sandeel growth rates and seabird breeding success was also available. We focussed on the peak period of energy demand for the seabirds, i.e. the mid-point of the chick-rearing period (Drent & Daan 1980). For shags this was estimated directly from median chick ringing date as this occurs midway through the chick-rearing period. For guillemots and razorbills we used the species- and year-specific median laying date plus the average incubation period plus the average chick-rearing period/2, while for kittiwakes and puffins we used first egg date plus average difference between first and median egg dates plus average incubation period plus the average chick-rearing period/2. Values for incubation and fledging periods were obtained from Cramp & Simmons (1978, 1983). The average difference between first and median egg dates was 11 d for kittiwake (range: 6 to 18 d, n = 10) and 12 d for puffin (range: 6 to 17 d, n = 15).

The sandeel model (Frederiksen et al. 2011) estimated mean hatch dates and growth rates, from which daily size of juvenile sandeels was then estimated. We compared relationships between the timing of mid-chick-rearing in seabirds and 2 phenological metrics for sandeels: hatch dates and the date each year that 0-group sandeels reached a predicted mean threshold length of 55 mm. This was undertaken because many phenological studies investigate the timing of appearance of prey (hatch dates), but we also wanted to test whether phenology of sandeel size and hence prey quality was more relevant to seabird predators. Other threshold sizes were also analysed (Fig. S1 in the supplement at www.int-res.com/articles/suppl/m454p119_supp.pdf), and model fit was found to increase with sandeel size, with 55 mm being the largest threshold size that sandeels attained in all years of the study. Thus, this was a useful measure to compare with timing of mid-chick-rearing for each seabird species. Linear regression with year was used to assess whether the date sandeels reached 55 mm showed evidence of a temporal trend.

In order to evaluate whether the timing of seabird mid-chick-rearing had become decoupled from the timing of availability of quality sandeel prey over the study period, a 'mismatch index' was calculated as the difference (in days) between the date of the mid-point of chick-rearing for each seabird species and the date that mean sandeel size was predicted to reach the threshold of 55 mm. We emphasise that as the mismatch index is based on a threshold sandeel size, a mismatch index of 0 does not indicate perfect matching of predator and prey timing. Instead positive values of the index indicate that the seabirds' peak energy demand occurred after sandeels reached 55 mm, while negative values indicated that peak demand preceded this threshold being attained. Thus, more positive values potentially indicated better matching with higher quality prey (larger fish) and more negative values indicated peak demand coinciding with poorer quality prey. We assessed temporal changes in this mismatch index for each seabird species using linear regressions with year. Finally, we estimated mean sandeel size at mid-chick-rearing to quantify the effects of mismatch on prey energy value using the equation relating sandeel length to energy value from Hislop et al. (1991). Due to the non-linear nature of this relationship, declines in size of large fish are more energetically costly than similar declines in smaller fish. Linear regression with year assessed whether there had been any systematic change in sandeel size at this time.

Generalised linear modelling was used to evaluate whether changes in seabird breeding success were associated with sandeel phenology and mismatch parameters, selecting models by Akaike's information criterion corrected for small sample sizes (AICc; Hurvich & Tsai 1989, Burnham & Anderson 2002). Breeding success was defined to be the ratio of the total number of chicks fledged to the total number of chicks that could potentially have fledged (a proportion). The total number of chicks that could potentially have fledged is equal to the maximum brood size multiplied by the total number of nests at which eggs were laid. Maximum brood size is invariably 1 for guillemots, razorbills and puffins, and typically 3 for kittiwake and 4 for shag (Cramp & Simmons 1978, 1983). Details of sample sizes and field methodology for monitoring breeding success are given in Harris et al. (2005). In addition to the sandeel phenology and mismatch parameters (sandeel hatch date, sandeel growth rate, length of sandeels at the mid-point of chick-rearing and mismatch index) we also included in model selection the following extrinsic factors that have previously been shown to correlate with breeding success for these seabird species on the Isle of May (Frederiksen et al. 2004b, 2006): lagged sandeel biomass index (an annual index modelled from the probability of sandeel larvae occurring in CPR samples and summed mass of larvae in a sample; see Frederiksen et al. 2006 for details); lagged SST (previous year) and sandeel fishery presence (kittiwake only; Frederiksen et al. 2008).

As the sandeel variables (apart from sandeel biomass index) arise from the same statistical model (Frederiksen et al. 2011; see Table S3 in the supplement at www.int-res.com/articles/suppl/m454p119_supp.pdf) we included at most one of these variables in each model. We used summed Akaike weights to calculate the relative strength of support for each of the potential predictors. Note that sandeel phenology and mismatch parameters each appeared in 8 of the 40 models within the candidate set (a prior weight of 0.2), whereas the variables relating to extrinsic factors each appeared in 20 of the 40 models (a prior weight of 0.5) — this difference must be taken into account when drawing comparisons between the 2 groups of variables.

Regression models were applied to logit-transformed data on breeding success for guillemot, razorbill and puffin, and to log-transformed data for

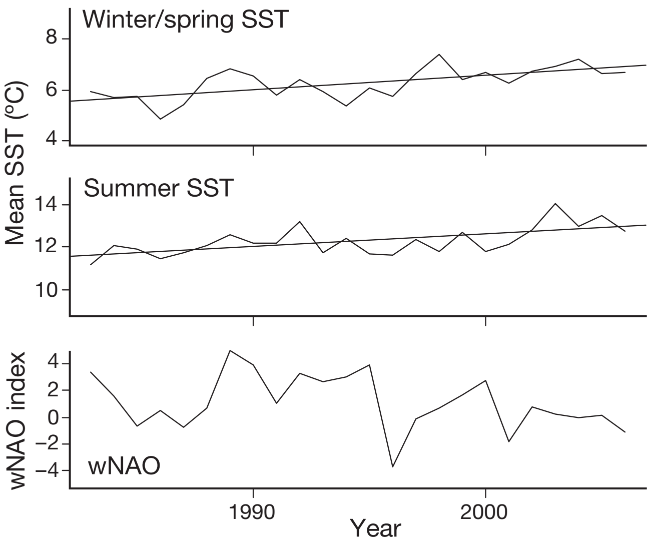

Fig. 2. Mean winter/spring and summer sea-surface temperature (SST) values, and the winter North Atlantic Oscillation (wNAO) index score over the study period. Fitted lines show significant regressions

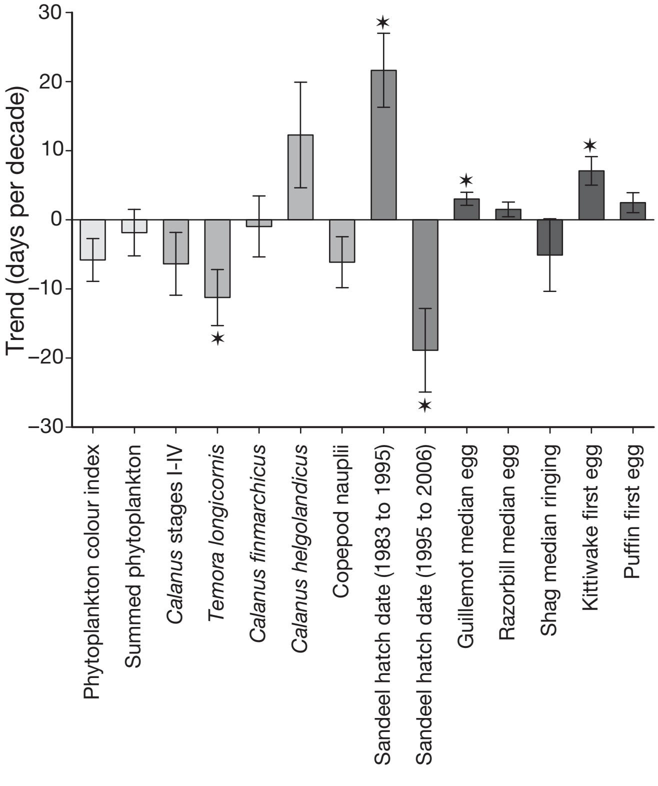

Fig. 3. Phenology trends (negative values below the line indicate timing becoming earlier, and positive values above the line indicate timing becoming later; n = 23 for plankton species and n = 24 for sandeel and seabirds) for species/groups from the 4 trophic levels with standard errors (trophic levels are shaded differently: palest grey: primary producers; darkest grey: top predators) in a North Sea pelagic food web between 1983 and 2006. *Significant trends after correction ($p < 0.05$)

kittiwake and shag, as well as being applied to untransformed data for all species. The same models (i.e. the same sets of explanatory variables) were selected by AICc for both transformed and untransformed data; we present the results for the untransformed data solely in order to allow direct comparison with the results of Frederiksen et al. (2006). We considered the inclusion of quadratic, as well as linear, relationships and sandeel parameters lagged by 1 yr, but found no support for inclusion of these terms. Spurious relationships between an explanatory variable and the response variable can arise if both are correlated with a third variable, particularly time (Grosbois et al. 2008). We therefore included year as an explanatory variable in order to assess whether the same best model was selected once year was included, and whether the addition of year improved model fit.

RESULTS

Climate

Winter/spring SST increased by an average (±SE) of 0.056 ± 0.014°C yr^{-1}; $p < 0.001$, an increase of 1.34°C over the study period. Summer SST also increased significantly (overall increase: 1.42°C; 0.059 ± 0.016°C yr^{-1}; $p = 0.002$). In contrast, there was no significant trend in the wNAO (estimate: −0.097 ± 0.060; $p = 0.118$; Fig. 2).

Phenological trends

For primary producers, neither the timing of the seasonal peak of overall summed phytoplankton abundance, nor that of the colour index showed a statistically significant trend (Fig. 3). Similarly, phenology of primary consumers appeared to be largely unchanged and only 1 species, *Temora longicornis*, showed a significant advancement in timing. Sandeel *Ammodytes marinus* hatch date showed, within the piecewise regression model, a highly significant break-point in 1995 (95% CI from 1991 to 1998, $p = 0.001$; model $R^2 = 0.452$), with hatching initially becoming later and then becoming earlier (Fig. 3). With the exception of shags, whose timing varied greatly from year to year, seabird breeding tended to become later, with significant trends for guillemot and kittiwake (Fig. 3). All significant trends remained significant after the Benjamini and Hochberg correction factor was applied to this set of models.

Table 1. Linear regressions of phenology against mean winter/spring sea-surface temperature (SST) and winter North Atlantic Oscillation (wNAO), together with uncorrected p-values. Significant regressions (at the 5 % level, after applying the Benjamini and Hochberg correction factor) are highlighted in bold. *T*: central tendency for monthly plankton data

Phenology measure	n	Day of year		Spring SST				wNAO			
		Mean	SD	Slope estimate	SE	p	R^2 (%)	Slope estimate	SE	p	R^2 (%)
Phytoplankton colour *T*	23	103.00	11.09	−1.89	3.82	0.63	1.16	2.54	1.04	0.02	22.20
Summed phytoplankton *T*	23	98.35	11.24	−1.32	3.88	0.74	0.55	−0.86	1.18	0.47	2.50
Calanus spp. Stages I to IV *T*	23	115.65	15.73	−10.40	4.95	0.05	17.35	1.18	1.65	0.48	2.39
Temora longicornis T	23	120.35	15.72	−12.64	4.70	0.01	25.66	0.29	1.67	0.86	0.14
C. finmarchicus T	23	96.09	14.65	−3.66	5.01	0.47	2.48	−0.37	1.55	0.82	0.26
C. helgolandicus T	23	66.70	26.82	12.64	8.88	0.17	8.81	3.97	2.71	0.16	9.26
Copepod nauplii *T*	23	123.87	13.00	0.80	4.50	0.86	0.15	−0.28	1.38	0.84	0.20
Sandeel hatch date	24	71.44	9.03	0.52	3.12	0.87	0.13	0.93	0.90	0.31	4.65
Date sandeels reach 55 mm	24	162.17	16.45	7.62	5.45	0.18	8.18	−1.88	1.62	0.26	5.79
Guillemot median egg	24	128.13	3.79	0.71	1.30	0.59	1.33	−0.93	0.33	0.01	26.28
Razorbill median egg	24	130.17	3.69	−0.76	1.26	0.55	1.63	−0.76	0.34	0.03	18.93
Shag median ringing	22	132.55	19.82	−7.14	5.96	0.24	6.13	0.71	1.80	0.70	0.70
Kittiwake first egg	24	131.50	8.46	1.37	2.91	0.64	0.99	**−2.35**	**0.70**	**0.00**	**34.14**
Puffin first egg	24	99.88	5.10	1.59	1.73	0.37	3.68	−0.70	0.50	0.17	8.41

Phenological regressions with climate

Overall there was little evidence that trends in phenology were associated with either of the climate variables. Significant relationships between phenology and winter/spring SST (see Table 1) for *Temora longicornis* and *Calanus* spp. Stages I to IV were apparent, but did not remain significant after applying the Benjamini and Hochberg correction to this set of models. None of the regressions were significant between seabird egg-laying phenology and winter/spring SST (Table 1) or summer SST (guillemot: $t = 0.50$, $p = 0.62$; razorbill: $t = -1.22$, $p = 0.24$; shag: $t = -0.69$, $p = 0.50$; kittiwake: $t = 0.911$, $p = 0.37$; puffin: $t = 0.40$, $p = 0.70$). Phytoplankton colour index, but not summed abundance, was positively related to wNAO, while timing of guillemots, razorbills and kittiwakes showed a negative relationship. Only the regression with kittiwake phenology remained significant once the correction factor had been applied to this set of models. However, this model also showed some evidence of autocorrelation when model residuals were examined and hence should be interpreted with caution.

Table 2. Linear regressions of phenology of upper trophic level species/group against that of the relevant lower trophic level, together with uncorrected p-values. Results for summed total phytoplankton abundance were similar to the colour index (see Table S2 in the supplement at www.int-res.com/articles/suppl/m454p119_supp.pdf). *T* is the central tendency for monthly plankton data

Response	Explanatory	Slope estimate	SE	*t*	p
Calanus finmarchicus T	Phytoplankton colour *T*	−0.476	0.269	−1.768	0.092
C. helgolandicus T	Phytoplankton colour *T*	−0.119	0.527	−0.227	0.823
Calanus stages T	Phytoplankton colour *T*	0.277	0.304	0.914	0.371
Temora longicornis T	Phytoplankton colour *T*	0.282	0.303	0.929	0.363
Copepod nauplii *T*	Phytoplankton colour *T*	0.258	0.250	1.032	0.314
Sandeel hatch	*C. finmarchicus T*	0.038	0.111	0.344	0.734
Sandeel hatch	*C. helgolandicus T*	0.128	0.054	2.377	0.027
Sandeel hatch	*Calanus stages T*	0.096	0.101	0.949	0.354
Sandeel hatch	*T. longicornis T*	−0.011	0.103	−0.110	0.913
Sandeel hatch	Copepod nauplii *T*	−0.175	0.119	−1.469	0.157
Sandeel hatch	Phytoplankton colour *T*	−0.056	0.146	−0.380	0.708
Guillemot median egg	Sandeel hatch	0.034	0.089	0.376	0.711
Razorbill median egg	Sandeel hatch	0.075	0.086	0.874	0.392
Shag median ring	Sandeel hatch	−0.332	0.414	−0.802	0.431
Kittiwake first egg	Sandeel hatch	0.088	0.199	0.440	0.664
Puffin first egg	Sandeel hatch	0.106	0.118	0.893	0.382

Comparisons of phenological change among trophic levels

There was no evidence that predator and prey phenologies were related, with no significant pairwise regressions between any of the trophic comparisons (the significant relationship between sandeel hatch and timing of peak abundance of *Calanus helgolandicus* was no longer significant after correction (Table 2 and Table S2 in the supplement at www.int-res.com/articles/suppl/m454p119_supp.pdf).

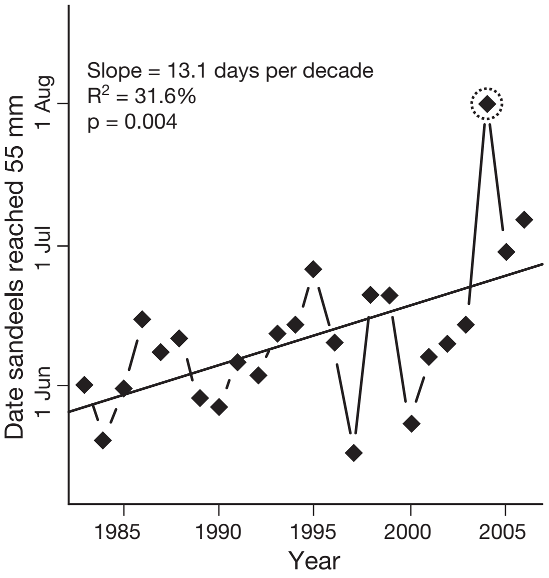

Fig. 4. Regression between the date that mean sizes of sandeel *Ammodytes marinus* are predicted to attain a threshold of 55 mm and year. The line shows the significant fitted regression. Relationship remained significant even when the latest date sandeels reached 55 mm (in 2004, dotted circle) was removed from the analysis

Trophic mismatch in seabirds and sandeels

The date at which 0-group sandeels reached a predicted mean threshold length of 55 mm became significantly later, at an average rate of 13.1 d decade^{-1} over the study period (Fig. 4). The date of mid-chick-rearing was significantly related to the estimated date this threshold length was reached for 4 of the seabird species (guillemot, razorbill, puffin and kittiwake; Fig. 5), and relationships for guillemot, razorbill and kittiwake remained significant even when year was also included in the model. However, the regression coefficient (slope) of mid-chick-rearing against the date sandeel threshold length was reached was substantially less than unity for these species (Fig. 5). This indicated that although mid-chick-rearing had become later in these 4 species, the shift in timing of sandeel size had been even faster. Razorbills showed the slowest rate of change in timing of breeding, and kittiwakes, the fastest. In contrast, shags showed no temporal trend in breeding phenology or relationship with sandeel size phenology (Fig. 5).

In addition to differing rates of phenological change, there was also interspecific variation in the

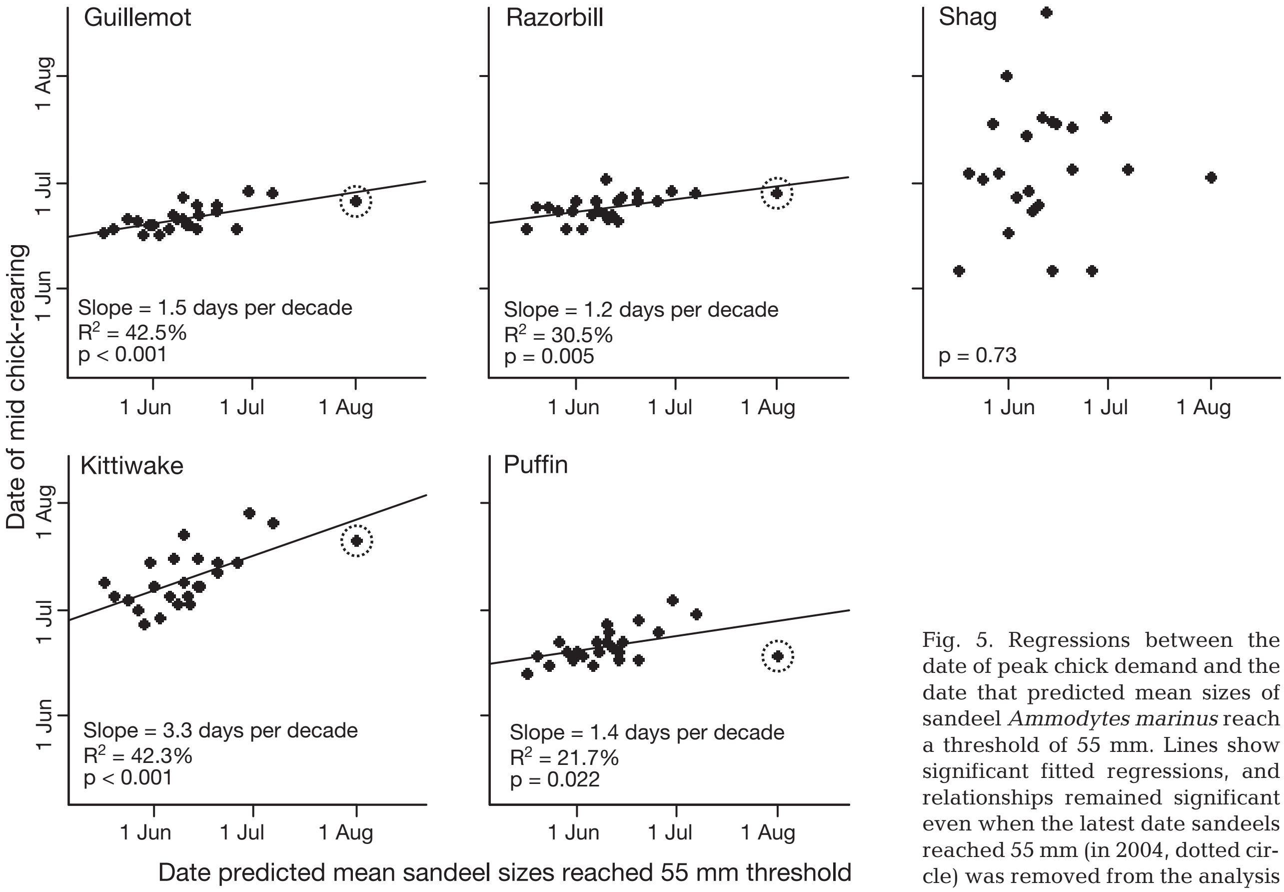

Fig. 5. Regressions between the date of peak chick demand and the date that predicted mean sizes of sandeel *Ammodytes marinus* reach a threshold of 55 mm. Lines show significant fitted regressions, and relationships remained significant even when the latest date sandeels reached 55 mm (in 2004, dotted circle) was removed from the analysis

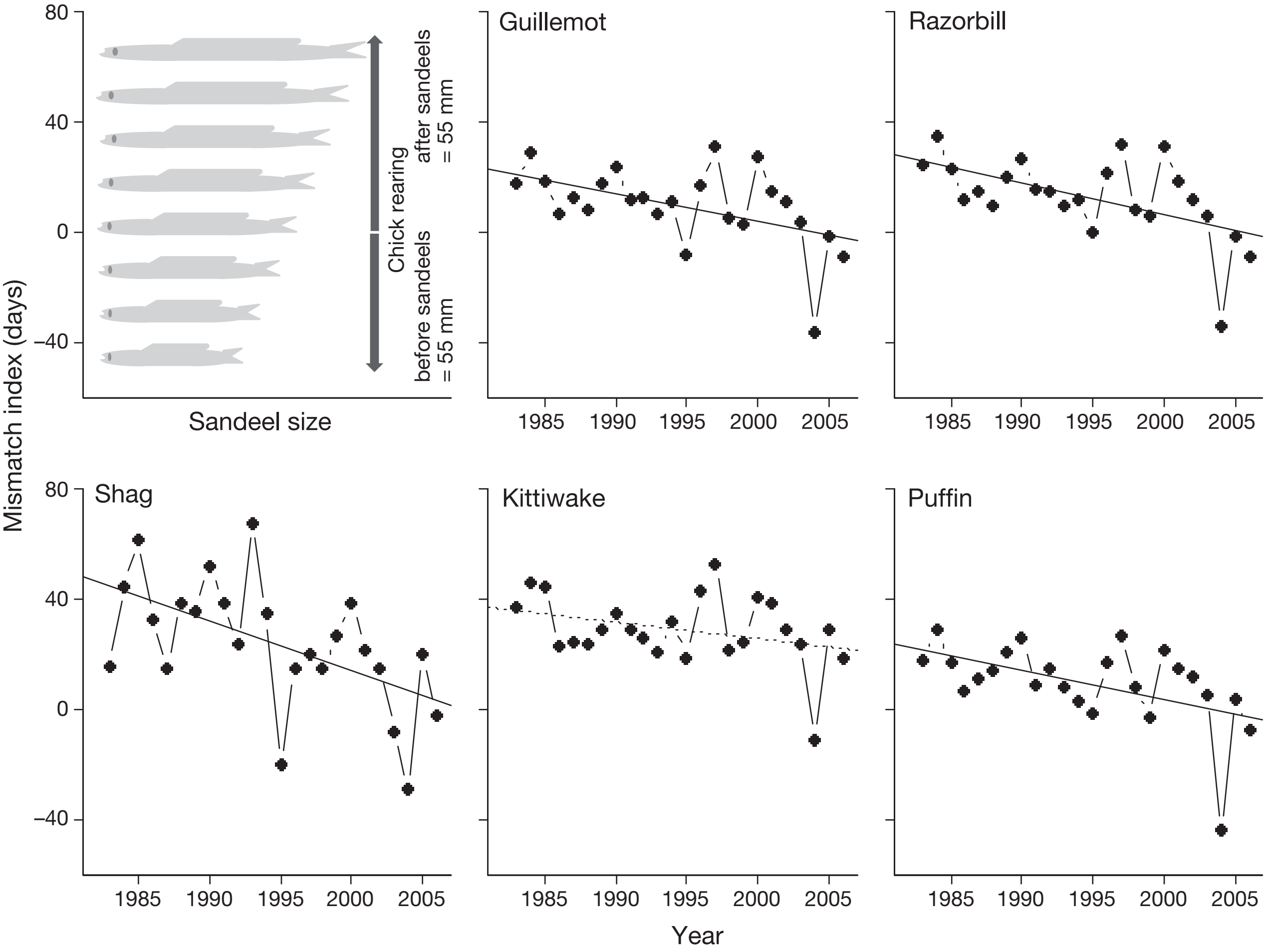

Fig. 6. Temporal changes in mismatch index (difference in days between timing of seabird mid-chick-rearing and the mean date that sandeels *Ammodytes marinus* were predicted to reach a threshold of 55 mm). As shown in upper left panel, a negative index means that mid-chick-rearing occurred before sandeels attained a threshold length of 55 mm; hence, sandeels would have been 55 mm and smaller during chick-rearing. Positive index values indicate that mid-chick-rearing occurred after this threshold; hence, sandeels would have been 55 mm or larger during chick-rearing. Solid lines: significant fitted regressions; dashed line (kittiwakes): non-significant. We emphasise that because the mismatch index is based on a threshold size of sandeel, a value of 0 for the mismatch index does not indicate perfect matching between seabirds and sandeels; rather the higher the mismatch index the larger the sandeels available

absolute timing of breeding. Ranking of the timing of breeding for 4 of the 5 seabird species was generally constant across the study period, with puffins and guillemots breeding earliest, followed by razorbills, and with kittiwakes breeding last. In contrast, shag mid-chick-rearing was highly variable, being the earliest studied bird in 3 of the years and the latest in 9 of the years.

These disparities in absolute timing and rates of change in seabird breeding schedules and sandeel sizes were integrated in the mismatch index (Fig. 6). Thus, in the 1980s, mid-chick-rearing for all the species considered occurred well after 0-group sandeels reached 55 mm (positive values of the mismatch index), whereas, in recent years, mid-chick-rearing coincided with (mismatch index around 0) or occurred before (negative values) the date at which sandeels had attained this size in 4 of the 5 seabird species. Kittiwakes were the exception; they bred latest and hence had generally higher mismatch index values than the other species (Fig. 6). As a result, the mean length of 0-group sandeels at mid-chick-rearing has significantly decreased over the study period in all seabird species (Fig. 7). The total estimated decrease over 24 yr and rates of decline (±SE) were as follows: for guillemots: 10.2 mm, –0.44 (±0.16) mm yr^{-1}; for razorbills: 12.4 mm, –0.54 (±0.16) mm yr^{-1}; for shags: 21.7 mm, –0.94 (±0.28) mm yr^{-1}; for kittiwakes: 10.2 mm, –0.44 (±0.19) mm yr^{-1}; and for puffins: 10.7 mm, –0.47 (±0.15) mm

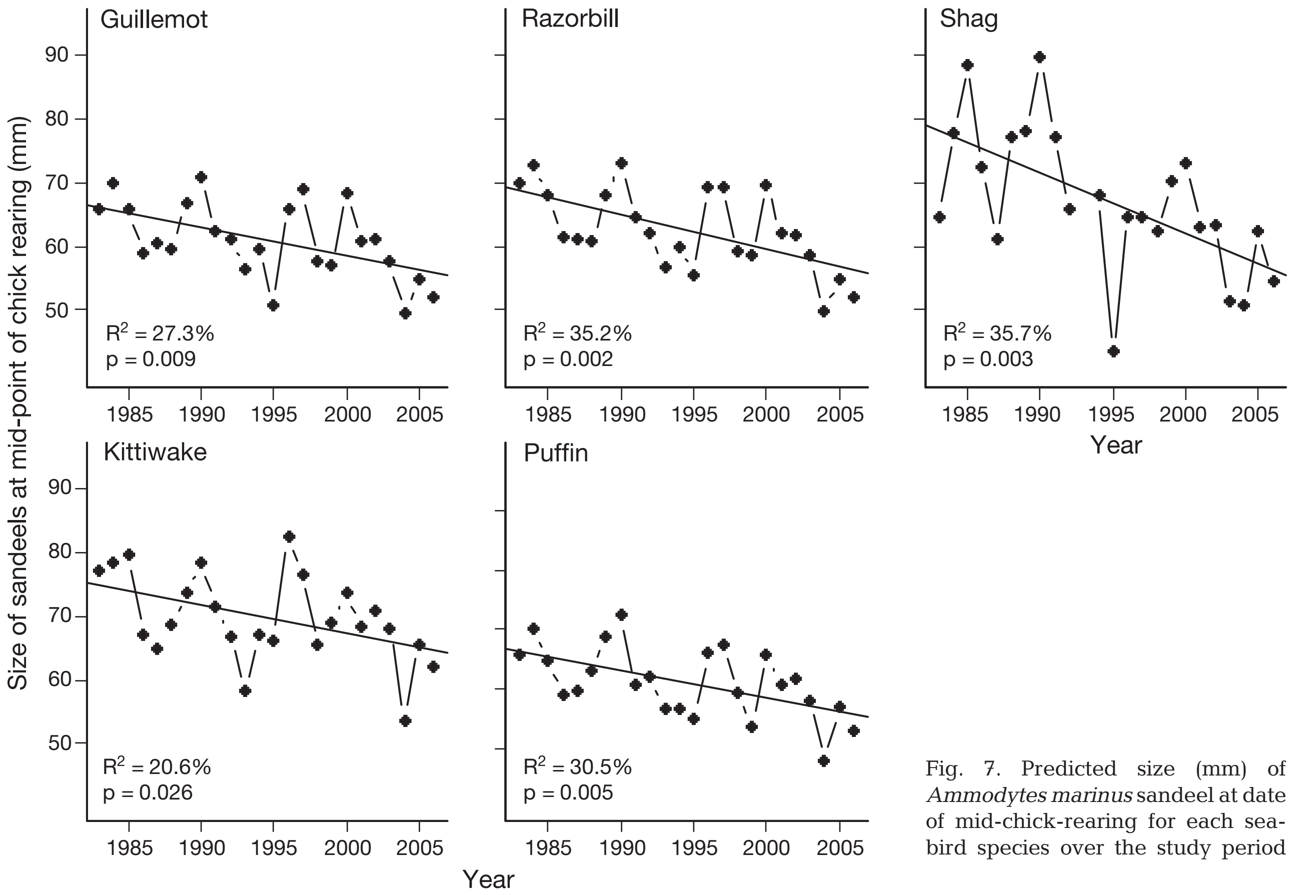

Fig. 7. Predicted size (mm) of *Ammodytes marinus* sandeel at date of mid-chick-rearing for each seabird species over the study period

yr^{-1}. Shags, with the steepest rate of predicted decline, showed the highest net reduction in energetic value of fish over the 24 yr study period (4.80 kJ, a 70.4 % decline from 1983). Despite kittiwakes having the lowest rate of decline in sandeel size, this species showed the next highest overall reduction in net energetic value of 2.46 kJ (42.2 % decline from 1983). As the latest breeding seabird, mid-chick-rearing of kittiwakes occurred when sandeels were predicted to be larger and, due to the non-linear nature of the relationship between sandeel length and energetic content, declines in the length of large fish are more energetically costly than equivalent declines in smaller fish. Net declines in the energetic value of fish were 1.70 kJ (46.7 %) for guillemot, 2.21 kJ (52.4 %) for razorbill and 1.79 kJ (48.2 %) for puffin.

Consequences of mismatch for seabird breeding success

Despite the energetic implications associated with the pronounced decline in 0-group sandeel length at mid-chick-rearing, there was no evidence that this or sandeel hatch date had a significant effect on the breeding success of any of the 5 species of seabirds considered once other significant variables were included in the models. The breeding success of guillemot, razorbill and shag was, however, positively related to sandeel growth rates (slope estimates ± SE: 0.849 ± 0.204, 0.341 ± 0.193, and 0.729 ± 0.333, respectively) such that in years with poorer sandeel growth these species had poorer breeding success.

Breeding success for shags, kittiwakes and puffins was poorer in years following a year with warmer winter/spring SST (slope estimates ± SE: −0.101 ± 0.042, −0.126 ± 0.030, −0.108 ± 0.028, respectively) and higher following years with a high sandeel biomass index (slope estimates ± SE: 0.047 ± 0.020, 0.035 ± 0.018, and 0.032 ± 0.013, respectively). All species except kittiwake showed evidence of a linear trend (negative for all species except shag) in success over time that was not accounted for by the other model variables (Table 3). The inclusion of quadratic or lagged sandeel terms did not lead to models with lower AICc values.

DISCUSSION

Phenological changes across trophic levels

To our knowledge, this is the first direct comparison of phenologies across multiple trophic levels of the North Sea pelagic food web. We found contrasting trends across the 4 trophic levels that were suggestive of trophic mismatch, supporting the assertion from other studies that this phenomenon is widespread (Visser & Both 2005). However, in contrast to mismatch theory for marine systems (Cushing 1990) and empirical results from terrestrial studies (Visser & Both 2005, Both et al. 2009), we found no evidence of strong pairwise relationships between predator and prey phenologies, except for timing of mid-chick-rearing in some seabird species and threshold size of 0-group sandeels *Ammodytes marinus*, and hence no evidence of matching in this system. This suggests that phenologies of North Sea species may have been mismatched since at least 1983, which is possible as most of our study followed the abrupt increase in SST and regime shift in the late 1980s (Beaugrand 2004).

Contrasting phenological responses can arise for several reasons. For example, if organisms at different trophic levels vary in their ability to respond to climate warming or in the extent to which their phenology is influenced by alternative drivers. The absence of significant relationships between any of the phenology metrics considered and SST, apart from suggestive relationships with *Calanus* spp. stages and *Temora longicornis*, suggests that differential responses to climate warming may be unimportant, at least in this part of the western North Sea. Alternatively winter/spring or summer SST may not be at the appropriate temporal or spatial scale for elucidating such responses. Indeed, there was evidence that timing of breeding for 3 of the 4 seabirds that disperse outside the North Sea in winter (kittiwakes, guillemot and razorbills, but not puffins) was related to broader scale climate cues (wNAO), particularly in the case of the kittiwake which exhibits the widest dispersal (Wernham et al. 2002, Bogdanova et al. 2011). High abundance and/or broad peaks of seasonal prey can potentially mask phenological relationships (Durant et al. 2005), with phenological matching likely to be particularly apparent when prey abundance is reduced or only available for a short duration of time. In the North Sea, dramatic changes in abundance and spatial distributions of phytoplankton and copepods (Beaugrand et al. 2009) have been observed. However, patterns of change are not consistent within trophic levels, with increases apparent for some species (for example *C. helgolandicus*), while others are decreasing (e.g. *C. finmarchicus*) (Planque & Fromentin 1996). Thus it is unclear to what extent changing abundance may be masking phenological matching in our system. Finally, there may potentially be lagged responses of predators to prey phenology such that comparison of phenologies in the same year does not elucidate relationships. For example, phenology of juvenile zooplankton abundance is related to the reproductive timing of parent generations (Ellertsen et al. 1987).

Table 3. Importance of variables associated with seabird breeding success, based upon summed Akaike weights (range from 0 to 1; high values indicate strong support), were calculated using the full candidate set of n = 40 models (see Table S4 in the supplement at www.int-res.com/articles/suppl/m454p119_supp.pdf. Note that parameters derived from the sandeel model (hatch date, growth rate, size and mismatch index) were present in 8 of the 40 models within the candidate set, whereas the remaining predictors were present in 20 models — the prior weights for these variables are therefore 0.2 and 0.5, respectively, and this difference needs to be taken into account when drawing comparisons between the 2 groups of variables. Predictors included in the model with the lowest value of the corrected Akaike's information criterion (AICc) for each species are shown in **bold**, and we report the overall R^2 values for these models. SST: sea-surface temperature

Predictor	No. of models	Guillemot	Razorbill	Shag	Kittiwake	Puffin
Sandeel size	**8 / 40**	0.001	0.125	0.083	0.135	0.125
Sandeel hatch date	**8 / 40**	0.025	0.090	0.099	0.071	0.171
Sandeel growth rate	**8 / 40**	**0.966**	**0.364**	**0.319**	0.176	0.097
Mismatch index	**8 / 40**	**0.004**	**0.135**	**0.110**	0.019	0.121
Sandeel biomass index lagged	20 / 40	0.169	0.237	**0.560**	**0.872**	**0.679**
SST lagged	20 / 40	0.177	0.116	**0.477**	**0.985**	**0.979**
Year (linear time trend)	20 / 40	**0.956**	**0.924**	**0.507**		**0.585**
Sandeel fishery presence	20 / 40				**0.847**	
R^2 for model with lowest AICc (%)		71.80	50.85	49.9	65.38	71.30
n (yr)		24	24	21	22	24

It is also possible that sampling differences between the trophic levels could potentially result in phenology measures that are too crude to identify correlations. The plankton data were at a lower temporal resolution and broader spatial scale than the sandeel and seabird data, and central tendency estimates of plankton phenology are known to have low sensitivity if timing shifts are small (Ji et al. 2010). Moreover, copepods may respond to timing of critical abundance thresholds of diatoms, rather than to seasonal peaks (Runge et al. 2005). In addition, we considered mean phenological values at a broad spatial scale, whereas changes in prey distributions can lead to localised spatial mismatch (Schweiger et al. 2008). Ideally future analyses of phenological trends and mismatch in this system should account for annual variation in prey abundance by investigating overlap between distributions of prey availability and predator peak energetic demands rather than treating them as point estimates.

Trophic mismatch between seabirds and sandeels

A key finding of the present study was that, for most of the Isle of May seabird populations considered, the timing of seabird mid-chick-rearing tracked the timing of 0-group sandeels attaining a threshold size, rather than sandeel hatch dates per se. The rate at which mid-chick-rearing was delayed varied among the species, but in all cases was insufficient to keep pace with the delayed date at which sandeels attained a threshold size. The net result was that for all 5 seabird species the size of 0-group sandeels around the mid-point of chick-rearing, when energetic requirements are likely to be greatest, has significantly declined.

The seabird species we considered differed to some extent as to the importance of 0-group sandeels in adult and chick diets, with the likely ranking in decreasing order of reliance being kittiwake, puffin, razorbill, guillemot and shag (Daunt et al. 2008). This ranking reflects the species-specific differences apparent in mismatching, with kittiwakes, which show the greatest reliance on the 0-group, tracking changes in size most closely, while shags, for which the 0-group is a minor part of the diet, showed no trend in their breeding phenology. However, the predicted net energetic reduction in 0-group sandeel prey was higher for kittiwakes than for the other seabird species that were also tracking changes in sandeel size, despite kittiwakes showing the greatest phenological shifts in response to changing sandeel timing. This is because variation in net energetic costs of reductions in sandeel size also depends on the absolute timing of breeding. As the consistently latest breeding seabird on the Isle of May, kittiwake mid-chick-rearing occurred when sandeels were predicted to be larger and, due to the non-linear nature of the relationship between sandeel length and energetic content, declines in the length of large fish are more energetically costly than equivalent declines in smaller fish.

Although the results presented here pertain to seabirds from the Isle of May, the order and annual timing of breeding for the species considered were consistent and varied in parallel with another North Sea colony 90 km distant (Wanless et al. 2009). This suggests consistency, at least at the local scale, with seabirds from these 2 colonies potentially foraging on the same sandeel stock. However, qualitative data from other UK seabird colonies suggests that breeding phenology may vary considerably between locations (Wanless et al. 2009). Moreover, sandeel populations also exhibit significant regional variation in growth rates, length-at-age and abundance (Boulcott et al. 2006), and further work is needed to identify whether interactions between seabirds and sandeel phenology vary regionally.

Very few other studies have considered the role of prey quality in trophic mismatch. However, Beaugrand et al. (2003) found a mismatch between the size of larval cod *Gadus morhua* relative to the size of their calanoid copepod prey, resulting in poorer cod survival. Similarly, in a terrestrial system, caribou *Rangifer tarandus* births had become mismatched from the onset of newly emergent nutrient-rich plant growth, resulting in reduced offspring survival (Post & Forchhammer 2008). There are several potential reasons why Isle of May seabirds are failing to track changes in the timing of 0-group sandeel size. Firstly, the cues used by the birds to time their breeding may not accurately predict 0-group sandeel phenology. Secondly, there may be trade-offs between the benefits of delaying breeding to maintain 0-group sandeel size and the fitness benefits of early breeding (Daunt et al. 2007, Harris et al. 2007). Thirdly, the birds may be constrained in their ability to alter their phenology due to having a photoperiodically controlled physiological window of breeding timing (Dawson 2008). Finally, adult birds may compensate for the lower energy value of 0-group sandeels by increasing foraging effort and/or switching to alternative prey. It is probable that some, possibly all, of these factors are operating in our study system.

Despite the apparently serious implications in terms of the reduced energy value of prey associated with changes in 0-group sandeel length at the time of chick-rearing, particularly for kittiwakes, there was no evidence that this was related to poorer breeding success. This contrasts with studies from a Norwegian seabird colony where breeding success of puffins was positively related to the size of herring prey (Durant et al. 2003) and from a Japanese colony where rhinoceros auklet *Cerorhinca monocerata* breeding success was poorer in years when birds were mismatched from the availability of their prey, Japanese anchovy *Engraulis japonicus* (Watanuki et al. 2009). The reason for this disparity is currently unclear, but may well be linked to differences in the life-history traits of the species involved, hydrobiological characteristics of the study systems — with both the mismatch examples given above being from a conveyor-type system where prey availability is affected by the timing of currents — and whether other factors such as predation or severe weather exert a major effect on breeding success.

It is also plausible that breeding success of some Isle of May seabirds is more closely linked to the scheduling and/or abundance of one or more alternative prey species. The main alternative prey species for Isle of May seabirds are 1+-group sandeels, clupeids (predominantly sprats *Sprattus sprattus*) and butterfish *Pholis gunellus* (Daunt et al. 2008). Time series data on abundance or phenology for these species are lacking; thus, it is impossible to repeat the approach used to look for matching between seabird breeding and 0-group sandeels. Previous findings suggest that the timing of 1+-group sandeel abundance is potentially important for kittiwakes, guillemots and shags (Frederiksen et al. 2004b). Our analyses of breeding success included a range of potentially important variables, and results indicated that these differed among the species. Sandeel abundance as indicated by a sandeel biomass index and the sandeel growth rate, which may be linked with behavioural changes and hence availability of sandeel to seabirds, emerged as being consistently important. However, we emphasise that investigating breeding phenology in relation to prey phenology assumes that this is the single critical activity under selection (Visser & Both 2005). In reality, the entire life-cycle is under selection and responding to multiple environmental drivers, such that breeding phenology may be the outcome of trade-offs between several selection pressures. Ideally, in future work, multiple life-history traits should be investigated at the individual level to understand whether predators are adequately responding to changes in prey phenology and the fitness costs of mismatch.

CONCLUSIONS

Quantifying the shift in the phenology of a prey species has been suggested as an appropriate yardstick for interpreting whether a predator is shifting its phenology adequately to match the change in its environment often as a result of climate change (Visser & Both 2005). Our study followed this approach to assess phenological changes across multiple trophic levels of the pelagic food web in the western North Sea. At a broad spatial scale we found contrasting phenological trends between trophic levels that may indicate that the system is currently experiencing trophic mismatching. By developing a novel approach we also explored finer scale data on the timing of peak energy for avian predators in relation to temporal changes in the energy value of an important piscivorous prey. This analysis highlighted significant changes over 24 yr in temporal matching of the chick-rearing periods of 5 species of seabirds and in the size of 0-group sandeels such that prey length, and hence energy value of individual items, have declined significantly. To date, there is no evidence that these changes are impacting on the breeding success of any of the seabird species considered, but further changes, particularly if alternative prey are also affected adversely, could well have population level consequences for the North Sea seabird community.

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Contribution to the Theme Section 'Seabirds and climate change'

Differential advancement of breeding phenology in response to climate may alter staggered breeding among sympatric pygoscelid penguins

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ABSTRACT: Numerous studies link climate change with advancing breeding phenology in birds, but less frequently considered are the joint impacts on sympatrically breeding communities of birds. We used data on clutch initiation dates (CID) from 4 sites along the Western Antarctic Peninsula for 3 congeneric and sympatrically breeding penguin species (Adélie *Pygoscelis adeliae*, gentoo *P. papua* and chinstrap *P. antarcticus*) to understand what factors correlate with the phenology and synchrony of breeding and how these factors might change with the recent warming experienced in this region. We found that clutch initiation was most significantly correlated with October air temperatures such that all 3 species advanced clutch initiation to varying degrees in warmer years. Gentoo penguins were able to advance CID almost twice as much (3.2 d $°C^{-1}$) as Adélie (1.7 d $°C^{-1}$) and chinstrap penguins (1.8 d $°C^{-1}$). Beyond the variation explained by mean October temperatures, there was an unexplained trend to earlier clutch initiation of 0.15 ± 0.05 d yr^{-1}. Greater plasticity in gentoo breeding phenology compressed the mean interval between Adélie and gentoo breeding in warm years and this may increase competition for nesting space in mixed colonies. Our results suggest that differential responses in breeding phenology to changing temperatures represent an additional mechanism by which climate change may affect competitive interactions and, consequently, pygoscelid penguins on the Antarctic Peninsula.

KEY WORDS: Breeding phenology · Climate change · Pygoscelid · Breeding asynchrony · Adélie penguin · Chinstrap penguin · Gentoo penguin · Interannual variability

INTRODUCTION

To understand the biological effects of climate change, scientists need to understand not only the direct effects of climate change on individual species (reviewed in Parmesan 2006), but also how changing climate may affect complex interspecific interactions (Van der Putten et al. 2010). The most frequently studied interactions are 'trophic mismatches' in which disparate phenological changes between trophic levels affect species interactions (e.g. Visser & Both 2005 and references therein). Less frequently considered are intratrophic interactions that may be affected by climate change (exceptions include Chadwick et al. 2006, Ahola et al. 2007). Climate change can alter the relative timing of breeding and the ecological interactions among species that utilize a shared set of limited resources (food, breeding

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space, etc.). This effect may be particularly acute where migratory species co-exist with resident species, the latter of which are in a better position to respond to changing conditions at the breeding location and are therefore at a competitive advantage (Ahola et al. 2007). Although the effect of climate change on breeding phenology in birds has been considered in many studies (e.g. Brown et al. 1999, Crick & Sparks 1999, Przybylo et al. 2000, Both et al. 2004), the subsequent impacts of these phenological changes on interspecific competition among sympatrically-breeding bird species has only recently been addressed (Schaefer et al. 2006, Ahola et al. 2007). Although imperfect, biological responses to interannual variability in climate are perhaps the best indication available of how populations might respond to long-term changes due to regional climate change (Trathan et al. 2007). Breeding synchrony among individuals in a population, although bestowing a number of potential benefits for colonially nesting seabirds (Birkhead 1977, Hatchwell 1991, Murphy & Schauer 1996), may constrain a population from responding adequately to environmental variability (Reed et al. 2006) and, ultimately, adapting to longer-term climate change. Additionally, migration away from the breeding colony during non-breeding months may preclude a timely assessment of environmental conditions at the breeding site and thus may prevent an adequate phenological response to interannual or long-term climate change (e.g. Both & Visser 2001, Both et al. 2006).

Few places on the planet have warmed as quickly as the Western Antarctic Peninsula (WAP) (Vaughan et al. 2003), and abundant empirical evidence links the changing climate in this region to observed changes in physical (Smith & Stammerjohn 2001) as well as ecological systems (e.g. Croxall et al. 2002, Trathan et al. 2007, Clarke et al. 2007, Ducklow et al. 2007). Of particular interest is the impact of climate change on the WAP's 3 pygoscelid penguin species: Adélie (*Pygoscelis adeliae*), gentoo (*P. papua*) and chinstrap (*P. antarcticus*). The study of niche segregation among sympatric congeneric penguin species (e.g. Lishman 1985, Fraser et al. 1992, Lynnes et al. 2002, Wilson 2010) is complicated by the spatiotemporal heterogeneity of resources for which the species compete. Climate change introduces a dynamic element, as the ecological axes along which species are segregated adjust along with the resulting competitive relationships (Fraser et al. 1992, Croxall et al. 2002, Forcada et al. 2006). One such axis is breeding phenology, with Adélie, gentoo and chinstrap penguins breeding in sequence and over a restricted interval of 3 wk or less (Trivelpiece et al. 1987). The staggered timing of breeding among these species may reduce the extent of direct foraging competition during chick rearing (Croxall & Prince 1980, Lishman 1985, Trivelpiece et al. 1987), and the relative timing of arrival and nest building is an important factor for the ultimate distribution of limited snow-free nesting space, as gentoo and chinstrap penguins can outcompete Adélies for available space in mixed colonies (Trivelpiece & Volkman 1979, Trivelpiece et al. 1984, Carlini et al. 2005, Sander et al. 2007; see also Slagsvold 1975). Despite the potential for breeding phenology to mediate competitive interactions, relatively little quantitative work has been done to understand what environmental factors are correlated with the timing of breeding in pygoscelid penguins (exceptions include Bost & Jouventin 1990 and Barbraud & Weimerskirch 2006), how breeding phenology varies over the spatial scale of the peninsula, or the extent to which breeding synchrony may vary between species.

Building on an earlier study to develop predictive models of clutch initiation (Lynch et al. 2009), we used data on clutch initiation dates (CIDs) for all 3 species of pygoscelid penguin at 4 different sites on the WAP to address 3 specific hypotheses: (1) species differ in the degree of breeding synchrony within a colony, (2) interannual variation in pygoscelid penguin breeding phenology (as measured by CIDs) reflects interannual variation in environmental conditions immediately prior to clutch initiation, and (3) species differ in their phenological plasticity, and these differences reflect a dichotomy between those that are resident and migrant in the non-breeding period. In the Discussion, we use these results to understand how differential breeding plasticity and synchrony may impact interspecific interactions under a climate change scenario.

MATERIALS AND METHODS

Clutch initiation data were taken from long-term studies of penguin colonies at 3 penguin breeding locations (Table 1, Fig. 1): Cape Shirreff, Livingston Island (62° 28′ S, 60° 46′ W; 1997–2006); Admiralty Bay, King George Island (62° 10′ S, 58° 30′ W; 1991–2006); and Humble Island (64° 46′ S, 64° 06′ W; 1991–2000). Breeding phenology data were collected according to the CCAMLR Ecosystem Monitoring Program (CEMP) Standard Methods (Standard Method 9; CCAMLR 2004). Additional data were used from a short-term study at Petermann Island (65° 10′ S, 64° 10′ W;

Table 1. Details of study sites and clutch initiation data. n: range of clutch initiation dates (CIDs) recorded per year for each Species × Site combination (not including discarded CIDs; see 'Materials and methods' and Table S1 in the supplement at www.int-res.com/articles/suppl/m454p135_supp.pdf)

Site	Species	Period	n	Source
Admiralty Bay, King George Island (62° 10′ S, 58° 30′ W)	Adélie	1991–2006	83–194	W.Z.T. & S.G.T. (unpubl. data)
	Gentoo	1991–2006	38–199	W.Z.T. & S.G.T. (unpubl. data)
Cape Shirreff, Livingston Island (62° 28′ S, 60° 46′ W)	Chinstrap	1997–2006	57–99	W.Z.T. & S.G.T. (unpubl. data)
	Gentoo	1998–2004, 2006	23–53	W.Z.T. & S.G.T. (unpubl. data)
Humble Island (64° 46′ S, 64° 06′ W)	Adélie	1991–1996, 1999–2000	81–100	Fraser (2004)
Petermann Island (65° 10′ S, 64° 10′ W)	Gentoo	2005–2007	92–99	H.J.L., W.F.F. & R.N. (unpubl. data)
	Adélie	2005–2007	47–56	H.J.L., W.F.F. & R.N. (unpubl. data)

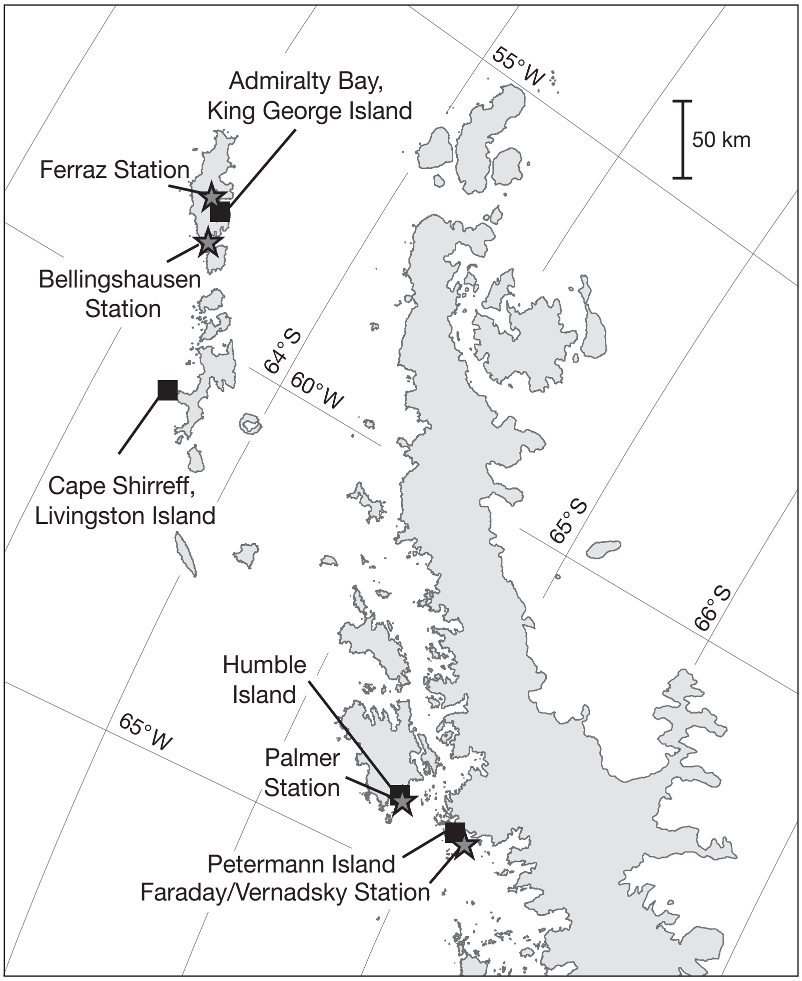

Fig. 1. The Antarctic Peninsula with sites (black squares) and weather stations (gray stars) used in this analysis

2005–2007); site details and field methods of the Petermann Island study may be found in Lynch et al. (2010). A total of 6108 CIDs were recorded. Of these, we discarded a small number (174) of CIDs because the first egg laid was not directly observed and CID had been inferred based on the timing of subsequent phenological events (e.g. second egg laid or first egg hatched). In all cases, new nests were chosen for observation each season, minimizing the potential for serial autocorrelation in CIDs.

We modeled mean clutch initiation (site j, year t) as a linear function of 3 *a priori* covariates — species (sp), latitude (lat) and year (measured relative to 2000) — and a suite of *a posteriori* environmental covariates. On the basis of previous studies reporting staggered breeding among sympatric pygoscelid penguins (e.g. Trivelpiece et al. 1987), we included species as a factor in our model. As latitudinal gradients have been found to be important in the breeding phenology of penguins (Warham 1972, Ainley 2002, Lynch et al. 2009) and other seabirds (Croxall 1984, Wanless et al. 2008), latitude was included as a covariate in the model. Year was included (as a fixed effect) to quantify any temporal trends in breeding phenology unaccounted for by trends in modeled environmental covariates. We considered 8 additional covariates representing various aspects of environmental conditions in the austral spring immediately prior to clutch initiation (August–October; Table 2). Monthly averages of mean air temperatures and sea-ice area were included for each of August, September and October. Both sea-surface temperature and monthly average Southern Oscillation Index were highly correlated between adjacent months and so a seasonal average (August–October) of these indices was used instead of separate monthly means. Models of CID at nest i, at site j, in year t took the form:

Table 2. Sources of environmental data considered in the model selection process.

	Source
Temperature	
King George Is.	Bellingshausen Stn (www.antarctica.ac.uk/met/gjma/)
Livingston Is.	
Petermann Is.	Vernadsky Stn (www.antarctica.ac.uk/met/gjma/)
Humble Is.	Palmer Station (LTER archive[a], http://pal.lternet.edu/)
SST	National Climatic Data Center Global Surface Temperature Anomalies Dataset (www.ncdc.noaa.gov/cmb-faq/anomalies.html)
SOI	University Center for Atmospheric Research Climate Analysis Section Data Catalogue (www.cgd.ucar.edu/cas/catalog/climind/SOI.signal.ascii)
Ice area	Palmer Station (LTER archive[b], http://pal.lternet.edu/)

[a] K. S. Baker (2008) Daily weather observations (air temperature, pressure, wind, precipitation) starting in April 1989

[b] S. Stammerjohn (2007) Mean monthly sea ice coverage for the PAL LTER region west of the Antarctic Peninsula derived from passive microwave

$$\mathrm{CID}_{i,j,t} \sim N(\mathrm{meanCID}_{i,j,t}, \tau^2_{\mathrm{sp}[i]}) \tag{1}$$

$$\begin{aligned}\mathrm{meanCID}_{i,j,t} \sim N(&\mathrm{sp}_i + \mathrm{lat}_j + \mathrm{year}_t + \\ &\text{additional covariate} \times \mathrm{sp}_i, \sigma^2_{j,t})\end{aligned} \tag{2}$$

where Eq. (1) links individual nest CID to population mean CID (meanCID) with a variance that depends on intraspecies breeding synchrony $\tau^2_{\mathrm{sp}[i]}$, and Eq. (2) links population mean CID to interannual variability in environmental conditions. The interaction between environmental conditions and species is included to account for potential differences in phenological response among the 3 pygoscelids. Note that empirical data for meanCID, and not model estimated meanCID from Eq. (2), are used in Eq. (1) to prevent error in Eq. (2) from inflating estimates of $\tau^2_{\mathrm{sp}[i]}$. All population-level mean CID data are given in Table S1 in the supplement at www.int-res.com/articles/suppl/m454p135_supp.pdf. Model parameters were given vague normal prior distributions and the precisions associated with model synchrony ($1/\tau^2$) and model error ($1/\sigma^2$) were given vague gamma distributions. Models were fit to the data using the software package WinBUGS (Spiegelhalter et al. 2003). We used a burn-in period of 1000 samples and drew our posterior distribution from the following 9000 samples in each of 3 overdispersed and randomly-initialized parallel Markov chain Monte Carlo chains. This was more than sufficient to achieve model convergence and adequate sampling of the posterior distribution. Models were compared using the deviance information criterion as described in Spiegelhalter et al. (2002).

RESULTS

There was overwhelming support for the model containing mean October temperature (Table 3). Mean October temperatures were significantly correlated with clutch initiation, and all 3 species showed an advanced schedule of breeding in response to warmer October temperatures (Table 4). CIDs were delayed 5 to 16 d in 1994 and 2002 because of unusually cold October temperatures (>2σ below the 1944–2006 mean at Bellingshausen Station). Although all 3 species demonstrated some degree of plasticity in breeding phenology, as defined by interannual variation in clutch initiation in response to environmental conditions, we found

Table 3. Models for CID ranked by fit to data. pD: rough measure of the effective number of parameters (Spiegelhalter et al. 2002); DIC: deviance information criterion; ΔDIC: difference between each model and the best model; w_i: model weight. The null model contains no environmental covariates and is included for comparison. sp: species; lat: latitude

Rank	Model: CID ~ sp + lat + year + covariates (see below) × sp	pD	DIC	ΔDIC	w_i
1	Mean October temperature	18.1	32600.6	0	~1.0
2	Mean August temperature	16.6	32641.1	40.5	<0.001
3	August–October average Southern Oscillation Index	17.7	32641.9	41.3	<0.001
4	August ice area	15.4	32642.3	41.7	<0.001
5	August–October average sea surface temperature	19.3	32644.3	43.7	<0.001
6	October ice area	13.6	32644.8	44.2	<0.001
7	September ice area	13.4	32646.0	45.4	<0.001
8	Mean September temperature	15.2	32647.7	47.1	<0.001
9	(No environmental covariates)	19.1	32649.3	48.7	<0.001

that gentoo penguins advanced breeding almost twice as much as either Adélies or chinstraps in response to warmer temperatures (Figs. 2 & 3, Table 4). In addition to the effect of warmer October temperatures on CIDs, we found an overall trend towards earlier reproduction of 0.15 ± 0.05 d yr^{-1} (posterior mean ± 1 SD) over the period for which data were available (1991–2007). This trend was significant for all of the models compared (Table 3) and, therefore, cannot be explained by underlying trends in any of the covariates not included in the final model. As such, the cause of this additional advance in CIDs is unknown.

Both species and latitude were significantly correlated with CIDs. Pygoscelid penguins bred in a predictable sequence, with Adélie penguins being the first to arrive and lay eggs, followed by the gentoos and then the chinstraps (Table 4, Fig. 2). At Admiralty Bay, model predicted mean CIDs in 2000 (mean October temperature = −2.0°C) were 29 October, 3 November and 19 November for Adélies, gentoos and chinstraps, respectively. Sites further south (negative latitude relative to Admiralty Bay) had delayed CIDs relative to more northerly sites (Table 4).

We found different levels of intraseason breeding synchrony among the 3 pygoscelid species (Table 4), with chinstraps showing the most synchronous breeding ($\tau = 2.7$ d), followed by Adélie penguins ($\tau = 3.6$ d) and then gentoo penguins ($\tau = 4.2$ d). All pairwise differences in synchrony were statistically significant (Table 4). Despite containing only 4 variables, our model for clutch initiation explained a large proportion of the variability in observed mean CID at the 4 study sites ($r^2 = 0.74$).

DISCUSSION

Despite strong similarities in breeding habitat, diet, clutch size and overall life history, breeding phenology is one niche axis along which the pygoscelid penguins are segregated. Our results provide strong evidence that climate change may significantly alter the absolute and relative timing of clutch initiation in these 3 species. Gentoo penguins are more asynchronous and demonstrate greater plasticity in breeding phenology than either Adélie or chinstrap penguins, with potential attendant consequences for interspecific interactions in mixed colonies.

There are compelling biological reasons why October temperatures might be expected to play a role in the timing of breeding of the 3 penguin species. All 3 study species at our study sites nest directly on rocks and breeding is conditional on the appearance of snow-free areas in October when penguins arrive to breed. Warm October temperatures hasten snow melt in breeding colonies and allow for earlier nest building and egg laying, although long-term trends in accumulation will reflect a balance between increased snow melt and changing patterns of precipitation (Thompson et al. 1994, Turner et al. 2005, Bracegirdle et al. 2008). Snow accumulation has been implicated as an important factor driving differential Adélie colony trends at the local (within-site) scale (Fraser & Patterson 1997, Patterson et al. 2003, Bricher et al. 2008), and the importance of snow-free areas to inter-season variability in the timing of gentoo breeding has been suggested by Gwynn (1953). In an Arctic analog, Moe et al. (2009) found that egg laying in ground-nesting little auks was strongly

Table 4. Model parameters, their interpretation and estimates (mean ± 1 SD of the posterior distribution). Clutch initiation dates (CIDs) are measured relative to 1 October (e.g. CID = 32 is 1 November), and latitude is measured relative to Admiralty Bay, King George Island (latitude is negative for sites further south). sp: species; lat: latitude; τ: standard deviation of intra-season intra-site breeding synchrony

Covariate	Interpretation of regression coefficient	Estimate
sp [Adélie]	Baseline CID for Adélie penguins	25.4 ± 0.6 d
sp [gentoo]	Baseline CID for gentoo penguins	27.6 ± 0.9 d
sp [chinstrap]	Baseline CID for chinstrap penguins	46.5 ± 1.4 d
lat	Effect of latitude	−5.2 ± 0.2 d deg^{-1}
Oct. temp. [Adélie]	Effect of mean Oct. temp. on CID for Adélie penguins	−1.7 ± 0.2 d $°C^{-1}$
Oct. temp. [gentoo]	Effect of mean Oct. temp. on CID for gentoo penguins	−3.2 ± 0.2 d $°C^{-1}$
Oct. temp. [chinstrap]	Effect of mean Oct. temp. on CID for chinstrap penguins	−1.8 ± 0.6 d $°C^{-1}$
year	Overall trend in CID shared by all 3 species	−0.15 ± 0.05 d yr^{-1}
τ [Adélie]	Within-site standard deviation of CID for Adélie penguins	3.62 ± 0.05 d
τ [gentoo]	Within-site standard deviation of CID for gentoo penguins	4.16 ± 0.06 d
τ [chinstrap]	Within-site standard deviation of CID for chinstrap penguins	2.73 ± 0.07 d

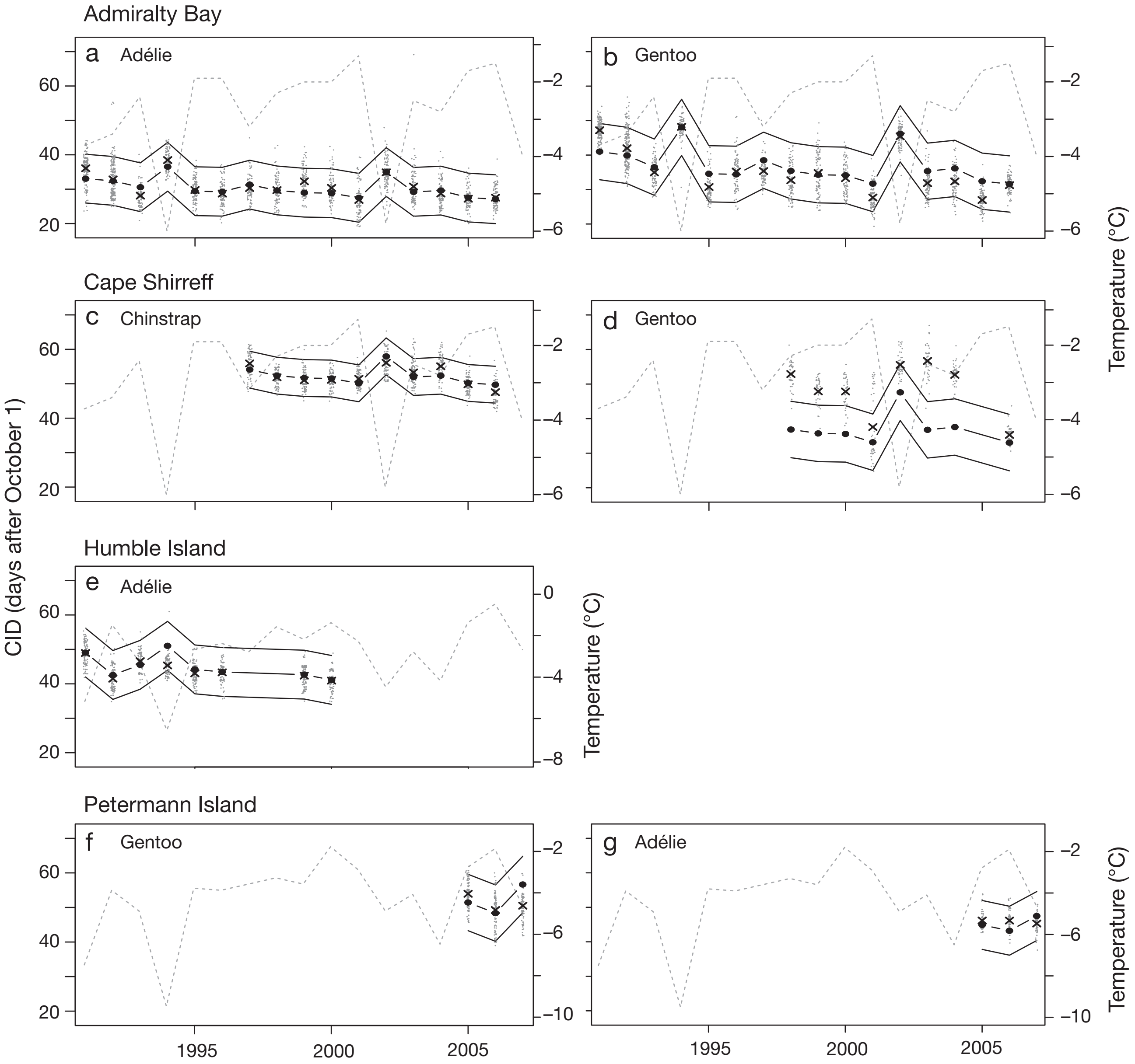

Fig. 2. Raw data and model results for (a) Adélie penguins at Admiralty Bay, (b) gentoo penguins at Admiralty Bay, (c) chinstrap penguins at Cape Shirreff, (d) gentoo penguins at Cape Shirreff, (e) Adélie penguins at Humble Island, (f) gentoo penguins at Petermann Island, (g) Adélie penguins at Petermann Island. The black solid circles and dashed lines represent the model estimate of the mean clutch initiation date (CID) and the solid lines above and below represent the mean CID ± 2τ (τ: standard deviation of intra-season breeding synchrony, see Table 4). Raw data are shown as gray dots (jittered for visual clarity) and the mean of the raw data indicated by black '×'s. Model fit can be assessed visually by comparing the mean CID predicted by the model (solid circles) with the mean of the raw CID data (black '×'s) and by comparing the separation between the upper and lower solid black lines with the temporal distribution of clutch initiation in the raw data (larger distribution = greater asynchrony in reproduction). October mean temperatures at Bellingshausen Station (a–d), Palmer Station (e) and Vernadsky Station (f,g) are plotted with a gray dotted line (scale on right axis). Panel rows (top to bottom) are arranged geographically, north to south

determined by the appearance of snow-free nesting sites and, as a consequence, found breeding phenology to be correlated with spring air temperature. Significant topography-mediated microscale variability makes it difficult to extrapolate snow depth at individual colonies from measurements recorded at the nearest meteorological station. Air temperature, although just one influence on spring snow melt, represents a useful proxy for modeling breeding phenology across a large latitudinal gradient.

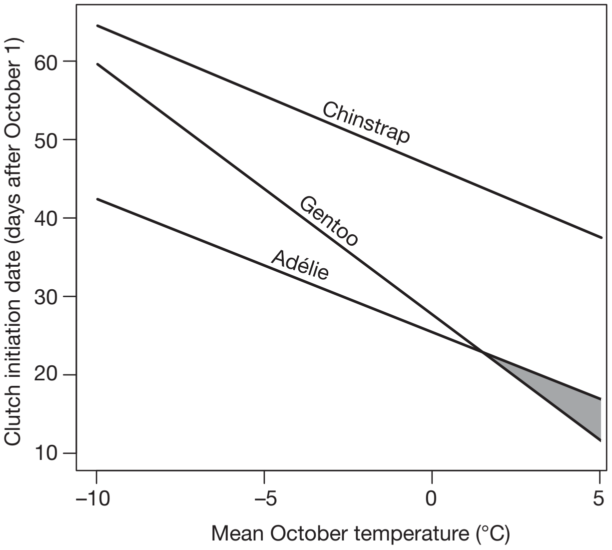

Fig. 3. Model-predicted clutch initiation dates (CIDs) for each species as a function of mean October temperature assuming a latitude equal to that at Admiralty Bay (62° 10' S) and the year 2000. At temperatures above 1.5°C, the mean CID for gentoos is predicted to occur before mean CID for Adélies by an amount represented by the gray shading

Potential effects of shifting phenology on competition and coexistence

In addition to being inshore feeders during the breeding season, gentoo penguins differ from Adélies and chinstraps by remaining in the waters near their breeding colonies throughout the austral winter (Wilson et al. 1998, Clausen & Pütz 2003, Tanton et al. 2004). For this reason, gentoos can be considered resident species relative to Adélies and chinstraps, both of which can migrate long distances from the colony in the non-breeding months (Davis et al. 1996, Fraser & Trivelpiece 1996, Trivelpiece et al. 2007, Ballard et al. 2010). The dichotomy between resident and migrant species is important in light of recent evidence that migrant species are often less able to respond appropriately to the phenological effects of climate change (Both & Visser 2001, Both et al. 2006, Rubolini et al. 2010), leading to disproportionate impacts on migrant species that can alter competitive relationships between resident and migrant bird species breeding at the same location (Ahola et al. 2007). Gentoo penguins, foraging in inshore waters near the breeding colony prior to the breeding season, are in a position to experience and take advantage of a warm spring and early snow melt whereas Adélies and chinstraps must decide when to return to the colony without the benefit of local information on breeding conditions.

Although differential foraging habitat use during the breeding season (diving depth and distance to shore) may mitigate interspecific competition for prey (Trivelpiece et al. 1987, Lynnes et al. 2002, Kokubun et al. 2010, Wilson 2010), penguins breeding in mixed-species colonies must still compete for snow-free breeding territory (Trivelpiece & Volkman 1979, Carlini et al. 2005). The average 2-day 'head-start' of Adélies over gentoos may not result in a significant temporal partitioning of prey resources during chick rearing, but it does allow Adélie penguins to establish nests in advance of the larger, and physically dominant, gentoo penguin. Gentoo penguins have been known to disturb adjacent Adélie penguins (H.J.L. & R.N., pers. obs.) and Adélie penguins nesting in gentoo-dominated colonies (>80% gentoo) have significantly lower reproductive success than those nesting in Adélie-dominated colonies (>80% Adélie) (H.J.L. unpubl. data). Likewise, other studies have reported that chinstrap penguins usurp nests from younger, less experienced and late-arriving Adélies, with adverse consequences on Adélie breeding success (Trivelpiece & Volkman 1979, Trivelpiece et al. 1984, Carlini et al. 2005). Thus, staggered arrival and clutch initiation may allow Adélie penguin populations to persist at gentoo-dominated sites (e.g. Booth Island, Petermann Island).

Our results show that the higher phenological plasticity of the gentoo penguin compresses the head-start of the Adélie penguin in warm years, which suggests that Adélie penguin populations will be disadvantaged as the WAP continues to warm. This may be one explanation for why small Adélie populations breeding in mixed colonies with gentoo penguins have been declining precipitously in recent years (Lynch et al. 2008). This effect — a climate-induced compression of the interval between the onset of breeding in sympatric species — is known to increase competition between species competing for limited resources (Slagsvold 1975, Slagsvold 1976, Ahola et al. 2007). The resident species, in this case the gentoo penguin, is expected to have a significant advantage over its 2 migratory congeners.

Breeding asynchrony and plasticity

We did not track CIDs of individual penguins across years and, therefore, we cannot unequivocally distinguish between phenotypic plasticity in individual response and microevolutionary change as a result of natural selection (see discussion of this dichotomy in Gienapp et al. 2008, Visser 2008). However, the time scale over which local populations responded to environmental cues (i.e. annually) relative to the generation time (8+ yr; Forcada & Trathan 2009) suggests that phenotypic plasticity played at least some role in the phenological variability observed in the present study; these results are consistent with other studies suggesting the same (Przybylo et al. 2000, Charmantier et al. 2008, Tøttrup et al. 2008, see also Forcada & Trathan 2009). Although population-level plasticity need not imply individual variability in phenotypic plasticity (Reed et al. 2006), there is evidence to suggest that individuals with more plasticity in breeding phenology may have a selective advantage over individuals less able to respond to local cues or environmental changes (Brommer et al. 2005, Nussey et al. 2005). However, highly synchronous colonial breeders derive many well-documented benefits from their synchrony (e.g. social foraging, reduced predation; Hoogland & Sherman 1976, Birkhead 1977, Ims 1990, Hatchwell 1991) that may select against highly plastic (and potentially asynchronous) individuals (Reed et al. 2006). Although all 3 of the penguin species studied are phenologically limited by the short austral summer on the Antarctic Peninsula, our results found significant differences in breeding synchrony, with gentoo penguins being the least synchronous and chinstraps the most synchronous of the pygoscelids. Without the constraints imposed by the more highly synchronous breeding strategy of the Adélies and chinstraps, gentoo penguins may be more free to respond to environmental cues.

The extent to which individual variation in timing of breeding (i.e. early or late relative to environmental cues or the colony's mean breeding date) affects reproductive success and, ultimately, fitness is unknown, but early breeding has been associated with higher breeding success in pygoscelids (Bost & Jouventin 1991, Viñuela et al. 1996) and other colonially nesting seabirds (Reed et al. 2006, 2009). Such differential breeding success would drive a population-level shift to earlier breeding even if individuals in a population showed a high degree of variability in phenological plasticity, although the strength of heritability in the timing of egg laying among pygoscelids remains unclear. On an interspecific level, we would expect that a species with a more plastic breeding phenology would be at an advantage over its less-plastic congeners, which is consistent with the rapid growth of gentoo penguin populations and sharp declines in Adélie and chinstrap populations where they overlap in the southern WAP (Ducklow et al. 2007, Lynch et al. 2008). The optimum balance between the advantages of plasticity in response to a changing climate and the advantages of breeding synchrony will differ across the wide environmental gradient inhabited by each of the 3 penguin species, but the rapidity of change on the WAP will likely tip the balance in favor of individuals, populations and species capable of adapting quickly.

Role of sympatric associations on breeding phenology

Despite broad agreement between the model and the data, our model fit poorly for gentoo penguins breeding at Cape Shirreff (Fig. 2d). If we removed gentoos at Cape Shirreff from consideration, the fit of mean predicted CID to the observed mean CID improved considerably (r^2 increases from 0.74 to 0.94). Gentoos at Cape Shirreff bred 14.8 d on average (and up to 25.9 d) later than gentoos only 130 km away at Admirality Bay (a difference nearly equal to the ~16 d gentoo laying period; Trivelpiece et al. 1987) and 19.9 d on average later than predicted by the model. One important difference between these 2 sites is the different sympatric associations involved. At Admirality Bay, gentoos breed alongside Adélie penguins, which are the earliest to breed of the 3 pygoscelid penguins, but at Cape Shirreff, gentoos breed alongside chinstrap penguins, which are the last of the 3 species to initiate breeding. It has been hypothesized that the staggered breeding of the pygoscelid penguins is a byproduct of dissimilar sea ice tolerances as reflected in the typical sea ice phenology of their disparate but overlapping ranges (Trivelpiece et al. 1987, Fraser et al. 1992). An alternative explanation is that staggered breeding facilitates the temporal partitioning of prey resources (Lishman 1985). The former explanation would predict no difference in the breeding phenology of gentoos at these 2 sites; therefore, our results are inconsistent with this explanation. In contrast, competitive interactions would predict that gentoos that breed at Cape Shirreff would breed earlier than gentoos at Admiralty Bay, but this is opposite of what we found. Neither of these explanations is consistent with the phenological differences between these 2 sites. A third possibility is that enhanced interspecific synchrony might be advantageous for predator swamping (Ims 1990). Gentoos may benefit from timing their breeding in synchrony with other penguins so as to minimize adult mortality by leopard seals

(*Hydrurga leptonyx*) and egg and chick mortality by skuas (*Catharacta* spp.). Actively brooding neighbors are also less likely to flush off the nest when disturbed and are thus less likely to trample or otherwise interfere with incubation than pre-breeders or non-breeders (Murphy & Schauer 1996). These hypotheses are currently being investigated.

Long-term forecasts

Current climate models for the Antarctic Peninsula predict a continued shift towards warmer and wetter conditions (Meehl et al. 2007). Our study of phenological responses to interannual variation imply that continued warming will cause additional advances in breeding phenology for all 3 pygoscelid species until gains are balanced by increased early spring snow (Thompson et al. 1994), temporal mismatches with prey resources (Trivelpiece et al. 1987), or physiological constraints of light or pre-season body condition (e.g. Ainley 2002). Although mean October air temperature explained much of the interannual variation in CIDs, the remaining trend of earlier laying (0.15 ± 0.05 d yr^{-1}) shared by all 3 species requires further investigation. Uncertainties regarding future climate change scenarios preclude long-term forecasts of breeding phenology on the WAP, although future efforts to understand population-wide changes should consider the potential role of shifting breeding phenologies and the effect such shifts may have on interspecific competition for resources.

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Contribution to the Theme Section 'Seabirds and climate change'

Effects of climate variability on breeding phenology and performance of tropical seabirds in the eastern Indian Ocean

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ABSTRACT: We compared 20 yr of seabird breeding data with oceanographic variables (sea level, sea-surface temperature) and a climate index (Southern Oscillation Index; SOI) for the lesser noddy *Anous tenuirostris*, brown noddy *A. stolidus*, sooty tern *Onychoprion fuscata* and wedge-tailed shearwater *Ardenna pacifica* at the Houtman Abrolhos, eastern Indian Ocean. We found that timing of breeding and performance of these species is related to climate variability, mediated by oceanographic conditions within the eastern boundary Leeuwin Current (LC). The 3 migratory species have breeding parameters which are correlated with sea level and the SOI, while the first egg date of the resident lesser noddy is correlated with SST during their pre-breeding phase. There was poor breeding performance for each species during El Niño Southern Oscillation (ENSO) conditions; moreover, poor breeding success was recorded for all species outside of ENSO events in the latter years of the study. In addition, breeding was delayed for all species during the time of the present study. The environmental conditions contributing to this appear to be fewer years of strong LC flow with associated high sea levels, warmer SSTs, stronger eddy energy and increased productivity. Migratory seabird species breeding at this location appear less able to respond to climate variability — and its influence upon prey availability — than the resident species. It is suggested that the resident lesser noddy may have an advantage due to its response to a localised environmental cue, SST, in the pre-breeding phase, which may be correlated with prey availability in the waters surrounding the Houtman Abrolhos.

KEY WORDS: Seabirds · Indian Ocean · ENSO · Climate · Variability · Leeuwin Current · Demography · Lesser noddy

INTRODUCTION

A diversity of breeding strategies are demonstrated by seabirds to accommodate local trophic connections and ensure that reproductive success is maximized (Lack 1968). However, seabird breeding parameters (e.g. phenology, participation rates and breeding success) are often affected by large-scale atmospheric climate phenomena, such as the El Niño Southern Oscillation (ENSO; Dunlop et al. 2002, Ramos et al. 2006, Surman & Nicholson 2009a,b) and the North Atlantic Oscillation (NAO; Frederiksen et al. 2004, Wanless et al. 2009), as well as localised weather conditions such as wind speed and sea-surface temperature (SST; Ramos et al. 2002, Smithers et al. 2003, Peck et al. 2004, Frederiksen et al. 2004, Jaquemet et al. 2007) that may limit the abilities of seabirds to adapt to changes in prey availability. Marine ecosystems are changing and are predicted to change substantially in response to climate change, with subsequent impacts to biodiversity and productivity (Poloczanska et al. 2007, Burrows et al. 2011). In particular, the timing of food availability is likely to shift in most marine environments, and seabirds will need to adjust their breeding phenology and/or trophic niche if they are to adapt to climate change.

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The ability to respond to climate variability, and variation in food availability (Ainley et al. 1995, Nicholson 2002, Surman & Nicholson 2009a,b), appears to be influenced by life-history traits. Response to changing regional cues by seabirds in 2 North Sea colonies showed contrasting patterns, with the breeding phenology of some species becoming earlier, some not changing at all, and still others becoming later, which appeared to reflect differing life-history traits such as foraging method and diet (Wanless et al. 2009). Life-history traits such as a protracted post-natal growth period can inhibit such plasticity in timing of breeding in response to environmental cues, in which case other breeding parameters such as participation and success decrease in response to low food availability. For example, the wedge-tailed shearwater *Ardenna pacifica* (previously *Puffinus pacificus*), a highly synchronous migrant tropical seabird species with protracted post-natal growth, experiences high variation in breeding productivity at 4 colonies located between 20° and 29° S in the eastern Indian Ocean, where poor years have been correlated with strong ENSO events, as measured by the Southern Oscillation Index (SOI; Dunlop et al. 2002, Nicholson 2002).

The degree to which a seabird can adjust their breeding phenology in response to climate variability may be dependent upon the environmental cues that they experience during their non-breeding phase. For example, migratory seabird species in the North Sea had an onset of breeding which was correlated with the NAO, whereas a resident species was more affected by localised SST (Frederiksen et al. 2004). Responding to more localised cues may confer some advantage for breeding success, as tropical seabird species breeding in the eastern Indian Ocean at 29°S experienced later onset of breeding and reduced productivity during seasons coinciding with ENSO events, although a resident species was less affected than the migratory species (Surman & Nicholson 2009a,b).

In the eastern Indian Ocean, interannual variability of the ENSO cycle induces changes in the mesoscale variability (e.g. eddy shedding) of the poleward flowing Leeuwin Current (LC; Fig. 1) (Feng et al. 2009); the LC is the primary driver of marine ecosystem productivity along the Western Australian coastline. The LC is sourced from the Pacific via the Indonesian Through-Flow, and flows between latitudes 22° and 34° S before turning eastwards and continuing into the Great Australian Bight. Seasonal and interannual variability of the LC is found to be a key factor influencing coastal SST, sea level, marine productivity and fisheries recruitments along the continental slope of the Western Australian coastline (Caputi et al. 2009, Feng et al. 2009, Thompson et al. 2011). This region is one of generally low biological productivity, as the low-density, warm waters of the LC flow southwards over the top of the cooler, denser, and northward-flowing Westralia Current, preventing upwellings of nutrient-rich waters into the photic zone (Feng et al. 2009). As a consequence, seabird abundance in the eastern Indian Ocean is much lower, and tropical species occur much further south, than at equivalent latitudes off the west coasts of Africa and South America, which possess northward-flowing currents and strong coastal upwellings (Wooller et al. 1991). The strength of flow of the LC and its eddy field varies seasonally, mostly due to variation of surface winds, as well as interannually (with the occurrence of ENSO events) in its cycle (Feng et al. 2009), with consequent effects upon marine pelagic production. During the austral winter and in La Niña (non-El Niño) years, the LC flow becomes more rapid, resulting in higher sea levels (by up to 20 cm at Fremantle; Feng et al. 2009) and warmer sea temperatures along shelf waters of the Western Australian coastline (Cresswell et al. 1989, Koslow et al. 2008, Thompson et al. 2011).

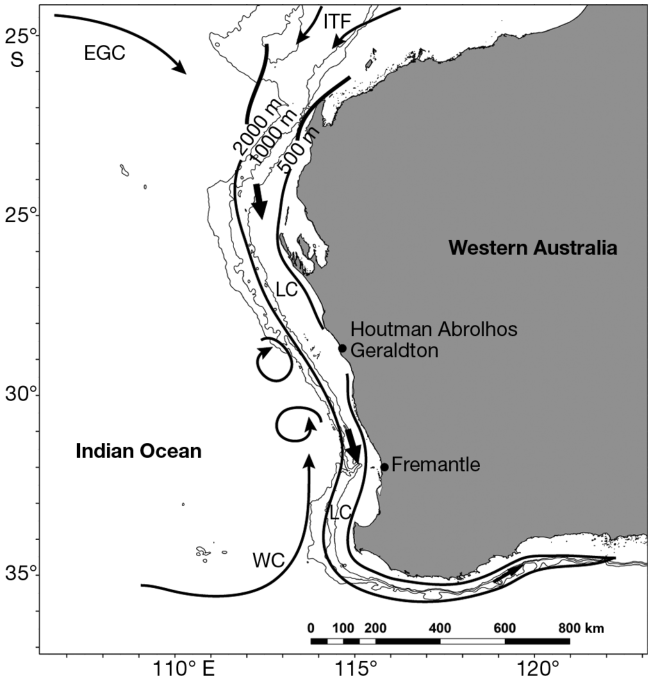

Fig. 1. Bathymetry of the Western Australian coastline, depicting the Indonesian Through-Flow (ITF), the Leeuwin Current (LC), the Eastern Gyral Current (EGC), the Westralia Current (WC) and the approximate positioning of the seasonal (autumn/winter) meso-scale eddies located near the Houtman Abrolhos

Strong annual and seasonal differences in marine pelagic productivity associated with the biophysical properties in LC mesoscale eddies have been identified (Koslow et al. 2008, Feng et al. 2009), particularly north and south of the Houtman Abrolhos region (29° S; Fig. 1). The Houtman Abrolhos is the central breeding area for the eastern Indian Ocean metapopulations of the lesser noddy *Anous tenuirostris*, brown noddy *A. stolidus*, sooty tern *Onychoprion fuscata* and wedge-tailed shearwater. This region contains one of the southernmost extensions of tropical marine flora and fauna in the Indian Ocean, principally due to the southward flow of the LC, which provides breeding seabirds with a mixture of tropical and temperate prey sources (Surman & Wooller 2003). In the present paper, we used 20 yr of data (1991 to 2010) to compare seabird response to large-scale, regional and fine-scale climatic signals, as indicated by variation in the breeding parameters of these 4 species. As we are interested in the ability of seabirds to respond to variation in climatic signals, as determined by life-history traits, these are outlined for each of the study species in Table 1 and include non-breeding distribution, timing of breeding, foraging distance from breeding colony and breeding diet.

Previous studies found that breeding success was severely reduced in all 4 seabird species during ENSO events, which coincided with reduced volumes of key prey species in regurgitates, particularly in the noddy species (Surman & Nicholson 2009a,b). Over time, increasing years of poor breeding performance for all species were recorded outside ENSO events, accompanied by a significant seasonal delay in the onset of breeding (date of first egg) in the 3 tern species (Surman & Nicholson 2009a). Years of poor breeding performance were not restricted to the Houtman Abrolhos seabird colonies, as wedge-tailed shearwater colonies between 20° and 29° S also had poor productivity in the same seasons (Dunlop et al. 2002), suggesting that these seabirds were all responding to the same large-scale environmental cue (ENSO variability). Therefore, our over-arching hypothesis is that timing of breeding and breeding performance by seabirds are related to climate variability, which is mediated by oceanographic conditions within the LC. Specifically, we predict that timing of breeding of the noddy and tern species (e.g. egg lay date) is frequently delayed in years characterized by lower sea levels, given that sea level is a proxy for the strength of the LC and that the LC flow is weaker during ENSO events. Furthermore, we postulate that a trend in later breeding dates of seabirds reflects changes in key prey resources (forage fish) that are governed by regional ocean conditions. To test this, we compared up to 20 yr of seabird breeding parameters with oceanographic variables (sea level, SST) and a climate index (SOI).

Table 1. The non-breeding distribution, timing of breeding, foraging distance from the colony while breeding and breeding diet (collected between 1991 and 2001) for 4 species of seabirds breeding on Pelsaert Island at the Houtman Abrolhos, based on Gaughan et al. (2002), Surman & Wooller (2003), Surman & Nicholson (2009a)

Species	Non-breeding distribution	Timing of breeding and mean lay date	Foraging distance (km)	Breeding diet
Sooty tern *Onychoprion fuscata*	Dispersal from colony, returning in late austral winter/early spring	Highly synchronous, flexible timing, austral spring in Oct–Nov	480–600	Wide variety of pelagic prey; >60 % squid, myctophids
Lesser noddy *Anous tenuirostris*	Over-winters at colony	Synchronous, flexible timing, austral spring in Oct–Nov	180	Larval ichthyoplankton, several species; >40 % inshore larval beaked salmon *Gonorynchus greyi*; 27 % black-spotted goatfish *Parupenseus signatus*
Brown noddy *Anous stolidus*	Dispersal from colony, returning in late austral winter/early spring	Synchronous, flexible timing, austral spring in Oct–Nov	180	Larval ichthyoplankton, approximately 70 % 1 species — inshore larval beaked salmon *Gonorynchus greyi*
Wedge-tailed shearwater *Ardenna pacifica*	Dispersal from colony, returning in late austral winter/early spring	Highly synchronous, static timing, first egg 17–23 Nov each year	Up to 400	Pelagic prey, few species; 60 % squid, adult scaly mackerel *Sardinella lemuru*

MATERIALS AND METHODS

Study location and species

The study was conducted on Pelsaert Island (28° 56′ S, 113° 58′ 30″ E), the southernmost and third largest of an archipelago of 192 islands, islets and rocks (the Houtman Abrolhos), 60 km off the mid-western coast of Australia (Fig. 1). Pelsaert Island (120 ha) is 12 km long, 50 to 500 m wide and very low (<3 m above high water), comprising sand and coral rubble on pavement limestone. On Pelsaert Island, the lesser noddy *Anous tenuirostris* (35 000 pairs) nests in white mangrove *Avicennia marina* trees, the brown noddy *Anous stolidus* (130 000 pairs) nests on low nitre bush *Nitraria billardierei* and samphire *Halosarcia halocnemoides* bushes, the sooty tern *Onychoprion fuscata* (260 000 pairs) nests on bare ground below herbaceous *Atriplex cinerea* and nitre bushes and the wedge-tailed shearwater *Ardenna pacifica* (75 000 pairs) digs burrows up to 1 m long in sandy areas throughout the southern portion of the island (Surman & Wooller 1995, 2003). All 4 seabird species breed during the austral spring/summer (Table 1). The Pelsaert Island colonies contain 99% of all brown noddies and 70% of all lesser noddies breeding along the Western Australian coastline, as well as the largest colonies of sooty terns and wedge-tailed shearwaters in the eastern Indian Ocean. The tern species share breeding times of between 75 and 85 d (Surman 1998), while the wedge-tailed shearwater has a much longer breeding time of 120 d (Serventy et al. 1971) and, as a consequence, has the least ability to shift timing of breeding. The lesser noddy is a resident species at this location, with the other 3 species migrating northwards during the austral winter (Surman 1997). Differences in the diet of these 4 species are given in Table 1.

Seasonal and interannual variability of the Leeuwin Current

The LC is a unique southward-flowing tropical eastern boundary current of warm (>24°C), low-salinity (<35‰) water which flows in a broad and shallow band (200 km wide by 50 m deep) at speeds of up to 2 km h^{-1}, along the continental shelf of Western Australia (Cresswell 1990, Pearce 1991). For the purposes of analysing seabird response to climatic variation mediated by the LC, we used the fine-scale climate signals of sea level at Geraldton and Fremantle (as Western Australian coastal sea level is a proxy for LC flow; Pearce 1991) and seasonal SST (austral winter, when LC flow is strongest, and austral spring, during the pre-breeding phase of the 4 study species) at the Houtman Abrolhos, as SST increases when LC flow is stronger (Feng et al. 2009).

Breeding phenology, participation and success

Nest sites of each species were selected at random and permanently marked. Nest contents were recorded weekly over the spring to summer period (September to May) between 1991 and 2001, and in more recent years (2002 and 2010), during several shorter visits between October and January of each year. There are some data gaps in these latter years which were excluded from analyses, and the resolution of breeding parameter data is higher for some of the study species, particularly in the latest 8 yr. The burrow contents of the wedge-tailed shearwater were determined using an electronic burrowscope (custom-made: model Nicholson 2010). Breeding participation was recorded as the percentage of the total sample size of nest sites or burrows that contained an egg, for each study species, during the breeding season. All 4 study species produce 1 egg clutch^{-1}, and only the noddy and tern species are capable of re-laying if an egg is lost, predated, or damaged. Egg-laying chronology was determined using lay dates of known age eggs, and the laying dates of other eggs were estimated by backdating, using egg-water loss techniques (Wooller & Dunlop 1980, Surman & Wooller 1995). Eggs known to be re-laid were excluded from calculations of the mean date of laying for each species. Chick age was estimated from growth curves described in Surman (1997).

Environmental parameters

Environmental data for the years 1991 to 2010 were used in all tests. ENSO events were measured using the SOI, which is based on the difference in atmospheric pressure between Tahiti, in the Pacific, and Darwin in northern Australia, and is expressed as positive values (La Niña) or negative values (El Niño) (Pearce & Walker 1991). The mean monthly and total annual SOI was obtained from the Australian Bureau of Meteorology (www.bom.gov.au).

The strength of flow of the LC was proxied using the mean monthly sea level at Fremantle and Geraldton, Western Australia; data were obtained from the National Tidal Facility, Flinders University, Australia.

Sea level height is a reliable indicator of the influence of the SOI upon the LC flow (Pearce 1991). Sea level is measured by remote tidal gauges in centimeters and presented in units of meters. Monthly mean SST (°C) was obtained using the Reynold's SST database for the latitude band at 28.5° S, between 113.5° and 114.5° E. For the purpose of comparison with breeding parameter data, SST was used for 2 pre-breeding periods (April to June and August to September). It was not the purpose of the present paper to look at potential effects of fine-scale fluctuations in SST during the breeding period for the 4 study species, but rather the oceanic conditions which may affect prey availability and distribution prior to breeding.

Analysis

Our first objective was to examine the relationship between ocean conditions and climate variability. To do this we used general linear regression to quantify the concordance among environmental variables within the LC. Our goal with this analysis was to describe the environmental state that seabirds experienced over a 20 yr period. Our second objective was to quantify and compare breeding parameters among seabird species to describe the patterns of breeding activity over the last 20 yr. It has previously been reported that the commencement of breeding was later between 2000 and 2007 when compared with 1991 to 1999 (Surman & Nicholson 2009a). To test if tern species were breeding later and were being less successful through time, we used a general linear regression to compare the date of first egg, mean lay date, breeding participation and breeding success over time for the years 1991 to 2010, inclusive. Breeding success was used as a measure of reproductive performance, by estimating the proportion of all eggs laid that resulted in a fledgling. Trends over time were not corrected for changes in population size. Our third objective was to determine if there are environmental conditions that can be used to predict changes in seabird breeding phenology. To conduct this analysis, we first removed trends in seabird metrics and environmental variables (Hudson 2010) because we are interested in quantifying the covariation between seabirds and environmental conditions at the interannual scale. We used a combination of linear regression and nonparametric correlation analysis to compare seabird breeding metrics with environmental variables. Significance of correlation analysis was estimated using a Monte Carlo randomization (n = 5000) procedure (Manly 2007).

RESULTS

Trends in timing of breeding, breeding participation and success

Wedge-tailed shearwaters commenced breeding on or near 17 November each year, with no discernable interannual variability. Commencement of breeding was more variable for the noddy and tern species (Fig. 2), with first egg dates becoming significantly later through time (Table 2). In addition, the

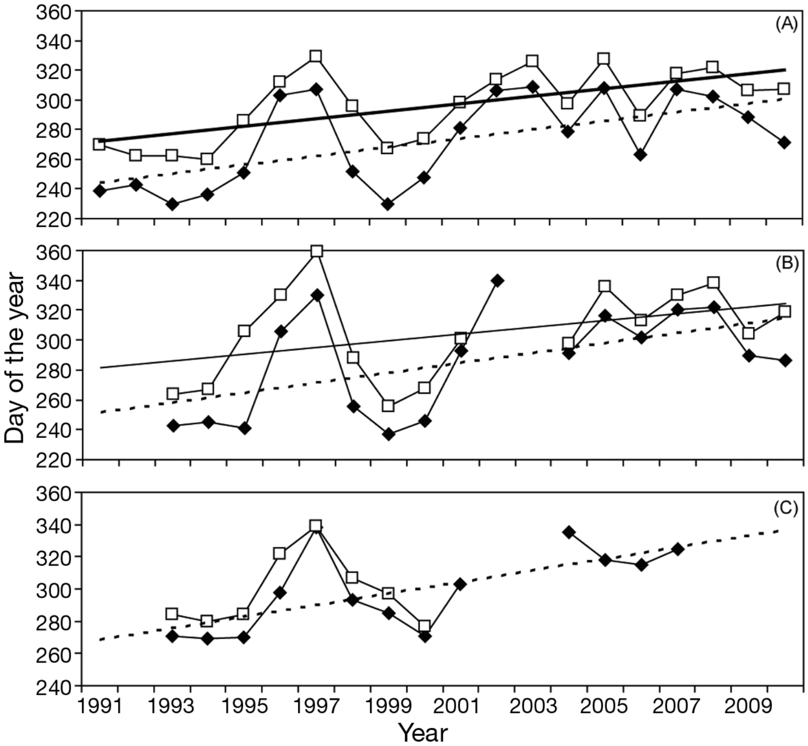

Fig. 2. Timing of breeding (day of the year, where 27 October = 300) as represented by the date of first egg (◆) and mean lay date (□) in (A) lesser noddy *Anous tenuirostris*, (B) brown noddy *Anous stolidus* and (C) sooty tern *Onychoprion fuscata* and wedge-tailed shearwater *Ardenna pacifica* (shown as a dashed line as there is no interannual variation within a 6 d period — 17 to 23 November) at Pelsaert Island, Houtman Abrolhos, Western Australia, between 1991 and 2010. In (A, B) the dashed line indicates the trend for first egg and the solid line for mean egg dates, respectively

Table 2. Trends over time (day of the year or percentage per year) for seabird breeding parameters from 1991 to 2010 for 4 species of seabirds breeding on Pelsaert Island, Houtman Abrolhos. Trends are uncorrected for changes in population size. An asterisk indicates insufficient data. Wedge-tailed shearwater egg dates not included as this species is highly synchronous and lays at the same time every year between 17 and 23 November. **Bold** values indicate significance at p ≤ 0.05

Seabird breeding parameters	N (yr)	*t*	p
Lesser noddy *Anous tenuirostris*			
First egg date	20	3.02	**0.007**
Mean lay date	20	3.45	**0.003**
Participation	19	0.29	0.78
Success	14	−0.89	0.39
Brown noddy *Anous stolidus*			
First egg date	17	2.41	**0.03**
Mean lay date	16	1.73	0.10
Participation	17	−0.02	0.98
Success	14	0.10	0.92
Sooty tern *Onychoprion fuscata*			
First egg date	13	3.03	**0.01**
Mean lay date	8	0.39	0.08
Participation	11	0.47	0.64
Success	*	*	*
Wedge-tailed shearwater *Ardenna pacifica*			
Participation	15	−3.45	**0.004**
Success	10	−2.29	**0.05**

phenology of both noddy species was delayed significantly during the 1996-97 and 1997-98 austral summers, with mean lay dates 65 d later (lesser noddy) and 98 d later (brown noddy) than during preceding years (Fig. 2). Variability in the onset of breeding was greatest for brown noddies, with a range of 103 d. In contrast, mean lay date for shearwaters varied by a single day each year (Fig. 2). While mean lay date became later for both noddy species, it was only significantly delayed for the lesser noddy (Table 2). Delays in breeding dates over time are also demonstrated by considering relative laying dates each year, measured as the difference between the long-term lay date (mean or first) and the annual mean date of laying (Fig. 3). There was a significant positive regression between the long-term mean date of first egg and the first egg date for each year between 1991 and 2010 in the lesser noddy ($t_{18} = 3.03$, $p = 0.069$, $r^2 = 0.34$), brown noddy ($t_{15} = 2.41$, $p = 0.029$, $r^2 = 0.28$) and sooty tern ($t_{11} = 3.03$, $p = 0.014$, $r^2 = 0.46$) (Fig. 3). There was also a significant positive regression between the running long-term mean lay date and the mean lay date for each year between 1991 and 2010 in the lesser noddy ($t_{18} = 3.45$, $p = 0.003$, $r^2 = 0.39$).

During 1991 to 2010, delayed breeding was accompanied by a decline in the proportion of the noddy and tern population participating per year (Fig. 4A). Wedge-tailed shearwater breeding participation declined significantly over time (Table 2). The lowest breeding participation was evident in 1996-97 for the sooty tern and lesser noddy (Fig. 4A). Wedge-tailed shearwaters, brown noddies and sooty terns did not attempt to breed during the 1997-98 ENSO event, and also showed low breeding participation during the 2002-03 ENSO event. The lesser noddy appeared to be the least affected during ENSO conditions, with breeding participation increasing during 1997-98 and 2002-03 compared with the previous seasons (Fig. 4A).

Breeding success data for all study species was not continuous after 2002. For the 2 noddy species, breeding success did not decline significantly over time (Table 2), but was low in the 1996-97, 1997-98, 2002-03 and 2004-05 seasons, coinciding with negative SOI values during these years (Fig. 4B). Poor breeding success occurred for all species outside probable ENSO events as well. Brown noddy breeding success was <10 % in 2007-08 (La Niña conditions) and in 2009-10, while lesser noddy breeding success was >40 and 30 %, respectively, in the same years. Wedge-tailed shearwater breeding success significantly declined over time (Table 2), and was zero for the 1997-98, 2007-08 and 2009-10 seasons (Fig. 4B).

Relationships between climate signals

As expected from the published literature, sea level at Geraldton and Fremantle was positively correlated with the SOI (Table 3, Fig. 5); higher sea levels were associated with positive SOI values reflective of La Niña conditions, while lower sea levels were associated with negative SOI values reflective of El Niño conditions. SST in the austral autumn of each year (when the LC becomes strongest in its annual cycle) was positively correlated with coastal sea levels in Geraldton and Fremantle, as well as with the SOI. The correlation between these signals was not significant within the late austral winter/early spring period (Table 3). The SST in the late austral winter/early spring was significantly and negatively correlated with SST in autumn so that higher SST in autumn was associated with lower SST in late winter/early spring, when the study species are present at the colony and preparing to breed.

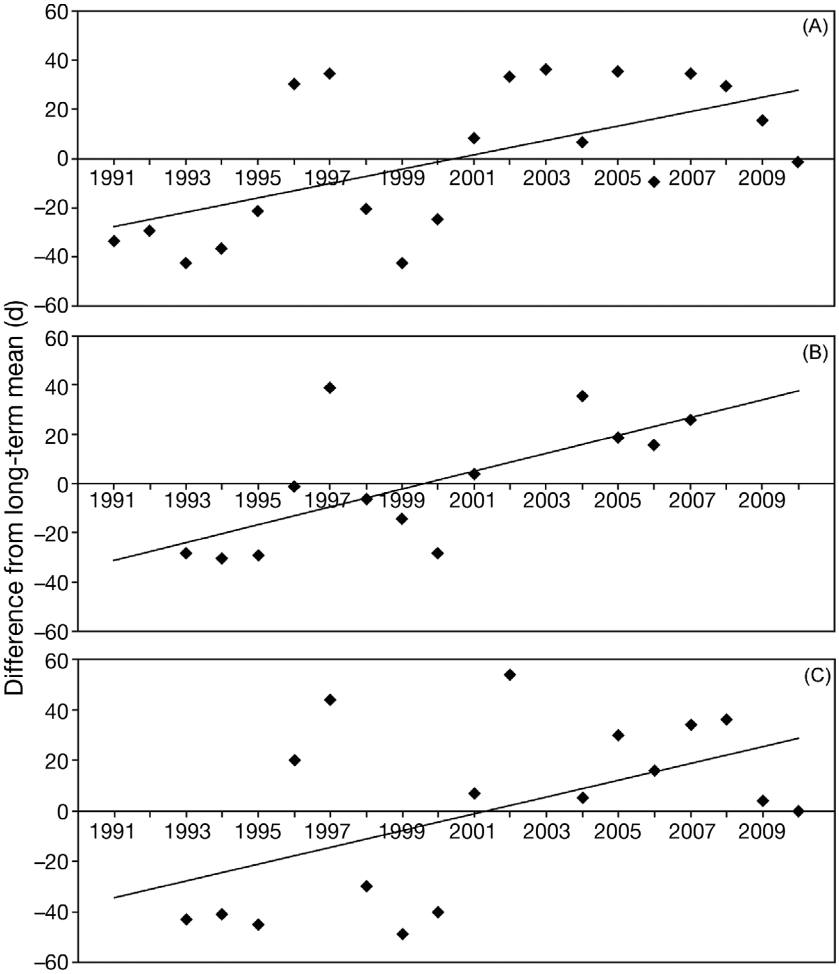

Fig. 3. *Anous tenuirostris, Onychoprion fuscata,* and *Anous stolidus*. Difference (in days) of the date of first egg from the long-term mean for the (A) lesser noddy, (B) sooty tern and (C) brown noddy at Pelsaert Island, Houtman Abrolhos, Western Australia, between 1991 and 2010

Relationships between environmental variables and breeding seabirds

We removed trends in order to examine the relationships among seabird breeding parameters and environmental variables. We found that first egg date of the brown noddy and sooty tern was inversely correlated to sea level at Geraldton (Table 4). First egg date of the lesser noddy was inversely correlated with SST during the pre-breeding months of August to September (Table 4); cooler SST in late winter/early spring results in later lay dates. Breeding success of the wedge-tailed shearwater and brown noddy was significantly and positively correlated with sea level at Geraldton (and Fremantle for the wedge-tailed shearwater) and the SOI (Table 4), so that higher sea levels and SOI values resulted in more successful breeding seasons.

DISCUSSION

The timing of breeding and breeding performance of the seabirds at Houtman Abrolhos is related to climate variability, mediated by local oceanographic conditions within the LC off western Australia. Our first objective was to describe the environmental state that these eastern Indian Ocean seabirds have experienced over the past 20 yr. The relationships we found are as expected based on the literature (Pearce 1991, Feng et al. 2009). Local sea level was positively correlated with the SOI, with higher sea levels and autumn SSTs during positive periods of the SOI. When the SOI is positive, southward flow of the LC is stronger causing southward advection of warm subtropical waters from the Indonesian Flow-Through to the western Australian shelf (Cresswell et al. 1989, Koslow et al. 2008, Thompson et al. 2011). In turn, during years of positive SOI, greater LC flow, higher sea level and warmer SST, 2 of the migratory seabirds experienced earlier breeding, all 3 migratory species experienced increased breeding participation and higher breeding success. Similarly, for the resident lesser noddy, earlier onset of breeding was associated with warmer SST in late winter/early spring. It can therefore be concluded that positive SOI conditions (as observed during La Niña) are better for seabird breeding performance at the Houtman Abrolhos.

Mechanistically, the LC carries greater surface nitrate than surrounding waters. When the LC is active, marine productivity is enhanced, with extensive autumn/winter shelf-scale phytoplankton blooms and increased fisheries production (Caputi et al. 2009, Thompson et al. 2011). However, despite the fact that the LC advects warmer waters into the system, the bloom is maintained by cooling and storms (Koslow et al. 2008). There is also greater eddy energy associated with stronger flow of the LC, which increases vertical nutrient mixing and

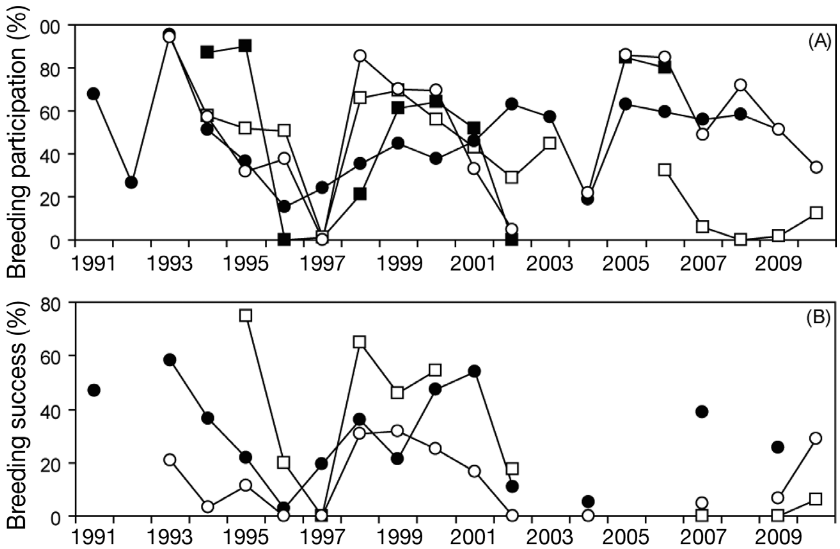

Fig. 4. (A) Breeding participation and (B) breeding success (both shown as percent) for the lesser noddy *Anous tenuirostris* (●), brown noddy *Anous stolidus* (○), sooty tern *Onychoprion fuscata* (■; in Panel A only) and wedge-tailed shearwater *Ardenna pacifica* (□) at Pelsaert Island, Houtman Abrolhos, Western Australia, between 1991 and 2010

Table 3. Spearman rank correlation among detrended environmental variables for 1991 to 2010. SOI: Southern Oscillation Index; SST: sea-surface temperature. **Bold** values indicate significance at $p < 0.05$

	Sea level		SOI	SST
	Geraldton	Fremantle		(Aug–Sep)
Sea level — Fremantle	**0.92**			
SOI	**0.85**	**0.88**		
SST (Aug–Sep)	0.06	−0.05	−0.03	
SST (Apr–Jun)	**0.54**	**0.52**	**0.52**	**−0.45**

nutrient flux into the upper ocean and the transport of nutrients from shelf to pelagic waters (Moore et al. 2007, Feng et al. 2009). Enhanced production of zooplankton may result (Waite et al. 2007, Thompson et al. 2011). Some eddies within seabird foraging range of the Houtman Abrolhos have been observed to last for 5 mo (Moore et al. 2007), which would extend these conditions of higher productivity into the austral summer, during the study species' breeding season. In contrast, primary productivity and fisheries recruitment in the eastern Indian Ocean have been found to decline during ENSO conditions, when the LC flow is weaker and there is less eddy-energy (Koslow et al. 2008, Feng et al. 2009). This corresponds to our study in which breeding performance was reduced for all seabird species during ENSO.

Our second objective was to describe breeding activities for our 4 seabird species (*Anous tenuirostris*, *A. stolidus*, *Onzchoprion fuscata* and *Ardenna pacifica*) over the last 20 yr. Breeding participation and breeding success have been highly variable for each species as a result of the climate variability discussed above. However, we also found trends in the first egg dates (later) for the 2 noddy species and the sooty tern, as well as a long-term delay in the mean laying date for the lesser noddy. The species with the greatest variability in onset of breeding was the brown noddy. In addition to these trends in phenology, we found that breeding participation and breeding success of wedge-tailed shearwater declined over time. The association between sea level and lay date/breeding success for the migratory species and between trending early spring SST and lay date for the resident lesser noddy suggests that lay date and breeding success for these species could be a proxy for a warming trend in SST, which is predicted to continue (Feng et al. 2004, Caputi et al. 2009).

Since the mid-1970s there have been more El Niño than La Niña events due to a climate regime shift in the Pacific Ocean (Feng et al. 2004), which has resulted in more years of a weak LC (and associated lower sea levels and lower SST) in recent decades (Caputi et al. 2009). The long-term increase in ENSO conditions may be a factor contributing to the significant negative changes in seabird parameters that we have recorded over a 20 yr period. Another contributing factor could be a 50 yr warming trend, with later peak timing, in the austral autumn/winter SST off the lower west coast of Australia (Caputi et al. 2009). The SST has increased by 0.02 to 0.035°C yr^{-1}, or an approximately 1°C increase overall, while the spring to summer period shows little increase (Caputi et al. 2009). Over the 50 yr period, the timing of the peak temperature has become delayed by 10 to 20 d, which may also delay the processes influencing peak prey availability for spring/summer breeding seabirds. This delay could contribute to the significantly later first egg dates of the lesser noddy, given the significant correlation of this parameter with winter/spring SST.

Our third objective was to identify environmental conditions, or cues, that could be used to predict changes in seabird breeding phenology. The first egg

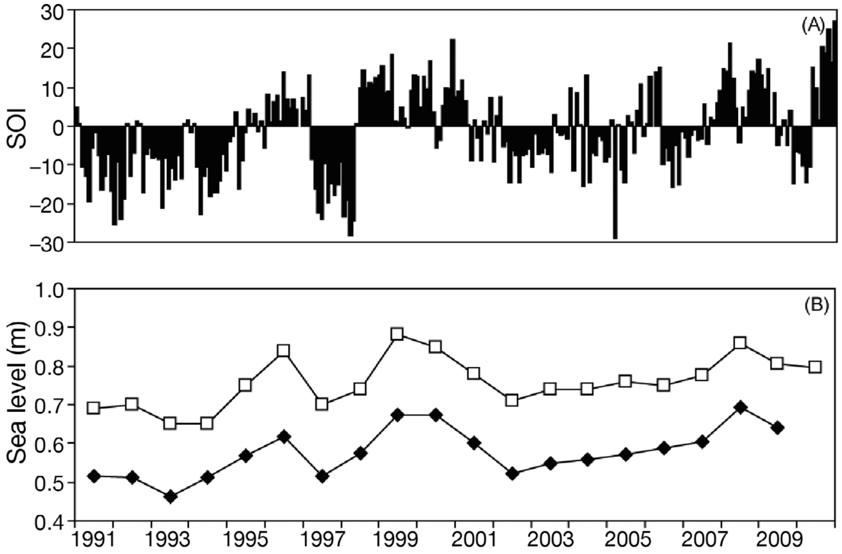

Fig. 5. (A) Southern Oscillation Index (SOI) and (B) sea levels at Geraldton (◆) and Fremantle (☐), Western Australia. El Niño Southern Oscillation events are associated with negative SOI values and lower sea levels

Table 4. Spearman rank correlations between detrended seabird breeding parameters and environmental variables from 1991 to 2010 for 4 species of seabirds breeding on Pelsaert Island, Houtman Abrolhos. SOI: Southern Oscillation Index; SST: sea-surface temperature. **Bold** values indicate statistical significance at $p < 0.05$

Seabird breeding parameters	Sea level		SOI	SST	
	Geraldton	Fremantle		Aug–Sep	Apr–Jun
Lesser noddy *Anous tenuirostris*					
First egg date	−0.28	−0.05	−0.12	**−0.72**	0.30
Mean lay date	−0.24	0.00	−0.09	−0.34	0.18
Participation	−0.38	−0.39	−0.18	−0.30	0.02
Success	0.19	0.08	0.16	−0.08	−0.04
Brown noddy *Anous stolidus*					
First egg date	**−0.50**	−0.31	−0.38	−0.18	−0.12
Mean lay date	−0.08	0.06	−0.12	−0.30	−0.09
Participation	0.24	0.07	0.24	−0.01	0.22
Success	**0.47**	0.44	**0.54**	−0.11	0.35
Sooty tern *Onychoprion fuscata*					
First egg date	**−0.50**	−0.23	−0.36	−0.32	−0.09
Mean lay date	−0.19	0.14	−0.10	−0.05	−0.17
Participation	0.35	0.04	0.14	0.03	−0.21
Wedge-tailed shearwater *Ardenna pacifica*					
Participation	0.17	0.16	0.30	0.19	0.45
Success	**0.62**	**0.53**	**0.56**	0.09	0.34

date of the migratory brown noddy and the migratory sooty tern was significantly correlated with sea level at Geraldton (29° S), with later laying associated with lower sea levels. The first egg date of the resident lesser noddy was significantly correlated with SST during the late austral winter/early spring, coinciding with the pre-breeding phase, with later laying associated with warmer SST. Breeding success of the wedge-tailed shearwater was significantly correlated with sea level at both Geraldton and Fremantle (32° S), while, for the brown noddy, breeding success was significantly correlated with sea level at Geraldton, with poor breeding success associated with lower sea levels. Breeding success of both these species was also significantly related to the SOI, with poor years associated with negative SOI values.

Breeding phenology and success in tropical seabird colonies has frequently been linked to both localised and large-scale oceanographic events. In the western Indian Ocean, the colony productivity of roseate terns *Sterna dougallii* on Aride Island was related to intensity and timing of phytoplankton blooms during breeding (Monticelli et al. 2007), SST (Ramos et al. 2002) and the Multivariate El Niño Index (Ramos et al. 2002, Monticelli et al. 2007). ENSO events and severe La Niña years were found to have a strong influence upon brown noddies in the western Indian Ocean, where there was evidence of strong variation in food availability with poor breeding success (Ramos et al. 2006). Breeding phenology of sooty tern colonies coincided with a large monthly change in SST (an indicator of the annual phytoplankton bloom) just before the beginning of reproduction in the southwestern Indian Ocean (Jaquemet et al. 2007). Similarly, in the western Indian Ocean a roseate tern colony was found to be sensitive to inter-annual variations in the intensity and timing of a localised phytoplankton bloom (Monticelli et al. 2007). Breeding phenology and performance of tropical seabird species breeding in the eastern Indian Ocean (Dunlop et al. 2002, Surman & Nicholson 2009a,b) and western Indian Ocean (Ramos et al. 2006) were influenced by the large-scale oceanographic cues associated with ENSO events. At least 2 other studies of tropical seabird species, one at the Great Barrier Reef, north-eastern Australia, and the other in the Seychelles, western

Indian Ocean, found that breeding success was influenced by both large-scale (ENSO) and localised (SST) oceanographic conditions (Ramos et al. 2002, Peck et al. 2004).

The data presented here suggest that the breeding parameters of our study species are decoupling from the strong negative influence of ENSO events reported previously (Surman 1998, Surman & Nicholson 2009a), as there seems to be a cumulative effect of consecutive poor seasons upon breeding performance, and a reduction in the ability to have a successful season even when conditions appear favourable. It would appear that the environmental trigger for the arrival of prey for seabirds, perhaps as a result of a delayed autumn SST peak (Caputi et al. 2009), has shifted and has pushed seabirds to significantly later breeding. The resident lesser noddy was found to be the most resilient of the 4 species, as it adapted to later onset of breeding and was able to fledge chicks in the later years of our study when the other species had relatively poor breeding success. Local knowledge of the foraging grounds at the Houtman Abrolhos may be buffering the lesser noddy against variation in food availability to a greater extent than the other species, as the lesser noddy is able to switch prey in poor years so that it has rarely suffered complete breeding failure to the same extent as the brown noddy or sooty tern (Surman & Nicholson 2009a). The correlation between first egg date and early spring SST for the lesser noddy suggests that this localised cue is indicative of food availability during the breeding season.

The effects of climate variability upon the LC and its eddy cycle in the past 20 yr appear to have affected the availability of key seabird prey resources and seabird breeding cycles at the Houtman Abrolhos. As increased SST warming and increasing ENSO conditions are predicted to continue (Feng et al. 2004, Caputi et al. 2009), it is difficult to predict whether migratory seabirds can adapt to this variability in the long term and continue to successfully breed at the Houtman Abrolhos.

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Contribution to the Theme Section 'Seabirds and climate change'

Phenology of pelagic seabird abundance relative to marine climate change in the Alaska Gyre

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ABSTRACT: In relation to climate change, a common finding from long-term studies on marine ecosystems is earlier annual peaks of abundance for many organisms. Here, we test the hypothesis of unidirectional change in the seasonal abundance of pelagic seabirds in association with change in marine climate and primary productivity in the Alaska Gyre. To test this hypothesis, we analyzed data on hydrographic conditions and seasonal at-sea abundance of seabirds along a 1425 km transect (Line P) over 11 yr, 1996 to 2006. Long-term sea surface temperature (SST) data show warming in the study region, advanced and delayed temperature peaks and northwestward isotherm displacement. Using negative binomial regression, we tested seasonal trends in the relative abundance of 15 seabird species and compared abundances to a multivariate ocean climate index we developed with principal component analysis from *in situ* measurements of water temperature, salinity, density and nitrate concentrations. Overall, 5 species showed no change, 1 declined, and 9 species as well as all species combined showed increasing abundance. By season, 3 species increased in winter, 7 in late spring, and 6 in late summer. Eight of 15 species showed relationships with our environmental index. Increases in seasonal seabird abundance may be related to lengthening of the 'growing season', as demonstrated by temporal temperature shifts and expansion of peak chlorophyll concentrations. Seabirds of the Alaska Gyre are probably responding to changes in forage nekton that are related to this extended growing season by shifting their migration to later dates.

KEY WORDS: Birds · Climate · Chlorophyll · Growing season · Migration timing · Sub-arctic ecosystem

INTRODUCTION

Climate change affects marine ecosystems worldwide, with impacts on distribution and abundance, phenology, and productivity of species, and, in turn, species interactions, community organization, and ecosystem functions and services (reviewed by Hoegh-Guldberg & Bruno 2010, Doney et al. 2012). To date, one of the most robust findings from long-term marine observations is earlier seasonality of abundance in plankton populations (Edwards & Richardson 2004, Beaugrand & Kirby 2010, Ji et al. 2010). Such effects have been particularly well-documented in the North Atlantic. Fewer studies have been conducted in the North Pacific, but similar findings have been obtained, showing, for example, earlier seasonal peaks in abundance of large, energy-rich *Neocalanus* copepods in the Gulf of Alaska (Mackas et al. 1998, Bertram et al. 2001, Batten & Mackas 2009). The phenology of plankton abundance is critical to trophic interactions; if plankton are not available at the right time and place, the

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foraging ecology of predatory nekton may be compromised, possibly leading to reduced recruitment and population declines in upper trophic-level species (Cushing 1990, Mackas et al. 2007, Sydeman et al. 2009, Dorman et al. 2011).

Seabirds are the most conspicuous marine organisms living at the interface of the ocean and atmosphere and have been put forth as reliable indicators of variability of the abundance of plankton and forage nekton populations (Piatt et al. 2007). As an ecotone, the surface and near-surface habitats of seabirds may be affected by climate change as global warming heats the atmosphere thereby affecting these upper ocean habitats (Levitus et al. 2005). While there have been many studies of climate change impacts on seabird phenology at colonies, examining parameters such as date of colony arrival (Barbraud & Weimerskirch 2006) and hatching dates of eggs (Byrd et al. 2008), long-term observational studies of seabird communities at sea are few, and almost none are conducted across multiple seasons (but see Hyrenbach & Veit 2003, Sydeman et al. 2010). Most studies of seabird populations at sea have, however, demonstrated responses to marine climate variability and change over multiple time scales (Hyrenbach & Veit 2003, Sydeman et al. 2009, Ainley & Hyrenbach 2010), so assuming that seasonal changes in abundance should also be observed is logical. To date, though, no study has attempted to corroborate the key findings on plankton described above using upper trophic-level species. We define variation in the phenology of seabirds at sea as a change in seasonal abundance through time. This may reflect changes in migration timing, especially for southern hemisphere species, or changes in wintering ecology for resident breeders.

In the North Pacific, the Gulf of Alaska (GoA) marine ecosystem is comprised of coastal and offshore waters from southern British Columbia north to Cook Inlet, Alaska, and west to the outer Aleutian Islands. The GoA is a highly productive marine ecosystem with substantial fisheries resources. In the southeastern sector, the Canadian 'Line P' survey (Fig. 1; www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/line-p/index-eng.htm) is one of only 2 long-term (>50 yr) interdisciplinary studies in the Northeast Pacific; the other is the California Cooperative Oceanic Fisheries Investigations (CalCOFI) off southern California (Hsieh et al. 2009). The Line P program has provided a wealth of information about change in ocean climate in the southeastern GoA. Key findings include: (1) increasing temperature and decreasing salinity (i.e. freshening of the surface layer, Freeland et al. 1997); (2) increasing density stratification due to surface layer warming and freshening (Crawford et al. 2007); (3) shoaling of winter pycnocline depth (Freeland & Cummins 2005); and (4) reduced annual re-supply of macronutrients (Whitney & Freeland 1999, see Sarkar et al. 2005 for similar information about the northern GoA). Changes in phenology of the zooplankton described above are likely related to these changes in the physical environment along Line P. Moreover, interannual variation in the abundance of many commonly occurring seabirds is substantial (Yen et al. 2005). Seabird distribution and abundance in this region has been related to gradients in sea surface temperature (SST) associated with frontal structures (O'Hara et al. 2006). While Yen et al. (2005) and O'Hara et al. (2006) provide initial information on this seabird community, a thorough investigation of seabird populations relative to ocean climate along Line P has yet to be conducted.

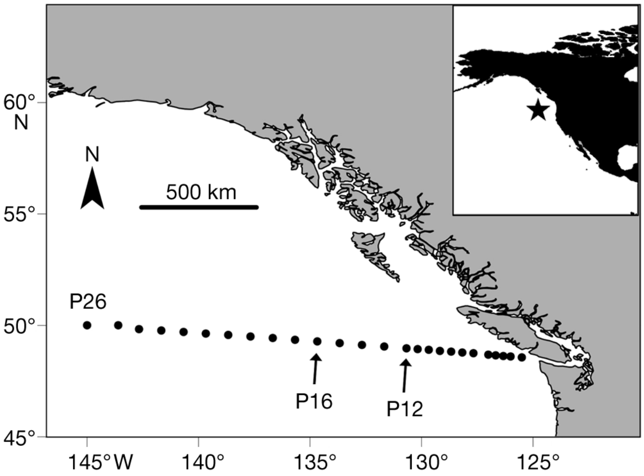

Fig. 1. Northeast Pacific. Position of the Line P survey transect and the locations of survey stations. Physical data were collected at Stns P12 (48.97° N, 130.67° W), P16 (49.28° N, 134.67° W) and P26 (Station Papa; 50.00° N, 145.00° W)

We present an analysis of seasonal variation in the abundance of seabirds in the Alaska Gyre to test the hypothesis of unidirectional change in the seasonality of pelagic seabird abundance in association with trends in marine climate and primary productivity as measured through chlorophyll *a* (chl *a*) concentration. Changes in SST are presented on a broad temporal and spatial scale using Hadley Center data. To test our hypothesis, we analyzed data on the at-sea abundance of seabirds and concurrent hydrographic conditions along the Line P transect in 3 seasons over 11 yr (1996 through 2006). Specifically, we examine if there were trends in the abundance of 15 seabird species relative to an environmental index and seasonality. This study is important as the potential effect of climate variability and change on seabird communities in the GoA has yet to be investigated, and this ecosystem may provide interesting contrasts to the adjacent California Current where we have concurrent data on the seasonal abundance of seabirds from the CalCOFI region (Hyrenbach & Veit 2003, Sydeman et al. 2009).

MATERIALS AND METHODS

Variability and change in ocean climate

We used SST data from 1960 through 2009 to assess broad-scale temperature change (°C yr^{-1}), the ‘velocity’ of climate change (isotherm displacement in km yr^{-1}) and seasonal shifts in temperature (d $decade^{-1}$) for April and October focused on the Alaska Gyre. Data were obtained from the Hadley Center (HadISST; badc.nerc.ac.uk/view/badc.nerc.ac.uk__ATOM__dataent_hadisst) and processed as described by Burrows et al. (2011). We extracted temperature data from the 1° × 1° pixels that encompass the locations of the Line P survey stations listed below.

Locally, measurements of temperature (°C), practical salinity, and nitrate concentrations (µmol l^{-1}) were measured *in situ* by Niskin bottles and CTD (Seabird SBE 911+) casts at stations along the Line P transect from 1996 through 2006. To simplify the analysis, we used data from 3 main offshore stations: P12 (48.97° N, 130.67° W), P16 (49.28° N, 134.67° W), and P26 (Ocean Station Papa; 50.00° N, 145.00° W; Fig. 1). Data from these stations were used previously in studies of temporal environmental variability of the Alaska Gyre (Lipsen et al. 2007, Peña & Varela 2007, Wong et al. 2007). Water column density (sigma-t) was calculated from temperature, salinity and pressure. Data were summarized for 10 m depth intervals and averaged to produce seasonal values. In addition, seasonal averages were calculated and used to proxy missing values (seasons) in the data set. Finally, the 1996–2006 seasonal averages were subtracted from seasonal values to produce anomaly statistics that were used in analyses.

Ocean surface chlorophyll

Satellite remotely-sensed chlorophyll concentration (mg m^{-3}) data were obtained from the Sea-viewing Wide Field-of-View Sensor (SeaWiFS) for 1998 to 2006. For consistency with measurements of hydrographic conditions, we used monthly composites of 9 × 9 km cells situated at the coordinates of Stns P12, P16 and P26. We averaged the chlorophyll values for the cell closest to the coordinates of the station and cells immediately to the east, south, and southeast to produce an overall estimate for 324 km^2 of ocean habitat at each station. The average concentration from the 4 cells at each station was averaged across the 3 stations to produce a single value for each seasonal Line P survey.

Seabird surveys

From June 1996 to June 2006, we conducted 28 seabird surveys along the Line P transect. Most surveys were conducted over 10 to 20 d aboard the Canadian Coast Guard Ship ‘John P. Tully’. The timing of winter (February), late spring (June), and late summer (August to September) seasonal surveys was variable, but did not change systematically over the 11 yr ($p > 0.1$ for each season). The median date of each survey is listed in Appendix Table 1. There was variability in the length of surveys, but the duration of surveys did not change significantly through time ($p > 0.05$). Related in part to survey duration, there was substantial variation in the area of ocean habitat surveyed for seabirds, but again we found no trend in coverage over the study period ($p > 0.2$).

Data on seabird populations were collected as described by Yen et al. (2005) and O’Hara et al. (2006). Briefly, birds were counted by an experienced observer positioned on the flying bridge, ~15 m above the water surface. Surveys were conducted using the standard strip transect method (Tasker et al. 1984). All birds sighted within 250 m of the ship in a 90° arc from the bow to amidship on the side of the ship with least glare were identified and enumerated. Surveys were conducted during daylight hours while the ship was underway at >5 knot; observations were halted during periods of inclement weather or when visibility or ability to spot and identify birds out to 250 m was compromised.

We summarized seabird observations into daily counts and converted them into density estimates (birds km^{-2}) by dividing counts by the area surveyed each day. We included species with at least 200 individuals observed over the duration of our study to exclude species with insufficient data for trend analyses. We did not conduct a power analysis on these data because the variance structure was unknown *a priori*. This procedure resulted in selection of 15 species

(Appendix Table A2), as well as a total for all species. Due to difficulties in distinguishing sooty shearwaters (*Puffinus griseus*) and short-tailed shearwaters (*P. tenuirostris*), these species were identified as 'dark' shearwaters for analysis. In terms of the use of 'day' as our fundamental sampling unit, in comparison to the finer spatio-temporal resolutions that others have used, we used daily counts to avoid problems of pseudo-replication, excessive sample size, and spatial autocorrelation (see Yen et al. 2005 for an analysis of spatial autocorrelation for this seabird data set). These issues affect estimates of probabilities on temporal trends as well as environmental (climate) correlates, as the degrees of freedom are unknown due to varying spatial autocorrelation functions between species. We avoided these problems by using 'day' as our sampling unit, which separated surveys by night-time hours when no seabird observations were made. Moreover, we excluded data collected during the first day of each survey to exclude observations from the coastal domain. In general, the vessel transits of coastal regions (shallow waters to ~1000 m depth) took <4 h. Daily density estimates (no. of birds km^{-2} d^{-1} +1) were log_{10} transformed for illustration.

Data analysis

Data were analyzed using Stata v. 11 (Stata). To test for trends in hydrography, we used Spearman rank correlations and linear regression. We used principal component analysis (PCA) to create a local multivariate marine climate index time series. The PCA was conducted on the 4 *in situ* hydrographic variables of temperature, salinity, sigma-t, and nitrate concentration. This analysis was restricted to data collected concurrently with seabird observations made during surveys from June 1996 to June 2006. The first principal component was retained for further analysis (environment PC1, hereafter '$PC1_{env}$'). We used rank correlations to test for trends in seasonal peak chlorophyll concentrations, changes in the timing of seasonal peaks, and a relationship between chlorophyll concentration and $PC1_{env}$. To look for trends in the timing of seasonal peaks, correlations were conducted on the month number of the peak across years. We calculated the number of months between the occurrences of the peaks and tested the difference over the time series to look for a trend in the temporal spacing of the peaks and length of the growing season.

We used negative binomial regression to test for trends in the seasonal abundance of seabirds. Negative binomial regression is designed for analysis of count data (Hilbe 2011), such as the seabird data described herein. Daily counts were used to test for trends, and 'area surveyed' was included as a covariate to adjust for survey effort. To investigate seabird–environment relationships, $PC1_{env}$ was aligned with the seasonal seabird count data and also lagged by 1 survey (i.e. a lag of 4 mo).

RESULTS

Trends in environment and seabirds

The HadISST data illustrate long-term and spatial patterns of change in the Northeast Pacific and Alaska Gyre (Fig. 2). Over 50 yr (1960 to 2009), there was an increase in temperature, a shift in isotherms toward the center of the Alaska Gyre, and earlier and later shifts in temperature. For each survey station, temperature increased significantly through time (P12: Spearman $\rho = 0.40$, $p = 0.0045$; P16: Spearman $\rho = 0.48$, $p = 0.0004$; P26: Spearman $\rho = 0.39$, $p = 0.0053$). The (mean ± SE) rate of temperature change for each station varied from 0.014 ± 0.005 (P26) to 0.019 ± 0.005 (P16)°C yr^{-1} (linear regression). We found no significance of quadratic fits to these data. For the central Gulf of Alaska and Line P region, isotherm displacement ranged from 5 to 10 km yr^{-1} (Fig. 2). Finally, these data indicate a seasonal shift in temperature, with an advance of ~8 d $decade^{-1}$ in April and a delay of ~3 d $decade^{-1}$ in October (Fig. 2).

$PC1_{env}$ captured 62% of the variance, with temperature and sigma-t loading most heavily (Table 1). Through time, $PC1_{env}$ was somewhat variable prior to 1999 and more stabilized thereafter (Fig. 3). The second principal component accounted for 25% of the variance and loaded very highly on nitrates (Table 1). We used the first principal component for our study as a representation of environmental conditions.

Monthly chlorophyll concentration over time is presented in Fig. 4. The seasonal cycle of early and late blooms is evident, with the highest values occurring in October 2005 and 2006. We found no change in the amplitude of peak values for each season. We found significant change in the timing of the peaks, with the early peak becoming earlier (Spearman $\rho = -0.718$, $p = 0.029$) and the late peak becoming later (Spearman $\rho = 0.572$, $p = 0.108$; see Table 2 for data). With the late spring peak becoming earlier and the late summer peak becoming later, the number of months between peaks increased (Spearman $\rho = 0.845$, $p = 0.004$). We found no significant correlations

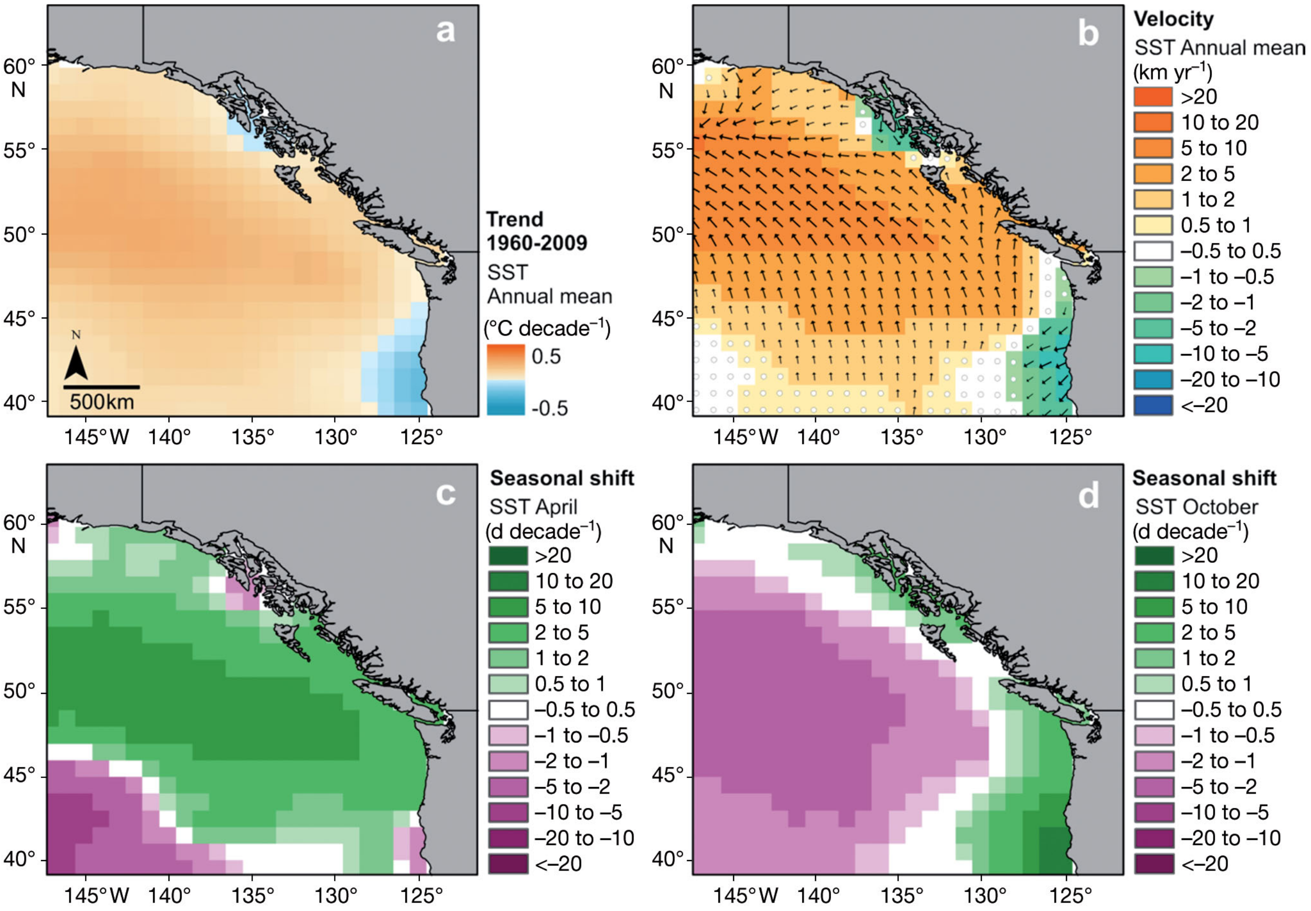

Fig. 2. Sea surface temperature trends (HadISST) in the Northeast Pacific. (a) Temperature trend for 1960 to 2009; the maximum change offshore = 0.25°C decade^{-1}. Note cooling along the coast of Oregon and northern California. (b) Directionality in the velocity of change in the mean annual sea-surface temperature (SST) isotherms; maximum change = 11.3 km yr^{-1}. The direction along Line P is northwestern, and the vectors shown generally are directed toward the center of the Alaska Gyre. Negative values indicate a decrease in temperature. Bottom panels: Phenological shifts of April and October SST. (c) Maximum advance (earlier occurrence) of April SST by ~8 d decade^{-1} shown, all corresponding to the Line P region in the Alaska Gyre. (d) Maximum delay of October SST by ~3 d decade^{-1}, particularly in the outer region of Line P. See Burrows et al. (2011) for methods of SST, velocity, and phenology shift calculations

between chlorophyll concentration and $PC1_{env}$.

We found seasonal variability and directional change in seabird species abundance (Table 3, Figs. 5, 6 & 7). Four species showed episodic high densities, illustrated by 1 or 2 disproportionately large bars in the density values (e.g. mottled petrel *Pterodroma inexpectata* peak in late spring 2002, Fig. 6; ancient murrelet *Synthliboramphus antiquus* peak in late spring 1997, Fig. 5; pink-footed shearwater *Puffinus creatopus* peak in late summer 2001, Fig. 6). Two species were completely absent from surveys in a season: pink-footed shearwaters (winter, Fig. 6) and ancient murrelet (late sum-

Table 1. Environmental principal component analysis (PCA). Variables included were seasonal anomalies of temperature, salinity, nitrates and sigma-t

Principal component	Eigenvalue	Difference	Proportion of variance	Cumulative variance
1	2.499	1.463	0.625	0.625
2	1.036	0.579	0.259	0.884
3	0.458	0.450	0.114	0.998
4	0.008		0.002	1.000
Eigenvector Variable	1	2	3	4
Temperature	−0.583	−0.152	0.523	0.603
Salinity	0.457	−0.509	0.676	−0.273
Nitrates	0.258	0.839	0.477	0.048
Sigma-t	0.621	−0.117	−0.205	0.748

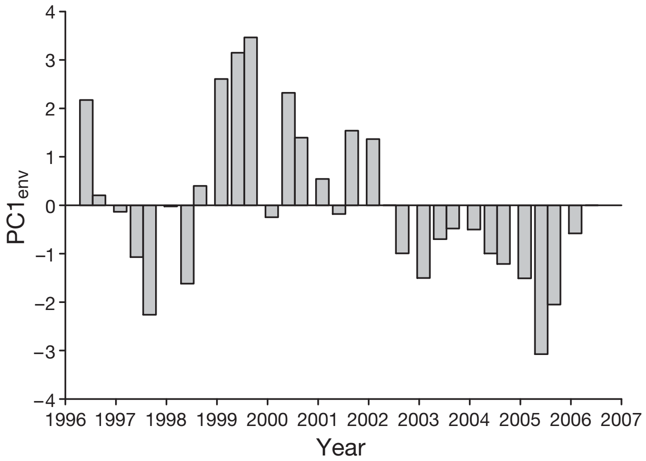

Fig. 3. Time series of principal component 1 ($PC1_{env}$), 1996 to 2006. Positive values of PC1 indicate cold periods, whereas negative values indicate warm periods

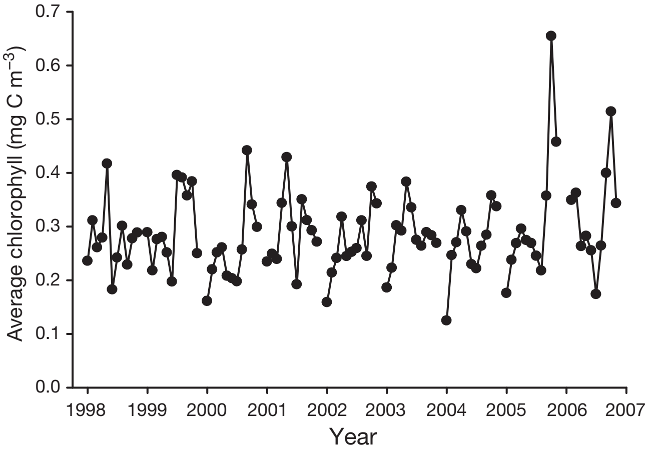

Fig. 4. Monthly chlorophyll concentrations on Line P, 1998 to 2006, derived from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS). Year ticks indicate January of each year

Table 2. Months of early and late peaks in chlorophyll concentration along Line P, 1998 to 2006 and the amount of time between the peak concentrations

Year	Month of early peak	Month of late peak	Time between peaks (no. of mo)
1998	May	August	3
1999	July	October	3
2000	April	September	5
2001	May	August	3
2002	April	October	6
2003	May	September	4
2004	April	October	6
2005	April	October	6
2006	March	October	7

mer, Fig. 5). Four species were excluded from the negative binomial regression analysis in 1 season because of very low counts: black-legged kittiwake *Rissa tridactyla* in late spring, dark shearwaters and Leach's storm-petrel *Oceanodroma leucorhoa* in winter, and Laysan albatross *Phoebastria immutabilis* in late summer. After omitting these species from analysis, we found winter had the fewest trends in seabird abundance while late summer had the most (Table 3). Laysan albatross (winter, Fig. 7) was the only species to show a significant decrease in abundance (Table 3). Two-thirds of the species showed increasing abundance. Total (all species) abundance increased overall as well as in every season, as did rhinoceros auklet *Cerorhinca monocerata* abundance (Table 3, Fig. 5).

Relationships between seabird abundance and the environment

The seasonal abundances of 4 species (rhinoceros auklet, glaucous-winged gull *Larus glaucescens*, dark shearwaters and Leach's storm-petrel) and all species combined correlated with $PC1_{env}$ at lags of both 0 and 4 mo (Table 4). Four species were negatively correlated with $PC1_{env}$ at either lag 0 or lag 4 mo: ancient murrelet and Cassin's auklet *Ptychoramphus aleuticus* at lag 0 (concurrent environmental and seabird measurements) and black-footed albatross *Phoebastria nigripes* and fork-tailed storm-petrel *Oceanodroma furcata* at lag 4 mo (environment leading seabirds; Table 4). Seven species (common murre *Uria aalge*, tufted puffin *Fratercula cirrhata*, black-legged kittiwake, mottled petrel, northern fulmar *Fulmarus glacialis*, pink-footed shearwater and Laysan albatross) had no significant relationships (Table 4). We found a significant correlation between the length of the growing season (as indexed by the number of months between early and late chlorophyll peaks) and total bird abundance in the late spring (Spearman rho = 0.725, p = 0.027), but no significant relationships for winter or late summer abundances (respectively, Spearman rho = 0.207, p = 0.593 and rho = 0.075, p = 0.873).

DISCUSSION

We investigated the hypothesis of change in the seasonal abundance of pelagic seabirds relative to change in marine climate and productivity (indexed by chl *a* concentrations) in the Alaska Gyre. Using the HadISST data, we demonstrated warming, poleward shifts in isotherms and seasonal shifts in average temperature, indicating long-term environmental change that may be attributable to anthropogenic global warming. Despite a relatively short time-series of seabird observations (11 yr) punctuated with the characteristic episodic variability in seabird densities observed in many studies (e.g. Ainley & Hyrenbach 2010), our primary result is an increase in the relative abundance of seabirds in the study region (10 of 15 species), with the most compelling change occurring during late summer (August to September). Increasing abundance of all species combined was found in all seasons. In winter (February) Laysan albatross abundance decreased, while 3 species (rhinoceros auklet, tufted puffin, and glaucous-winged gull) increased. In late spring (June), 4 species (Cassin's auklet, dark shearwaters, fork-tailed storm-petrels and Leach's storm-petrels) increased; in late summer, 6 species (common murre, rhinoceros auklet, dark shearwaters, black-footed albatross and both species of storm-petrels) increased. Four species (ancient murrelet, black-legged kittiwake, mottled petrel and northern fulmar) did not show any change in abundance. Overall, there appears to have been a general increase in seabird abundance in the study region over the 11 yr, with the greatest shift towards increasing abundance later in late summer.

Internal and external drivers of change

The population changes demonstrated here could reflect internal (species- or population-specific) or external (environmental) factors. Recent studies indicate the following population trends for locally-breeding seabirds in British Columbia: tufted puffin breeding populations are stable, rhinoceros auklet populations are increasing, and Cassin's auklet and common murre populations are declining (1984–2009; Rodway & Lemon 2011). Hipfner (2005) attributes the change in murre populations (2003–2004) to differences in colony attendance driven by the presence or absence of predatory bald eagles *Haliaeetus leucocephalus*. Information on locally-breeding fork-tailed storm-petrel population is inadequate to assess trends (M. Hipfner pers. comm.). Population trends from breeding sites for the migrant species are also indicative, primarily, of declining trends. Sooty shearwaters have declined 37% over 27 yr (1969–1996) at breeding colonies in New Zealand (Scott et al. 2008), and pink-footed shearwaters have declined from colonies in Chile (Schlatter 1984).

Since many seabird species show population declines at colonies, yet we found increased abundance at sea in the Alaska Gyre, we suggest external factors may explain our observations, with environmental correlations supporting this supposition. There are, however, a number of caveats to this suggestion. (1) Most of the studies referenced above focused on breeding birds and did not consider the non-breeding component of these populations, which largely remain at sea throughout the year. For these species it is possible, though unlikely, that non-breeding birds increased while the breeding component did not, therefore resulting in an increase in relative abundance at sea. (2) A related point is that with deferred reproduction, breeding populations could decline while abundance at sea, if represented by non-breeders, could increase. However, there are also temporal limits to consider. Deferred reproduction and non-breeding for most of these seabird species lasts up to 6 to 8 yr, while the patterns of population change we observed extended over an 11 yr period.

Seabird–environmental correlates on multiple time scales

The environmental variables we measured during surveys were highly correlated with each other (results not shown) and thus could suitably be combined using PCA. This is expected since temperature and salinity are inversely related and sigma-t is a factor of temperature, salinity and pressure. Importantly, these data came from measurements well offshore and away from freshwater sources that would affect salinity. The resulting multivariate indicator, $PC1_{env}$, reflects interannual variation in water column conditions. Temperature loaded negatively while salinity and sigma-t loaded positively on $PC1_{env}$. Temperature and sigma-t probably contributed most to the correlations between seabird abundance and this principal component.

Regarding interannual variability, we found few correlations between seabird abundances and individual hydrographic measurements (S. A. Thompson & W. J. Sydeman unpubl. data). However, we found significant correlations between $PC1_{env}$ and seabird abundances; 8 of 15 species and all species combined showed significant relationships. In general, we found decreasing abundance of seabirds with increasing $PC1_{env}$. These inverse relationships reflect the 'PC1 space' that was created by combining the physical parameters using PCA. To reiterate, temperature was

Table 3. Negative binomial regression on seabird abundance over time by season (winter: 1997–2006; late spring: 1996–2004, 2006; and late summer: 1996, 1999–2005). The model for all seasons included terms for area, year (continuous), and season (categorical). The model for each season included terms area and year (continuous). The sign of any significant trend is noted next to species names (NC: no change). Dark shearwaters consist of both sooty and short-tailed species. nd: not detected; *p < 0.1, **p < 0.05, ***p < 0.01

	All seasons		Winter		Late spring		Late summer	
Species	Coefficient	*Z*-score	Coefficient	*Z*-score	Coefficient	*Z*-score	Coefficient	*Z*-score
All species (+)	0.151	7.21***	0.093	3.03***	0.167	4.7***	0.235	5.78***
Alcids								
Ancient murrelet (NC)	−0.016	−0.12	0.179	0.99	−0.189	−1.02	nd	nd
Cassin's auklet (+)	0.164	1.90*	0.133	0.84	0.344	2.79***	−0.036	−0.20
Common murre (+)	0.272	2.59***	0.196	1.34	0.178	1.27	0.904	3.21***
Rhinoceros auklet (+)	0.308	4.31***	0.394	3.56***	0.208	1.65*	0.373	2.78***
Tufted puffin (+)	0.057	1.21	0.175	2.88***	−0.018	−0.25	0.041	0.23
Larids								
Black-legged kittiwake (NC)	0.052	0.75	0.059	1.13	nd	nd	−0.284	−0.46
Glaucous-winged gull (+)	0.207	3.34***	0.191	3.51***	0.158	0.94	0.368	1.39
Procellarids								
Mottled petrel (NC)	0.044	0.57	−0.023	−0.29	0.101	0.54	0.112	0.52
Northern fulmar (NC)	0.072	1.58	0.042	1.08	0.148	1.30	0.003	0.02
Pink-footed shearwater (+)	0.761	2.14**	nd	nd	0.770	1.74*	0.463	0.64
Dark shearwaters (+)	0.283	4.76***	nd	nd	0.172	2.63***	0.454	4.34***
Albatrosses								
Black-footed albatross (+)	0.077	2.14**	−0.103	−1.37	0.104	1.70*	0.189	3.91***
Laysan albatross (–)	−0.169	−3.32***	−0.159	−2.90***	−0.216	−1.45	nd	nd
Storm-petrels								
Fork-tailed storm-Petrel (+)	0.100	3.38***	0.009	0.19	0.095	2.14**	0.237	3.88***
Leach's storm-Petrel (+)	0.150	4.77***	nd	nd	0.141	3.64***	0.167	3.12***

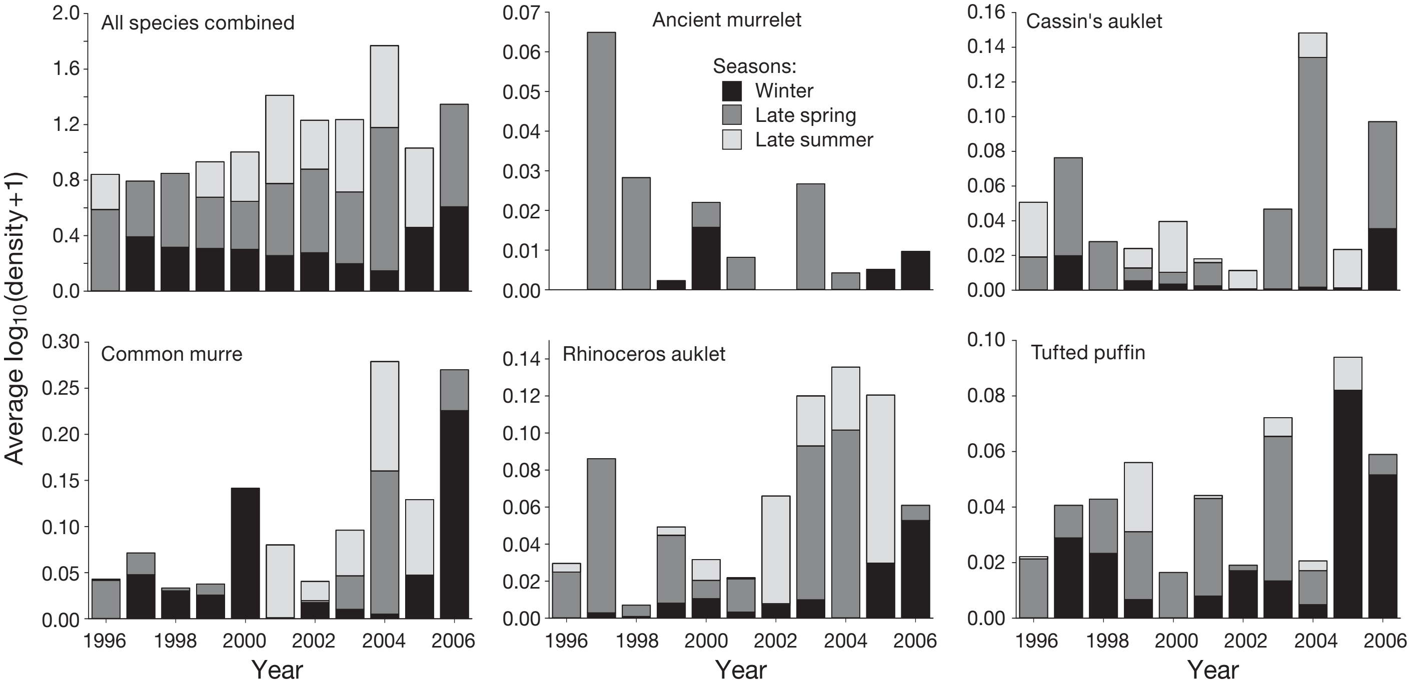

Fig. 5. *Synthliboramphus antiquus*, *Ptychoramphus aleuticus*, *Uria aalge*, *Cerorhinca monocerata*, and *Fratercula cirrhata.* Seasonal average $\log_{10}$(density + 1) of all species combined and alcids individually. Seasons see key

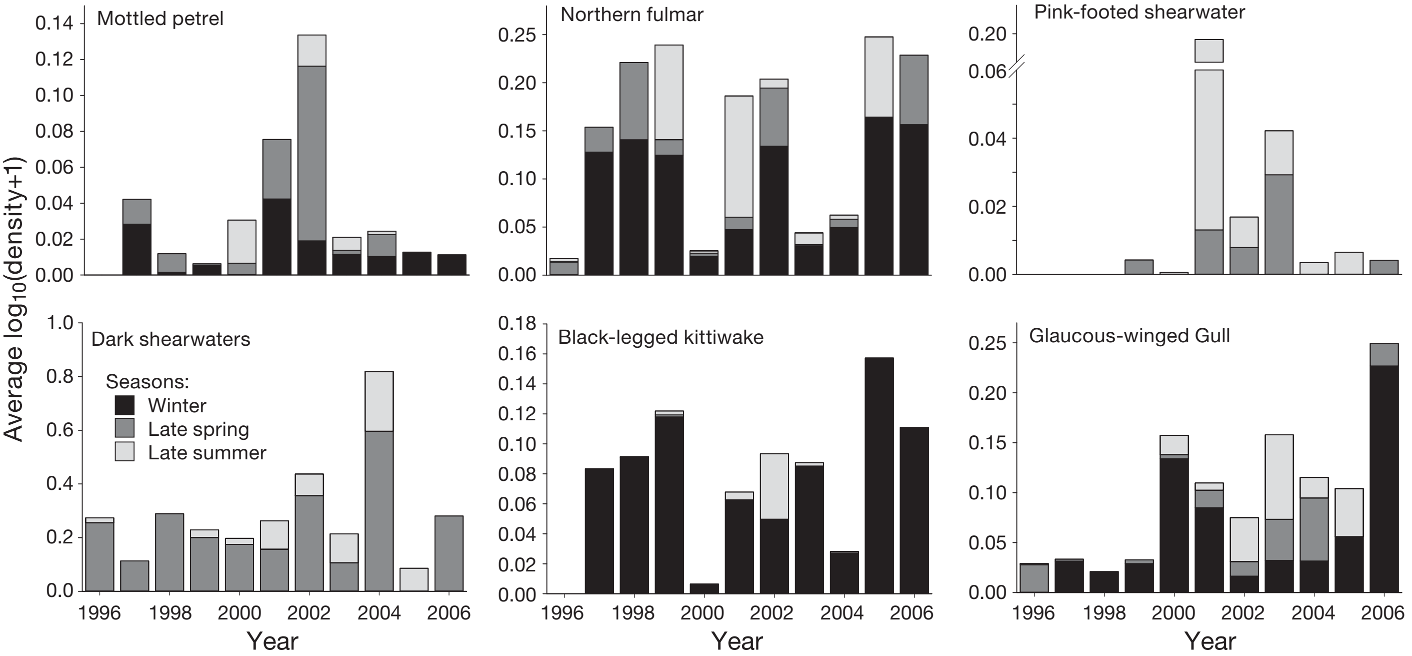

Fig. 6. Seasonal average log10(density + 1) of procellarids and larids. Seasons see key. Dark shearwaters consist of both sooty and short-tailed species. See Appendix Table A2 for scientific names

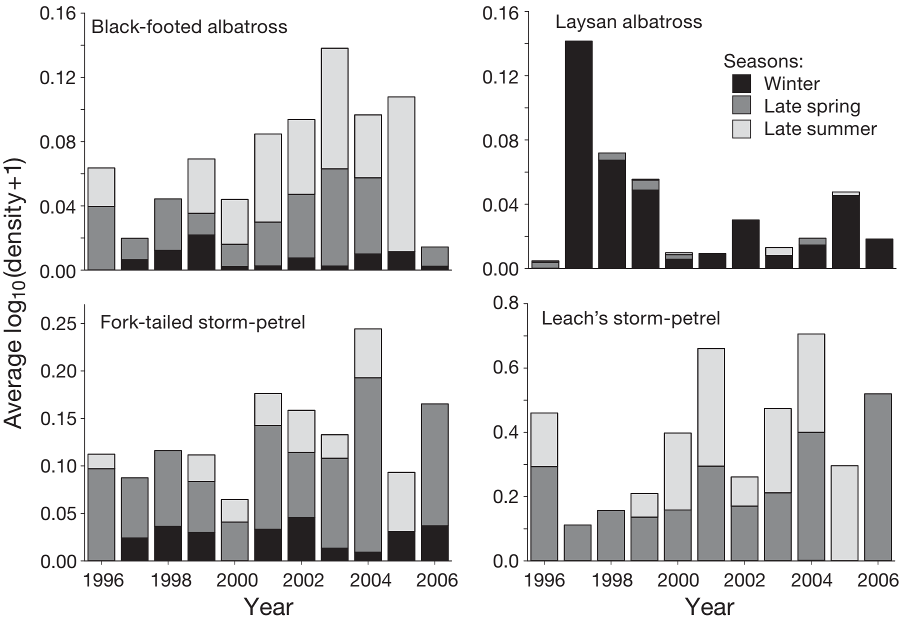

Fig. 7. *Phoebastria nigripes*, *P. immutabilis*, *Oceanodroma furcata* and *O. leucorhoa*. Seasonal average $\log_{10}$(density + 1) of albatrosses and storm-petrels. Seasons see key

negatively related to $PC1_{env}$ and salinity and sigma-t were positively related. This means that the relationships between seabird abundance and temperature were actually positive (negative in PC space), while the relationship with salinity and sigma-t was negative. So, while these results may appear to contradict other findings in this paper, notably a long-term increase in SST using the 50+ year HadISST data set and a decadal increase in seabird abundance, they do not. Temperature in PC space has the same relationship to seabirds on interannual and decadal scales, and in both cases the relationships were positive.

On the decadal scale, we found that seabird abundances were increasing, particularly in late summer, and suggest that this is related to the timing of peak chlorophyll concentrations, with shifts of late spring and late summer peaks occurring earlier and later in each year, respectively. Thus, we postulate that the length of the growing season in the Alaska Gyre has extended over the period of study. This is supported by the April (advance) and October (delay) temporal shifts in temperature (for more details see Burrows et al. 2011). Notably, as there were no trends in chlorophyll concentrations, the increases in seabird abundance observed in this study may be explained by changes in the timing of peak chlorophyll

Table 4. Negative binomial regression of seabird abundances against PC1$_{env}$. Models included terms area and season (categorical). Dark shearwaters consist of both sooty and short-tailed species. $^{*}p < 0.1$, $^{**}p < 0.05$, $^{***}p < 0.01$

	Lag 0 mo		Lag 4 mo	
Species	Coefficient	Z-score	Coefficient	Z-score
All species	−0.142	−1.72*	−0.165	−2.31**
Alcids				
Ancient murrelet	−0.773	−2.14**	0.023	0.08
Cassin's auklet	−0.343	−1.96**	−0.262	−1.44
Common murre	−0.182	−0.95	−0.217	−1.37
Rhinoceros auklet	−0.354	−2.43**	−0.323	−2.78***
Tufted puffin	0.033	0.27	−0.106	−0.85
Larids				
Black-legged kittiwake	−0.033	−0.17	−0.313	−1.54
Glaucous-winged gull	−0.452	−2.71***	−0.233	−1.88*
Procellarids				
Mottled petrel	−0.214	−0.86	0.326	1.49
Northern fulmar	0.066	0.38	−0.089	−0.45
Pink-footed shearwater	0.502	0.78	−0.419	−0.80
Dark shearwaters	−0.266	−2.00**	−0.344	−1.90*
Albatrosses				
Black-footed albatross	−0.038	−0.45	−0.186	−2.24**
Laysan albatross	0.002	0.99	-0.155	-0.80
Storm-petrels				
Fork-tailed Storm-petrel	−0.093	−1.16	−0.180	−2.25**
Leach's Storm-petrel	−0.154	−2.11**	−0.187	−2.39**

values alone. We are not suggesting that seabirds are responding directly to changes in phytoplankton, but rather that increased phytoplankton provide the basis for greater productivity and larger biomass of forage nekton, including fish and zooplankton. Our new working hypothesis is that the extended growing season enhances food availability in late summer, thus enticing seabirds to stay in the gyre longer during each year.

Re-distribution of seabirds to the Alaska Gyre?

Sydeman et al. (2009) compared overall seabird abundance and species richness from the CalCOFI (1987–2006) and Line P programs (1996–2006), and found a decline in abundance and diversity in the Southern California Bight and an increase in abundance and diversity in the southeastern Gulf of Alaska. To what extent could range expansions or contractions explain patterns of change in the Alaska Gyre seabird community? This study and others (Hyrenbach & Veit 2003, Woehler et al. 2003, Ainley & Hyrenbach 2010, Péron et al. 2010) have demonstrated changes in relative abundance of seabirds that could suggest large-scale re-distributions. In this case, locally-breeding and migrant seabirds appeared to be staying in the Alaska Gyre for a longer period of time each year, a pattern related to changes in the phenology of primary productivity and possibly 'bottom-up' trophic interactions. Northwestward isotherm displacement suggests possible improvements in habitat quality (warming) for seabirds in this region.

Studies of seabirds at sea have a distinct advantage over studies of seabirds at colonies in that environmental conditions can be measured concurrently at appropriate temporal and spatial scales, thereby facilitating mechanistic understanding of physical–biological coupling. The importance of this study lies in its broad spatial scale and seasonal sampling along with the hydrographic data collected in tandem and applied to multiple seabird species. With shipboard surveys one can map and assess changes in the distribution and abundance of multiple species simultaneously and attribute these changes to environmental conditions. We expect that additional insight will be provided by these sea-going programs, especially with increasing lengths of the time series in future years. This study provides key reference points for developing spatially explicit and seasonally sensitive models of climate–seabird interactions in the Northeast Pacific.

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Appendix 1

Table A1. Median survey date, number of survey days, and total area surveyed of each at-sea survey along Line P. No surveys took place in winter 1996, late spring 2005, or late summer 1997, 1998 and 2006

	Median survey date			No. of survey days			Total area surveyed (km^2)		
Year	Winter	Late spring	Late summer	Winter	Late spring	Late summer	Winter	Late spring	Late summer
1996		21 May	23 Aug		14	13		468	560
1997	21 Feb	18 Jun		10	16		200	555	
1998	24 Feb	15 Jun		10	18		467	716	
1999	20 Feb	13 Jun	4 Sep	12	17	17	437	652	540
2000	13 Feb	6 Jun	13 Sep	10	11	12	393	802	451
2001	14 Feb	12 Jun	27 Aug	13	25	10	401	902	405
2002	15 Feb	9 Jun	5 Sep	14	19	16	760	637	723
2003	12 Feb	6 Jun	7 Sep	13	18	13	742	506	296
2004	23 Feb	9 Jun	27 Aug	8	15	14	208	253	376
2005	18 Feb		25 Aug	15		15	385		482
2006	9 Feb	18 Jun		16	6		428	204	

Table A2. Abundances for 15 seabird species that were analyzed. Species with >200 observations were included in the study

Species	Scientific name	No. of birds	Species	Scientific name	No. of birds
Alcids			**Shearwaters and petrels**		
Ancient murrelet	*Synthliboramphus antiquus*	356	Mottled petrel	*Pterodroma inexpectata*	393
Cassin's auklet	*Ptychoramphus aleuticus*	1667	Northern fulmar	*Fulmarus glacialis*	2784
Common murre	*Uria aalge*	2730	Pink-footed shearwater	*Puffinus creatopus*	760
Rhinoceros auklet	*Cerorhinca monocerata*	1431	Dark shearwaters	*Puffinus griseus* and	13789
Tufted puffin	*Fratercula cirrhata*	611	(sooty and short-tailed)	*P. tenuirostris*	
Gulls			**Albatrosses and storm-petrels**		
Black-legged kittiwake	*Rissa tridactyla*	1375	Black-footed albatross	*Phoebastria nigripes*	1158
Glaucous-winged gull	*Larus glaucescens*	1386	Laysan albatross	*Phoebastria immutabilis*	382
			Fork-tailed storm-petrel	*Oceanodroma furcata*	2278
			Leach's storm-petrel	*Oceanodroma leucorhoa*	9225

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Contribution to the Theme Section 'Seabirds and climate change'

Seabird diet indicates changing Arctic marine communities in eastern Canada

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ABSTRACT: Changing climatic conditions are affecting ecosystems worldwide, but polar ecosystems are experiencing the most rapid changes as the extent of summer sea ice has diminished over the last several decades. In the Canadian Arctic, thick-billed murres *Uria lomvia* can be used as samplers of the marine environment, and we examined changes in the diet of the birds between recent and historical studies from the 1970s and 1980s. In the low Arctic, the amount of Arctic cod, an ice-dependent species, declined in the murre diet; and capelin, a subarctic species, has now become the primary prey item. In the mid-Arctic, where summer sea ice is still present during the summer, Arctic cod persists as an important prey item, but capelin is now regularly observed, marking an apparent northward expansion of this species over the last 30 yr. In the high Arctic, summer sea ice continues to dominate the seascape in most years, and Arctic cod continues to dominate the diets of the murres. Changes in Arctic cod in the bird diet were found to be more related to sea ice conditions averaged over multiple years rather than single-year indices, indicating that long-term changes in sea ice do impact this prey species. The diversity of the prey sampled by the birds has decreased, signaling a potential change in the number of prey species available. Overall, the birds illustrate changes occurring in the marine environment in areas where little other information is available.

KEY WORDS: Seabird · Arctic · Climate change · Diet shift · Fish community · Zooplankton · Thick-billed murre · *Uria lomvia* · Sea ice cover

INTRODUCTION

Changing climatic conditions are affecting biological systems worldwide (Edwards & Richardson 2004). High latitudes are expected to be particularly affected by changing atmospheric and oceanographic conditions, as a result of widespread changes in sea ice and snow cover (IPCC 2007). In the Canadian Arctic, an overall warming trend and a reduction in summer sea-ice cover have been observed over the last several decades (Barber et al. 2008). Such changes are likely going to fundamentally alter Arctic ecosystems, as sea ice plays a central role to marine organisms, and changes in sea ice have direct impacts on local species (Gaston et al. 2005a, Soreide et al. 2010). Tracking changes in sea-ice ecosystems over time can help us understand ecosystem dynamics as well as how changing climatic conditions may affect the polar regions.

Seabirds are considered ideal organisms for tracking changes in marine environments (Cairns 1987). They are highly visible, easy to count, and have a life history that is tightly coupled with the environment, and as a result have been useful in studying changes in fish populations in a number of ocean basins (Piatt et al. 2007). In the eastern Canadian Arctic, the thick-billed murre *Uria lomvia* (hereinafter referred to as 'murre') has been shown to be a useful indicator species for tracking changes in the marine environment, based on long-term monitoring programs (Gaston et al. 2005b, 2009).

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Starting in the mid-1970s, several studies examined the diet of adult murres throughout Canada's low-, mid-, and high-Arctic oceanographic zones as defined by Salomonsen (1965) (Bradstreet 1980, Gaston & Nettleship 1981, Gaston & Noble 1985). Historically, the diet of high-Arctic murres was dominated by Arctic cod *Boreogadus saida*, a cold-water schooling fish that spawns on the under-surface of ice (Craig et al. 1982), while low-Arctic murres also consumed Arctic cod along with a number of secondary prey items (Gaston & Bradstreet 1993).

Since these initial studies, several long-term monitoring programs have been established by Environment Canada in the Canadian Arctic to study murres, with a major part of the research focused on the murre colony at Coats Island, Nunavut (62° 57′ N, 82° 00′ W). In the 1980s and early 1990s, most food items delivered to nestlings by parents on Coats Island were Arctic cod (Gaston et al. 2003). However, beginning in the mid-1990s, capelin *Mallotus villosus*, a subarctic schooling fish species common off the coast of Atlantic Canada, became more common in the nestling diet, whereas the amount of Arctic cod declined. By 1997, capelin was the most common prey item delivered to nestlings (Gaston et al. 2003), a pattern that has persisted to date (A. J. Gaston unpubl. data).

In light of the changes observed in the nestling diet at Coats Island, and the changes in sea ice observed throughout the eastern Canadian Arctic, a reassessment of adult murre diet throughout the region was needed to detect potential widespread changes in murre diets. In the present study, in order to compare current murre diets with historical samples, murres were collected for stomach content analysis from 2007 to 2009 (International Polar Year) in the same areas and on similar dates as collections made in the 1970s and 1980s (see Table 1).

As sea ice conditions are a major factor structuring marine ecosystems in the Arctic, the diets of the birds were expected to show the greatest changes in the low Arctic, where dramatic changes have occurred in summer sea-ice cover over the last few decades (Barber et al. 2008). Diversity in prey items at the low-Arctic sites was expected to increase as subarctic species start to contribute more to the diversity of the murre diet. In the high Arctic, where sea ice continues to be present for much of the summer, murre diets were expected to show little or no change in composition or diversity, while in the mid-Arctic, changes were expected to be intermediate between those in the high- and low-Arctic zones (Gaston & Bradstreet 1993).

We also looked at how changes in the 2 main prey species, Arctic cod and capelin, in the murre diet were related to changes in local sea-ice conditions during the breeding season in the year of sampling and in the previous 2 yr. Due to the sympagic (ice-associated) nature of Arctic cod, changes in this fish species in the diet of the murres was expected to be more positively related to sea ice over several years as compared with any single year of ice cover. Conversely, as capelin is a subarctic species, and not dependent on sea ice, the presence of this species in the murre diet was expected to be more negatively related to sea ice cover over a period of several years.

MATERIALS AND METHODS

Stomach content analysis has limitations as a dietary study tool, as it is biased toward prey items with hard parts or those that have been recently ingested (Jackson & Ryan 1986). The retention time of prey items varies with species, and stomach contents usually reflect species preyed upon in the last 6 to 24 h (Brekke & Gabrielsen 1994, Hawkins et al. 1997). As a result, direct dietary comparisons are admissible only where they duplicate, as closely as possible, the methods of the earlier studies.

Collections

Adult murres were collected at 5 sites spread throughout the eastern Canadian Arctic. Birds were shot with a 12-gauge shotgun using steel shot from a small boat in areas where birds were seen to be actively feeding. During the 2007–09 breeding seasons, murres were collected from the waters around Akpatok Island (60° 25′ N, 68° 08′ W), Coats Island, and Digges Sound (62° 33′ N, 77° 35′ W) in the low Arctic; the Minarets (also known as Akpait; 66° 56′ N, 61° 46′ W) in the mid-Arctic; and Prince Leopold Island (74° 02′ N, 90° 00′ W) in the high Arctic (Fig. 1, Table 1). Murres were collected as close as possible to historical collection dates to minimize differences in diet due to seasonal patterns. After the collections were complete, carcasses were kept cool for 6 to 24 h, and then frozen until dissections were carried out.

Laboratory procedures

Each gastrointestinal tract (GIT) was cut longitudinally along the entire length of the tract. Once the

GIT was opened, the stomach was flushed with ethanol to remove all the items, taking care to remove all items in the folds of the stomach, and placed in 95% ethanol. Prey remains in each stomach sample were sorted, divided into smaller vials, and categorized using an MZ6 Leica binocular microscope.

Otoliths were viewed, measured, and photographed using the Leica microscope, a scope-mounted video camera, and image analysis software. All otoliths were identified using Campana (2004), and voucher otoliths were sent to Otolith Technologies' laboratory in Stillwater, Nova Scotia for confirmation of identification (www.marinebiodiversity.ca/otolith/english/home.htm). If 2 otoliths from a given stomach measured within 0.2 mm, they were considered to originate from the same fish (Bradstreet 1980). The minimum number of fish in each stomach was calculated as the number of matched otolith pairs plus the number of unmatched individual otoliths.

Intact zooplankton individuals, along with heads and tails for each taxon, were enumerated and identified to the lowest taxonomic level possible (Holmquist 1959, Clarke 1962, Tencati & Leung 1970, Baker et al. 1990, Klekowski & Weslawski 1991, Vinogradov et al. 1996, Audzijonyte & Vainola 2007). Abundance estimates were based on the sum of whole zooplankton and the number of heads or tails, whichever was more numerous, giving a minimum number for each stomach.

Polychaete jaws were identified as left or right, and the number of individual polychaetes present was determined from the maximum number of either right or left jaws. Squid numbers were estimated by the maximum number of beak hoods or rostrums present.

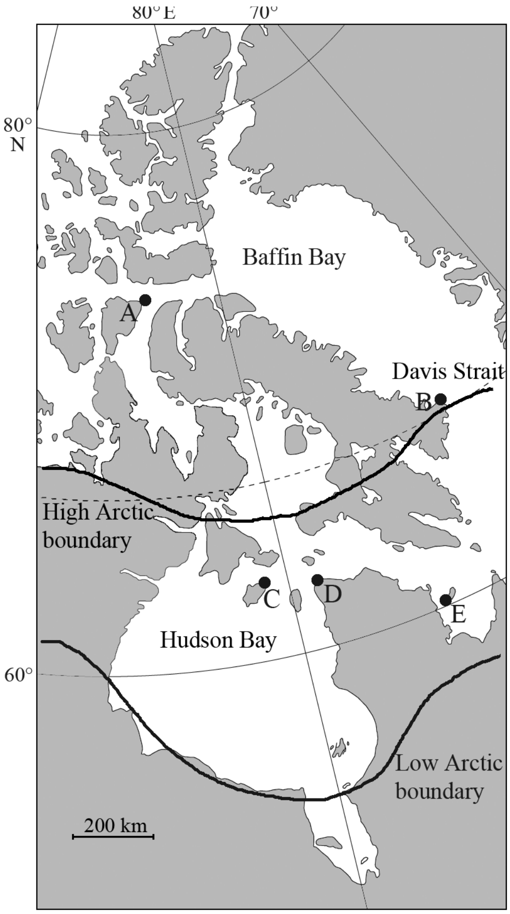

Fig. 1. *Uria lomvia*. Location of collections in the eastern Canadian Arctic in the 1970s–80s and 2007–09 and the boundaries of the low- and high-Arctic zones as described by Salomonsen (1965). The mid-Arctic zone is the area at the boundary between the low- and high-Arctic zones. A: Prince Leopold Island; B: the Minarets; C: Coats Island; D: Digges Sound; E: Akpatok Island

Table 1. Collections: Historic and current collections of thick-billed murres for dietary studies in the eastern Canadian Arctic

Colony	Collection date	Year	n	Source
Low Arctic				
Akpatok Island	August 7	1983	19	Gaston & Bradstreet (1993)
Akpatok Island	August 19	2008	31	Present study
Coats Island	July 27	2007	25	Present study
Digges Sound	July–August	1980	98	Gaston et al. (1985)
Digges Sound	July–August	1981	44	Gaston et al. (1985)
Digges Sound	June–August	1982	55	Gaston et al. (1985)
Digges Sound	August 11	2008	30	Present study
Digges Sound	July 28, August 1	2009	61	Present study
Mid Arctic				
The Minarets	late July	1985	17	Gaston & Smith (1985)
The Minarets	August 5	2007	30	Present study
The Minarets	August 3	2008	20	Present study
High Arctic				
Prince Leopold Island	June–August	1976	48	Gaston & Nettleship (1981)
Prince Leopold Island	June–August	1977	48	Gaston & Nettleship (1981)
Prince Leopold Island	June 5, August 9	2008	50	Present study

Diet data analysis

Sampling occurred at 5 colonies, but for dietary comparisons, only Digges Sound, the Minarets, and Prince Leopold Island are included, as these had both robust historic and current stomach samples. The 2007–08 dietary results for Coats Island and Akpatok Island are included and referred to for general discussion purposes, but due to a lack of historic stomach-contents data from Coats Island, and highly degraded current samples from Akpatok Island because of logistical challenges during collections, these colonies are not included in the diet-change analysis. The prey item results are presented as percent totals, which describe the proportion of prey items as a function of the total amount of prey items found in the birds at a given colony (see Fig. 2). Percent occurrence or incidence rate is given in the supplement (www.int-res.com/articles/suppl/m454p171_supp.pdf), describing the proportion of birds that contained at least one of the prey items as a function of the total number of birds collected during the sampling (i.e. incidence rate).

To test for differences in the proportion of fish and invertebrates consumed by the birds as a function of total prey items, a generalized linear mixed model was used ('Proc GLIMMIX': this and other procedures run in SAS version 9.2). Fish proportion of total prey consumed was modeled with time period (historic vs. new) and zone (low, mid-, and high Arctic) as explanatory variables. The effect of year nested within sampling periods was modeled as a random variable. Only those birds sampled during the chick-rearing season (July to mid-August) were included in this analysis to control for any seasonal difference in diet. The model was fitted with a binomial distribution and a logit function, and controlled for over-dispersion of the data by modeling residuals as a random variable ('random = residual' statement).

Counts within fish subgroups (e.g. Arctic cod, sandlance, sculpin) were modeled as response variables and tested for variation with time period and Arctic zone using a similar generalized linear mixed model. Again, the effect of year nested within time periods was modeled as a random variable. This model was fitted with a negative binomial distribution and log link function to control for over-dispersion in the data. Models failed to converge for capelin, sandlance, and the remaining fish categories pooled into a single category ('other') because of low occurrence in diets sampled in the high-Arctic zone, and for this reason we modeled these groups based on data from the low- and mid-Arctic zones only. When a significant interaction was found between time period and zone in the number of individuals within a fish category in the diet samples, LSMEANS statements were used for post hoc comparisons of fixed effects within this model.

The invertebrate diet data (hyperiids, gammarids, mysids, squid, other) were highly zero-inflated and over-dispersed, precluding the use of generalized linear mixed models. Instead, these data were modeled using maximum likelihood estimation ('Proc GENMOD') and a negative binomial distribution with a log link function. This modeling technique does not allow for the inclusion of year nested within time sample period as a random variable. When a significant interaction was found between time period and zone in the number of individuals within an invertebrate subgroup in the diet samples, LSMEANS statements were used for post hoc comparisons of fixed effects within this model.

Sea ice analysis

To examine the relationship between the sea ice and the main fish species found in the murres, we used the historical percentage of sea ice cover on 16 July from the area around the colonies as reported from the Canadian Sea Ice Service (using IceGraph 1.03, available at http://ice-glaces.ec.gc.ca/IceGraph103/?id=11874&lang=eng) as a linear explanatory variable for predicting diet composition in the murres. Sea ice on this date has been shown to be related to murre diet (Gaston et al. 2005b). These analyses were more complicated than comparing diet composition between sampling periods because prey populations are likely determined by ice conditions in previous years. For this reason, indices of ice conditions at variable lag-times were created as predictors for diet composition among the 3 Arctic zones. Indices of ice conditions used were conditions during the sample year (t_0), the year before sample (t_{-1}), and 2 yr before sample (t_{-2}), as well as mean indices combining sample year and the year prior to sample, $(t_0 + t_{-1})/2$, and mean combining sample year, year prior to sample, and 2 yr prior to sample, $(t_0 + t_{-1} + t_{-2})/3$.

To explore the relationship between the proportion of fish in overall diet and subgroup abundance with the various ice condition indices, we used maximum likelihood estimation and the Akaike information criterion (AIC) to guide our choice among the different indices. For the analysis based on fish proportion, we modeled with a logit link function and binary distribution for proportion of fish, and for both analyses based on the fish subgroup abundance data, we used a log link function and negative binomial distribution to account for over-dispersion within the data. All exploratory models included zone and interactions as explanatory parameters.

Once the best-fit ice index was determined for both proportion of fish in overall diet and fish subgroup abundance, we tested the relationship between the best-fit ice condition index with proportion of fish and subgroup abundance in diet samples among zones, again using 'Proc GENMOD' with logit link function and a binary distribution (proportion data), and with a log link function and a negative binomial distribution to correct for over-dispersion in the subgroup abundance data. Insignificant explanatory variables and higher-order variables were removed in the final model.

Prey diversity

Prey diversity for each site was examined using species-richness accumulation curves, which allow for standardized comparison of diversity across collections that differ in sample size (Gotelli & Colwell 2001). This approach was used to examine prey species diversity in murre diets at the 3 colonies with robust historic and current diet sampling (Digges Sound, the Minarets, and Prince Leopold Island). All birds sampled in July and August (the chick-rearing period) that contained at least 1 identified item in their GIT (leading to smaller sample sizes) were grouped together by colony and sampling period, and the prey abundances for each bird were put into a matrix in EcoSim (Gotelli & Entsminger 2009) to create a sample-based curve, with a rarefaction curve as the randomization algorithm and species richness as the prey species diversity index. Prey diversity curves were then produced in Excel in order to compare the species richness with 95 % confidence intervals. Non-overlapping endpoints outside of 95 % confidence interval curves indicate significantly different diversity levels.

RESULTS

During 2007–09, 247 GITs were examined, of which 191 were from Digges Sound, the Minarets, and Prince Leopold Island, compared with 331 from the 1970s and 1980s from the same sites (Gaston & Bradstreet 1993). In the present study, 12 488 prey items were identified (Tables S1 & S2 in the supplement at www.int-res.com/articles/suppl/m454p171_supp.pdf), with fish accounting for 21 % of the total number of prey items and invertebrates making up the rest. Most GITs contained >1 type of prey and only 14 (5.6 %) contained no identifiable prey remains.

Differences among colonies

The primary prey items identified varied among the 5 colonies sampled. At Prince Leopold Island, Arctic cod was predominant (Fig. 2); at the Minarets, it was Arctic cod and mysids, with other fish and invertebrates in smaller numbers; at Coats Island, hyperiid amphipods were the most numerous prey item, with capelin the most numerous fish; and at Digges Sound, sandlance and capelin were the most common fish and mysids the most abundant invertebrates. At Akpatok Island, the stomach contents were highly degraded due to an unexpected delay in preserving the birds, resulting in many of the otoliths not being identifiable. Hence most of the fish in the diet are unknown, but by numbers, hyperiid amphipods were the largest group of invertebrates consumed at Akpatok.

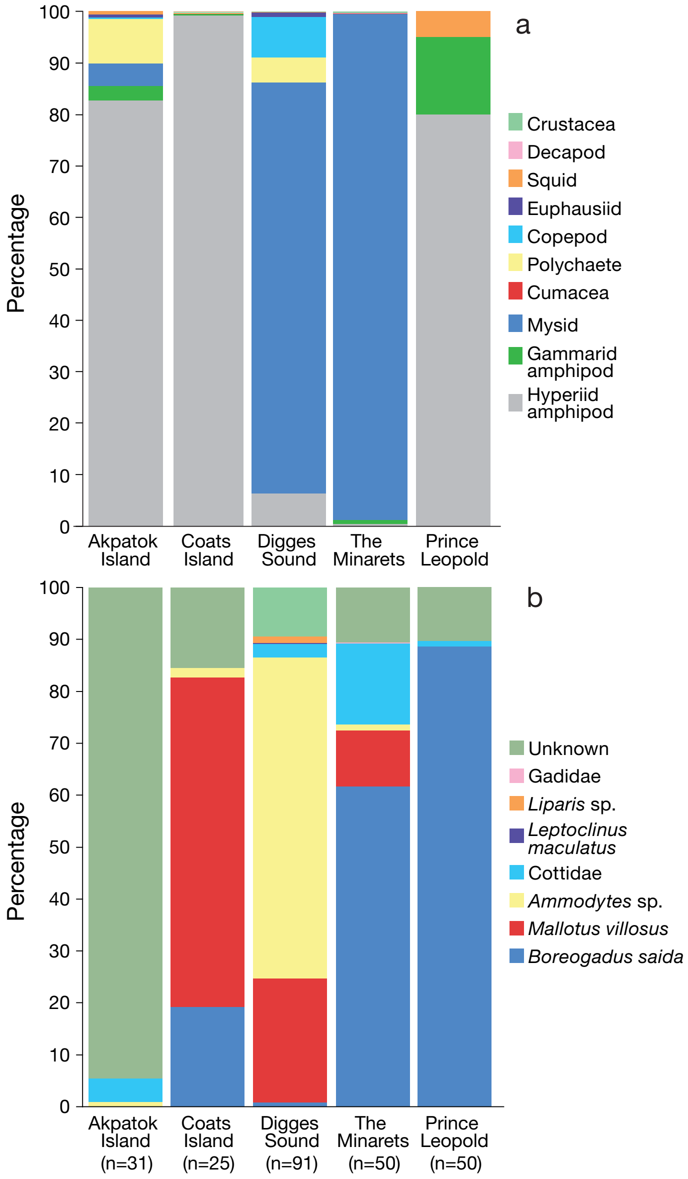

Fig. 2. *Uria lomvia*. Percent totals of (a) invertebrate and (b) fish prey items from eastern Canadian Arctic samples in 2007–09. Akpatok Island (n = 31), Coats Island (n = 25), and Digges Sound (n = 91) are in the low Arctic; the Minarets (n = 50) is in the mid-Arctic; and Prince Leopold Island (n = 50) is in the high Arctic

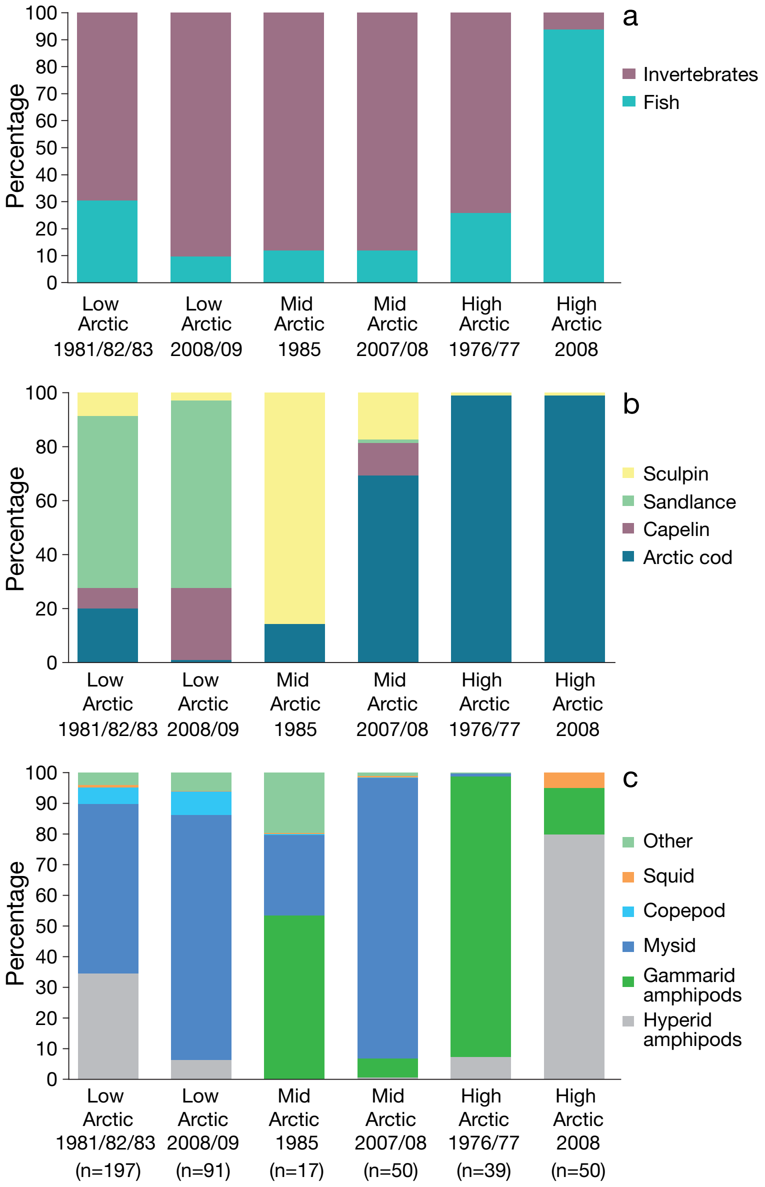

Fig. 3. *Uria lomvia*. Historic and current diet samples in the low Arctic (Digges Sound), mid-Arctic (the Minarets), and high Arctic (Prince Leopold Island). Percent total of (a) fish and invertebrates, (b) identified fish species, and (c) invertebrate prey items

Differences in prey composition between recent and earlier samples

Overall, fish proportion (mean ± SD) varied between sampling periods inconsistently among zones (Fig. 3; $F_{2,376} = 3.46$, $p = 0.032$). In particular, the proportion of fish decreased in the low-Arctic zone (historic: 0.40 ± 0.18; new: 0.055 ± 0.045; $t = 2.11$, df = 376, $p = 0.036$), did not change in the mid-Arctic zone ($t = 0.09$, $p = 0.93$), and in the high-Arctic zone it may have increased (old proportion: 0.43 ± 0.30; new proportion: 0.98 ± 0.05) but we failed to detect significance ($t = 1.56$, df = 376, $p = 0.12$).

Fish species abundance varied between time periods differently among the 3 Arctic zones for the 2 fish species with sufficient data to test (Arctic cod, sculpin). The proportion of Arctic cod differed significantly between time periods and among zones ($F_{2,304} = 6.91$, $p = 0.0012$). In the low Arctic, there was a significant decrease in the proportion of Arctic cod in the diet from 30% of the fish consumed to <5% ($t = -2.85$, df = 304, $p = 0.005$). In the mid-Arctic, Arctic cod increased from 15% of the fish consumed in 1985 to almost 70% ($t = 2.02$, df = 304, $p = 0.04$) in the 2007–08 sample. In the high Arctic, Arctic cod continued to be the main fish prey species ($t = 0.97$, df = 304, $p = 0.33$). Sculpins (family Cottidae) did not show a significant change over time ($F_{1,5} = 0.81$, $p = 0.41$).

Analyses based on capelin, sandlance, and 'other' fish data were restricted to murres sampled in the low- and mid-Arctic zones only, because of an extremely low rate of occurrence for these species in samples from the high Arctic. The number of capelin found in murre diets increased with time ($\chi^2_{1,265} = 17.8$, $p < 0.0001$) in both zones ($\chi^2_{1,264} = 3.34$, $p = 0.07$), from 0 to 12% in the mid-Arctic and from 8 to almost 30% in the low Arctic zone. A change in sandlance *Ammodytes* sp. abundance was not detected between time periods ($\chi^2_{1,264} = 1.23$, $p = 0.27$) or time periods and zones ($\chi^2_{1,265} = 0.03$, $p = 0.86$). There were no significant changes in analyses based on data pooled among the remaining fish species ('other'), likely because of small sample size.

Table 2. *Uria lomvia*. Summary of changes in prey items sampled in the 1970s–80s and 2007–09 diets in the low Arctic (Digges Sound), mid-Arctic (the Minarets), and high Arctic (Prince Leopold Island) based on significant changes in prey abundance. Only those prey items that showed a significant interaction over time are shown. '↑' denotes an increase, '↓' denotes a decrease, '=' denotes no change, and 'na' denotes not able to test

	Low Arctic	Mid-Arctic	High Arctic
Fish	↓	=	=
Arctic cod	↓	↑	=
Capelin	↑	↑	na
Mysids			
Hyperiid amphipods	↓	↑	=
Gammarid amphipods	↓	↓	↓

Overall invertebrates in the diet of the murres also changed over time (Fig. 3; $\chi^2 = 22.3$, df = 5, p = 0.0005). Both copepod and squid abundance in murre diet did not vary with time (copepod: $\chi^2 = 3.38$, df = 1, p = 0.070; squid: $\chi^2 = 1.51$, df = 1, p = 0.22) and did not vary with time period by zone interaction (copepod: $\chi^2 = 0.98$, df = 2, p = 0.61; squid: $\chi^2 = 3.65$, df = 2, p = 0.16). Gammarid amphipods decreased significantly with time period ($\chi^2 = 23.8$, df = 2, $p < 0.0001$) consistently among zones ($\chi^2 = 2.85$, df = 2, p = 0.24). Mysids also decreased significantly with time ($\chi^2 = 8.11$, df = 1, p = 0.0014) consistently among zones ($\chi^2 = 1.35$, df = 2, p = 0.51).

The amount of hyperiid amphipods in the diets of the murres varied inconsistently with time among the zones ($\chi^2 = 16.8$, df = 2, p = 0.0002). In the low Arctic, where hyperiid amphipods formed a relatively large portion of the murre diet in the earlier period, there was a significant decrease (from 30% of invertebrates to 8%: $\chi^2 = 20.48$, df = 1, $p < 0.0001$). In the mid-Arctic, hyperiids contributed a small amount to the bird's diet but showed a significant increase with time ($\chi^2 = 6498.3$, df = 1, $p < 0.0001$) (Fig. 3). In the high Arctic, hyperiid amphipods continued to contribute to the diet of the birds in very small numbers, with only 14 hyperiids found in 50 birds from the high Arctic in 2008 ($\chi^2 = 2.91$, df = 1, p = 0.09).

Other invertebrate prey items found in small numbers include annelids, cumaceans, decapods, and euphausiids. Grouped together, these prey items were found to account for <10% of total invertebrate prey items, except at the Minarets in 1985, where >20% of the invertebrates were from these 4 groups. Independently, changes in these groups could not be modeled due to limited numbers in the samples.

Considering all of the above changes, the greatest amount of change occurred in the diet of the murres in the low Arctic, with fewer changes in the mid-Arctic and the least amount of changes in the high Arctic (Table 2).

Changes in ice conditions

Between 1971 and 2010, the sea ice cover in northern Hudson Bay, around Digges Sound (low Arctic), decreased strongly, especially after 1993 (Fig. 4). On average, the extent on 16 July was 33% during the period 1971 to 1993 and only 7% after 1993, and the overall slope of the trend line for sea ice cover (mean ± SD) for this time period is $-7.45 \pm 5.13\%$ decade^{-1}, suggesting a long-term decrease in sea ice. In Davis Strait (mid-Arctic), summer sea ice showed only a small decline in sea ice over the last 40 yr (slope: $-3.36 \pm 2.11\%$ decade^{-1}), and in Lancaster Sound (high Arctic), sea ice cover showed substantial fluctuations and no strong trend (slope: $-2.60 \pm 7.49\%$ decade^{-1}) between 1971 and 2010.

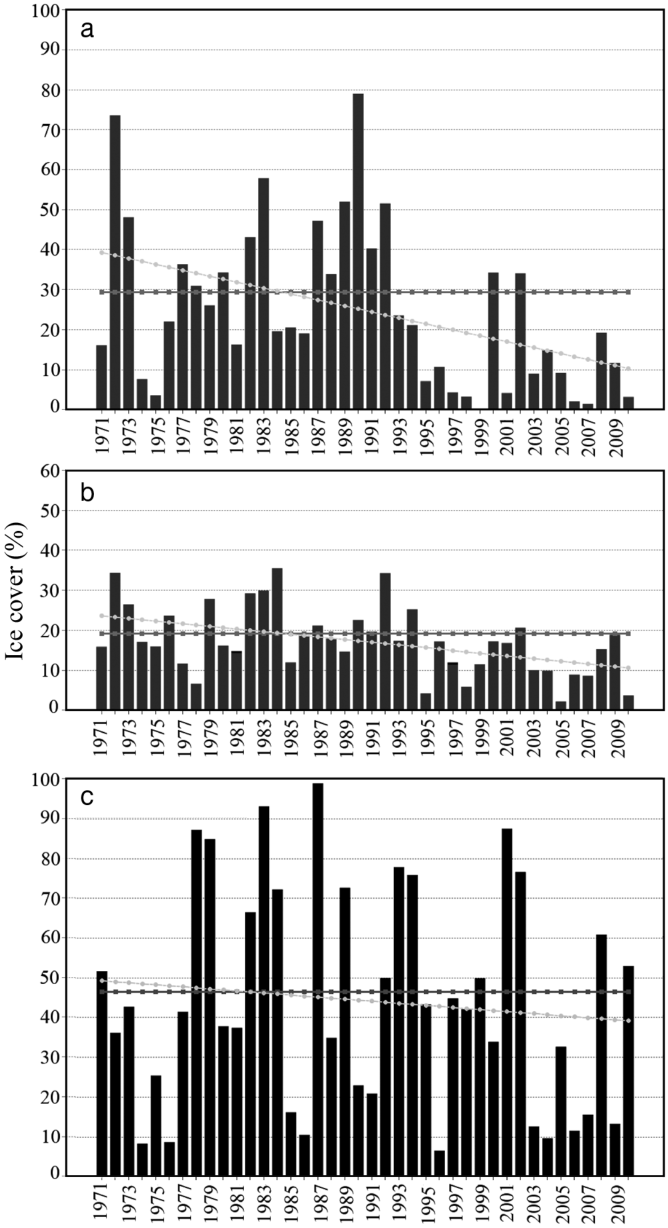

Fig. 4. *Uria lomvia*. Sea ice cover in the eastern Canadian Arctic during the chick-rearing period from 1971 to 2010 on 16 July of each year in (a) North Hudson Bay Narrows (low Arctic; slope: $-7.45 \pm 5.13\%$ decade^{-1}), (b) Davis Strait (mid-Arctic; slope: $-3.36 \pm 2.11\%$ decade^{-1}), (c) Lancaster Sound (high Arctic; slope: $-2.60 \pm 7.49\%$ decade^{-1}). The dark gray line indicates the average ice cover and the light gray indicates the overall trend in sea ice cover between 1971 and 2010. The slopes listed above are for the trend line for each region

Table 3. *Uria lomvia*. Model fit (Akaike information criterion) for various ice indices explaining variation in the proportion of fish in the diet and variation in abundance of Arctic cod and capelin in the diet. **Bold** text indicates the best fit model of the 5 tested as shown

	Sample year (t_0)	1 yr lag (t_{-1})	2 yr lag (t_{-2})	2 yr average $((t_{-1} + t_0)/2)$	3 yr average $((t_{-2} + t_{-1} + t_0)/3)$
Proportion of fish	12215.2	13448	**10790.2**	12789.5	11921.3
Arctic cod	1388.4	1327.3	1322.4	1363.8	**1319.6**
Capelin	630.7	642	**621.1**	639.4	631

Changes in local sea-ice conditions were significantly associated with changes in the proportion of fish in general and specifically with the 2 main fish prey species consumed by murres, Arctic cod and capelin, but the nature of this association varied among zones. The ice index reflecting ice conditions 2 yr prior to the sample year had the highest explanatory power for variation in the proportion of fish in murre diets (Table 3), the ice index reflecting ice conditions averaged over 3 yr up to and including the sample year was most effective for explaining variation in Arctic-cod abundance, and ice conditions prior to the sample year best predicted capelin abundance in murre diets.

Proportion of fish in the diet varied significantly with the best-fit ice index reflecting ice conditions 2 yr prior to sample year ($F_{2,381} = 9.45$, $p \leq 0.0001$), and most of this variation occurred in the low-Arctic zone where fish proportion decreased significantly with the decrease in sea ice ($t = 8.46$, df = 381, $p \leq 0.0001$). There was no significant relationship in the mid-Arctic zone ($t = 0.52$, df = 381, p = 0.60), and there was significant variation in the high Arctic where the proportion of fish decreased with more ice cover ($t = -2.02$, df = 381, p = 0.044). Capelin abundance varied significantly with the same best-fit ice index as overall fish proportion (ice conditions 2 yr prior to sample year) ($F_{1,370} = 26.6$, $p \leq 0.0001$), but this variation was consistent among Arctic zones for this species. Arctic cod abundance in the diet varied with the best-fit ice index averaged over the previous 3 yr including the sample year, and the nature of the relationship differed significantly among Arctic zones ($F_{2,368} = 45.8$, $p \leq 0.0001$). In the high Arctic, no significant change was detected in Arctic cod consumed by murres as the local ice conditions changed ($t = 0.16$, df = 368, p = 0.69), but in the low Arctic, Arctic cod increased in the murre diet with more sea ice ($t = 32.2$, df = 368, p = 0.0001), and in the mid-Arctic, Arctic cod decreased with increasing ice cover ($t = 15.0$, df = 368, p = 0.0001).

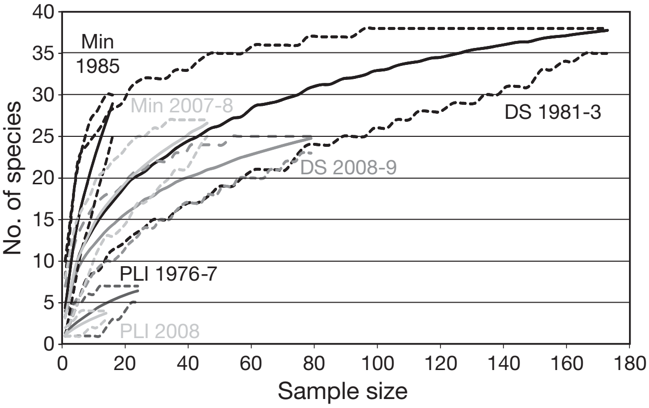

Fig. 5. *Uria lomvia*. Prey species richness curves (sample size vs. number of species) for diets compared between sampling in the 1970s–80s and again in the same locations in 2007–09 at Digges Sound (DS; 1981–83 black, 2008–09 mid-gray), the Minarets (Min; 1985 black, 2007–08 light gray), and Prince Leopold Island (PLI; 1976–77 dark gray, 2008 light gray). Dotted lines: 95% CIs

Changes in prey diversity

Diet diversity did not change between time periods in either the low Arctic (Digges Sound; 1980s: mean = 37.8, n = 178; 2000s: mean = 24.78, n = 81) or high Arctic (Prince Leopold Island; 1970s: mean = 3.73, n = 16; 2008: mean = 6.42, n = 29), with 95% confidence intervals overlapping in both cases (Fig. 5). Diversity did differ significantly in the mid-Arctic (the Minarets; 1985: mean = 28.94, n = 48; 2007–08: mean = 26.60, n = 17) as indicated by the non-overlapping endpoints of the diversity curves (Fig. 5). Differences in diversity were not related to number of prey items, or associated with any single group of prey for any colony, and the level of taxonomic differentiation was similar among all samples.

DISCUSSION

Changes in diet

Changes in the diet of murres between earlier and recent samples were found in all zones. These changes are difficult to interpret as we have only 2 collection points separated by 20 to 30 yr, with little information from the intervening time. One potential confounding factor in diet comparisons is timing, as adult birds have been shown to alter their prey spectrum over the breeding season (Elliott et al. 2009), thus we tried to repeat as near to the original sampling dates as possible, which still correspond to the bird's breeding phenology. Fisheries may also influence prey communities, but no commercial fisheries operate in any of the areas sampled, so it is unlikely that our results are in any way affected by fisheries. Competition among other top predators can also influence marine communities, but although razorbills and subarctic gulls have increased in the low Arctic (Gaston & Woo 2008), their numbers are negligible relative to the size of the large murre colonies (Brown et al. 1975, Gaston 1991). All these factors must be considered when examining and interpreting detectable changes in seabird diet, but their effects in the present study are likely to be small, allowing murres to be used as sentinels of changing marine ecosystems.

Arctic cod still dominates the diet of the high-Arctic murres. This supports our prediction that little change should have occurred in the diet of the high-Arctic murres as sea ice conditions, although variable, have shown no consistent trend or change during the murre's breeding season. Arctic cod was also still the main fish species in the murre diet in the mid-Arctic, where sea ice is also still present in the summer months. In the low Arctic, where summer sea ice has declined the most drastically, and is now rare or non-existent, Arctic cod has all but disappeared from recent murre diets. Very few Arctic cod were found in the recent sample from Digges Sound, and only slightly more in the birds from Coats Island. At Akpatok Island, where murre diet studies go back 6 decades, the recent sampling found no Arctic cod, whereas this species was found to be a main prey item fed to chicks in 1954 (Tuck & Squires 1955) and was still present in the murre diet in 1983 (Gaston & Bradstreet 1993). The decrease in Arctic cod in the murre diet is highly associated with ice conditions over 3 yr prior to and including the sample year in the low and mid-Arctic, suggesting that changes in this prey species in murre diets is more likely due to longer-term, chronic changes than episodic acute events.

The dependence of Arctic cod on sea ice (Craig et al. 1982), declining numbers of Arctic cod in murre diets in Digges Sound cumulatively related to sea ice changes, and the disappearance of Arctic cod from the diet of murres over the last half century at Akpatok Island indicate that changes in Arctic cod as a prey item in the low Arctic may be a consequence of changing sea-ice conditions over the long term. Given the decrease in Arctic cod observed in murre diets in the low Arctic, where summer sea ice is negligible or absent most years, and the variability of sea ice cover in the high Arctic, where Arctic cod continues to be the main food item, our results indicate that the presence or absence of sea ice is the largest factor in Arctic cod availability for murres, although percent cover is likely to be a contributing factor as well.

Alongside the decrease in Arctic cod, the increase in capelin in the diet of the murres sampled in 2007–08 in the low and mid-Arctic suggests that this subarctic fish is becoming an important prey item at these colonies. Capelin is an abundant item in seabird diets in Atlantic Canada (Davoren & Montevecchi 2003), but before the mid-1990s it was only observed as a secondary prey item for murres in the low Arctic (Gaston & Bradstreet 1993). Throughout the 1980s to the mid-1990s, capelin was a secondary prey item in northern Hudson Bay (Gaston et al. 2003), an area within the described range of this species (Leim & Scott 1966), but was not found among nestling diets at Hantzsch Island, off SE Baffin Island (Gaston & Noble 1985), an area just north of the described distribution of capelin at the time. While capelin was present in the low Arctic prior to the 1980s, no range maps for capelin extended north to the Arctic Archipelago, no records existed for capelin on Baffin Island, and no capelin were found in the diets of the mid-Arctic adults at the Minarets in 1985 (Tee-van 1948, Leim & Scott 1966, Gaston & Bradstreet 1993). Now, in 2007–09, capelin has become the dominant prey item at murre colonies in the low Arctic and is common at the Minarets in the mid-Arctic, which lies outside of the range described previously (Leim & Scott 1966), but within more recent range descriptions (Muss et al. 1999), suggesting a northward expansion in the range of this prey species.

In Hudson Bay, the change in sea ice has not been linear, but showed a more step-wise change in the mid-1990s (Scott & Marshall 2010, A. J. Gaston unpubl. data). The replacement of Arctic cod by capelin as the main constituent of food fed to nestling murres at Coats Island coincided with this decrease in sea ice in the low Arctic (Gaston et al. 2003). It is also important to note that prey stocks for murres are not likely to be solely determined by conditions in the year of collection, but as seen in our analysis can be affected by conditions over several years prior to sampling. Thus, a more thorough analysis of multiyear trends in sea ice may be more important to prey fauna availability than ice conditions in any particular year.

The decrease in Arctic cod in the diet with the simultaneous increase in capelin could be interpreted as a switch in preference by the murres, rather than a decrease in Arctic-cod numbers. However, this appears unlikely, because of the decline in the sea ice on which the Arctic cod depend, and because long-term monitoring from Coats Island suggests that during the period when the parents switched from Arctic cod to capelin for feeding their young, nestlings had reduced growth rates, indicating that this change in prey was not beneficial to the young (Gaston et al. 2005b).

Based on the increase of subarctic capelin at low-Arctic sites over the last decade, an increase in subarctic invertebrates was also expected in the diet of the low-Arctic birds. On the contrary, no invertebrate species characteristic of subarctic waters were identified, indicating that no general northward movement of invertebrate species has occurred to date. As most invertebrates are zooplankton and depend on the currents for dispersal, while fish can move of their own accord, subarctic zooplankton may take longer than fish to expand northwards. As ice conditions change, southern zooplankton species may be more likely to appear in Davis Strait (the Minarets) rather than in Hudson Bay, due to the direction of prevailing currents (Rekacewicz & Bournay 1998).

Some changes in invertebrates were observed. The proportion of hyperiid amphipods, previously mostly *Themisto libellula*, fell at Digges Sound. Where the cold-water hyperiid amphipods and Arctic cod used to dominate the diet in Digges Sound, now 2 subarctic fish species (capelin and sandlance) and mysids are the primary prey items, suggesting large-scale changes in the marine environment around this colony.

Several species of the ice-associated amphipod genus *Onisimus* (Horner et al. 1992), common in murre diets earlier (Gaston & Bradstreet 1993), were present in diets at the Minarets in 2007–08, suggesting that summer sea ice continues to influence the organisms found in this area during the murre breeding season. At Prince Leopold Island, the birds sampled in 1976–77 contained a large number of *Onisimus* spp. (Gaston & Nettleship 1981), but none was found in the recent samples. Sea ice is still present at Prince Leopold Island during the breeding season, and a number of the birds were collected while feeding among ice flows, so a decline in ice is not likely to account for the lack of *Onisimus* spp. amphipods in Lancaster Sound.

Changes in diversity

Contrary to our expectations, we found no evidence for an increase in species diversity in any of the 3 zones. The highest prey diversity in the historic samples was found at Digges Sound, but among the recent samples the highest diversity was found at the Minarets. However, at the latter colony, diversity was actually lower in 2007–08 than in 1985. As climatic conditions change, it has been predicted that high-latitude areas will likely be sensitive to changes in biodiversity (Cheung et al. 2009). Our results suggest that there has been no immediate effect on biodiversity with decreasing levels of summer sea ice, although much more comprehensive studies are needed.

Changes in trophic levels

The proportion of fish consumed by murres at low- and high-Arctic colonies was found to have significantly changed. Such changes may have caused a change in the overall trophic level of the murre diet since the last sampling period. The murres from the different colonies show a significantly different δN ratio in breast muscle tissue (J. F. Provencher & A. J. Gaston unpubl. data), suggesting that within the species, trophic level differs among colonies. If current dietary patterns persist, they may lead to the high-Arctic (Prince Leopold Island) murres feeding at a higher trophic level and low-Arctic (Digges Sound) murres feeding at a lower trophic level than in the past. Braune (2009) found that the murres from Coats Island (low Arctic) have shown a decrease in δN ratio in eggs since the early 1990s, suggesting that a change in trophic position on a colony-wide scale has occurred over the last 2 decades. Although historical diet information is not available from Coats Island and no historical stable-isotope data are available from Digges Sound, the change in trophic level at Coats Island supports the idea that the change in the proportion of fish in the diet at Digges Sound is potentially long-term, and has trophic-level implications. Furthermore, if the changes in the diet of the murres have led to a change in their trophic position, then our results have implications for the interpretation of pollutant loads, as trophic level influences biomagnification of contaminants such as mercury, and murres are an important monitoring species in the Canadian Arctic (Braune 2009).

CONCLUSIONS

With only 2 sampling periods to compare, changes in prey species need to be interpreted carefully, and more detailed sampling is needed to fully understand potential biodiversity changes in Arctic waters. However, the decrease in cold-water species across the low Arctic, along with the increase in capelin and mysids in the low and mid-Arctic, illustrates that the biota of these regions is undergoing dramatic changes.

The contrast between the changes in prey observed in the low Arctic and the much less dramatic changes in the diet of the murres in the mid-Arctic suggests that what has occurred in the low Arctic may represent a step-wise change in the marine ecosystem. While the low-Arctic areas in Hudson Bay seem to have shifted towards subarctic species over the last few years, the marine ecosystem of the mid-Arctic appears to be at an Arctic–subarctic transition period, with sympagic species still present but with subarctic species such as capelin and sandlance now becoming regular components of seabird diets.

Overall, we see the greatest change in murre diet in the low Arctic and the least in the high Arctic, with the mid-Arctic showing an intermediate amount of change, as predicted. When this change is compared with sea ice data, the greatest change in diet, specifically in ice-associated prey species, coincides with those areas where sea ice has declined and is no longer present while murres are provisioning their chicks. In the mid-Arctic, where the sea ice is still present during the chick-rearing period, changes in prey species are already occurring, with capelin and sandlance now found at more northern latitudes than previously reported and now being consumed by the birds in quantities similar to those observed in the low Arctic 25 yr ago, suggesting that change will continue in this location if summer sea ice continues to decline. Along with razorbills *Alca torda* (Gaston & Woo 2008) and great black-backed gulls *Larus marinus* (H. G. Gilchrist & J. F. Provencher unpubl.), 2 subarctic marine birds, the movement of capelin to more northern latitudes adds to our knowledge of subarctic species that have become more common in low- and mid-Arctic areas. These changes may have several different effects on the murre colonies of the Arctic Archipelago, and continued work in monitoring of populations will help detect long-term changes in this important human-hunted species.

Studying murres in the Canadian Arctic provides significant and relevant information on changes in the availability of a number of fish and invertebrate species where little or no other fisheries-assessment work is currently being done. The murre colonies in the eastern Canadian Arctic, where long-term studies have been established, are strategic study locations where continued monitoring will allow us to track potential changes in seabird populations and their prey species as changing climatic conditions continue to be observed.

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Contribution to the Theme Section 'Seabirds and climate change'

Climatic effects on breeding seabirds of the northern Japan Sea

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ABSTRACT: Seabirds as marine top predators have been put forth as reliable indicators of ecosystem change. To understand climate–ecosystem change in the northern Japan Sea, we studied the timing of breeding, chick diets, and breeding success of 3 seabird species almost continuously over 26 yr on Teuri Island, 1984 through 2009. Key climate drivers in this region are: (1) westerly winter winds that cool the atmosphere and the ocean and (2) the northward flowing Tsushima Current (TC) that warms the ocean in late spring and summer. Chick diet showed decadal changes in coastal pelagic fish, with a switch from sardine *Sardinops melanostictus* to anchovy *Engraulis japonicus* in the late 1980s corresponding to intensification of the TC. There were no long-term trends in the timing of breeding or breeding success of rhinoceros auklet *Cerorhinca monocerata* and Japanese cormorant *Phalacrocorax filamentosus*, but these variables were affected by interannual variation in spring air and sea temperatures, as well as the timing of TC warm water intrusions within the foraging range (~60 km from the colony) of the birds. Effects include: (1) freezing of the breeding grounds by winter winds limiting access to nesting grounds and (2) availability of anchovy and sandlance *Ammodytes personatus* affecting chick diet, growth, and breeding success. We did not detect relationships between chlorophyll *a* concentrations and the availability of prey species. The timing and success of black-tailed gulls *Larus crassirostris*, which fed mainly on sandlance, however, could not be explained by these factors. Our study indicates potential links between the Pacific Decadal Oscillation index and the flow rate of the TC, and between the Arctic Oscillation index and local wind stress, and suggests that broad-scale atmospheric pressure fields influence local weather, oceanography, and seabirds indirectly through changes in prey availability.

KEY WORDS: Auklet · Breeding performance · Chick diet · Cormorant · Gull · Prey availability · Regime shift · Timing of breeding

INTRODUCTION

Changes in wind stress (Aebischer et al. 1990), sea-ice extent (Loeb et al. 1997), sea-surface temperature (SST; Bertram et al. 2001, Frederiksen et al. 2006), and upwelling (Thayer & Sydeman 2007, Schroeder et al. 2009) affect the foraging and breeding of seabirds through changes in food web structure. In addition to these 'bottom-up' effects, changes in seasonal and spatial patterns of prey influences seabird diet and breeding performance (Durant et al. 2005, Grémillet et al. 2008). Adverse local weather (low air temperature, heavy rain or snow, or strong winds) may limit accessibility to nesting grounds (reviewed by Schreiber 2002). Thus, various mechanisms may underlie the responses of seabirds to climate variability and change.

To understand climatic drivers of marine ecosystem change, it is necessary to examine how seabird diet and breeding performance varies with climatic fac-

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tors on multiple spatial and temporal scales. Seabirds may respond to climate fluctuations on immediate to interannual (Gaston et al. 2009, Moe et al. 2009), decadal (regime shift) (Anderson & Piatt 1999, Durant et al. 2004), and long-term (ocean warming) (Jenouvrier et al. 2009) scales. Responses may also vary between regions (Frederiksen et al. 2007), depending on regional geography, marine physics, and ecosystems, and vary between species depending on the species-specific constraints (Furness & Tasker 2000). Thus, long-term information from multiple species in multiple regions is useful for testing mechanisms.

The Japan Sea lies between the Eurasian continent and Japan (Fig. 1). Here, increases in air temperature (www.data.kishou.go.jp/climate/cpdinfo/temp/an_jpn) and SST (Yeh et al. 2010) have been reported and related to global climate change. In addition, the warm Tsushima Current (TC) heats the sea during the late spring and summer, while westerly winds cool the ocean in winter (Hase et al. 1999, Chiba & Saino 2003). These latter factors vary at 2 time scales. (1) A decadal change in the surface air pressure in Siberia has influenced wind stress and SST; the SST was lower between the late 1970s and late 1980s and has been higher since then (Minobe et al. 2004, Yeh et al. 2010). This climatic regime shift induced a change in phytoplankton and zooplankton (Chiba & Saino 2003, Chiba et al. 2005), as well as pelagic fish communities (Tian et al. 2008). (2) Annual changes in SST are related to air pressure anomalies in the northwestern Pacific represented by variation of the Aleutian Low, which drives the warm TC northward, from the Tsushima Strait in the southern Japan Sea (Minobe et al. 2004).

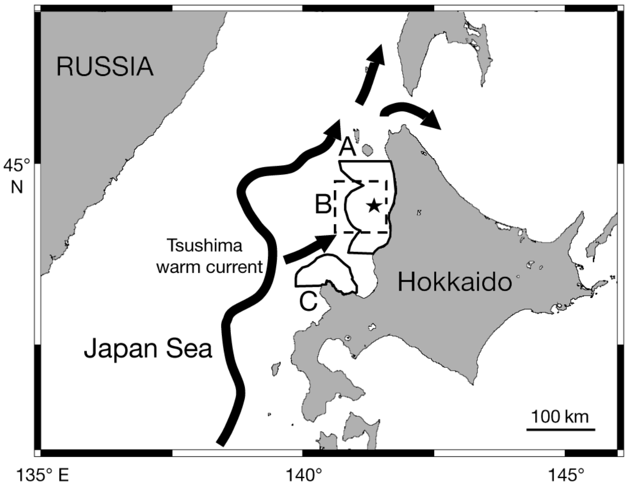

Fig. 1. Study area. ★ = Teuri Island. Around the colony, we measured local sea-surface temperature (SST) in Area A (60 × 150 km), chlorophyll *a* in Area B, and SST for determining the date of warm water arrival (WWA) within foraging range of rhinoceros auklets (Area C)

To understand the relationships between local and large-scale climate fluctuations and seabird biology in the Japan Sea we studied the chick diets and breeding performance of *Cerorhinca monocerata* (rhinoceros auklets, RHAU), *Phalacrocorax filamentosus* (Japanese cormorants, JCOM), and *Larus crassirostris* (black-tailed gulls, BTGL) on Teuri Island (Fig. 1) over 26 yr, 1984 through 2009. We examined long-term trends and the effects of interannual variation in air temperature, SST, other local climate factors, and prey availability on the timing of breeding, chick diets, and breeding success. We discuss how these local factors are influenced by broad-scale climate change.

MATERIALS AND METHODS

Study area and species

We conducted our study on Teuri Island (44° 25′ N, 141° 52′ E). Data were collected in 1984, 1985, and 1987, and from 1992 to 2009 (n = 21 yr). Additional data on the breeding of BTGL were collected in 1980. Table 1 summarizes the breeding biology and chick diets of the 3 studied species. The population sizes varied from year to year. RHAU feed on sandlance *Ammodytes personatus*, juvenile Japan Sea greenling *Pleurogrammus azonus*, and krill *Thysanoessa longipes* and *T. inermis* in spring (Ito et al. 2009) and on sandlance, sardine *Sardinops melanostictus*, and anchovy *Engraulis japonicus* in summer. JCOM feed on benthic fish in spring (M. Ito unpubl. data) and on epipelagic fish (sandlance and anchovy), benthic rock fish *Sebastes* spp., flat fish (Pleuronectiformes), and epibenthic greenlings in summer. BTGL feed on krill *T. inermis* and fish in spring (Tomita et al. 2009) and mainly on sandlance in summer. All 3 species spend winter around the Japan archipelago.

Study plots and breeding biology

RHAU nest in burrows 1 to 2 m deep on cliff shoulder slopes. JCOM nest on cliff ledges and rock stacks, and BTGL on glassy slopes. A single RHAU study plot (ca. 20 × 50 m) containing ~1000 burrows was set-up on a gentle slope in 1984. To increase the number of JCOM samples while minimizing plot size

Table 1. *Cerorhinca monocerata*, *Phalacrocorax filamentosus*, *Larus crassirostris.* Total number of nests, body mass, foraging pattern, and foraging range in rhinoceros auklets (RHAU) Japanese cormorants (JCOM) and black-tailed gulls (BTGL). Range of the annual mean values of the mass proportion of fish prey in chick diet, the timing of breeding (hatching date for RHAU, hatching date of the first chick in a brood for JCOM, clutch initiation date for BTGL), clutch size, and the number of fledglings per active nest (nests with ≥ 1 hatchling or egg)

	Rhinoceros auklet (RHAU)	Japanese cormorants (JCOM)	Black-tailed gull (BTGL)
No. of active nests	190,000–290,000[a]	500–1600[a]	2500–30,000[a]
Body mass (kg)	0.5–0.6[b]	2.3–3.2[e]	0.5–0.6[h]
Foraging mode	Wing-propelled diving	Foot-propelled diving	Surface feeding
Diving depth (m)	14.0 (median), 50 (max.)[b]	7.2–15.1 (mean), 26–39 (max.)[e]	–
Foraging range (km)	87 (0.5–164)[c]	10–22[f]	Around the island[i]
Wintering area	Along Japan archipelago[d]	Along Japan archipelago[g]	Along Japan archipelago[j]
Percent chick diet in 1984–2009 (median)[l]			
Sardine	0–24 (0)	0–19 (0)	0–53 (0)
Sandlance	2–57 (13)	3–92 (21)	8–86 (41)
Anchovy	1–95 (69)	0–49 (13)	0–65 (20)
Juvenile Japan Sea greenling	1–50 (9)	0 (0)	0 (0)
Greenlings	0 (0)	0–60 (22)	0–34 (0)
Demersal fish	0 (0)	3–69 (16)	0–12 (0)
Egg laying date[l]	1 Apr–24 Apr[k]	8 Apr–27 May[k]	5 May–28 May
Hatch date[l]	16 May–9 Jun	6 May–24 June	2 Jun–25 Jun[k]
Clutch size[l]	1	2.6–4.0	1.4–2.6
No. of fledglings per nest[l]	0.3–0.9 per nest with chick	0.5–2.6 per nest with egg	0.0–1.2 per nest with egg

[a]Osa & Watanuki (2002), Watanuki et al. (unpubl. data), [b]Kuroki et al. (2003), [c]Kato et al. (2003), [d]A. Takahashi (pers. comm.), [e]Watanuki et al. (1996), [f]Watanuki et al. (2004), [g]Nelson (2005), [h]Chochi et al. (2002), [i]Olssen & Larsson (2004), Y. Osa pers. comm., [j]Watanuki (1987a), [k]Calculated from incubation period: 46 d (median) for RHAU (Gaston & Jones 1998), 28 d (mean) for JCOM (E. Hayashi pers. comm.), and 28 d (mean) for BTGL (Niizuma et al. 2005), [l]Present study

and thus disturbance of BTGL, we set 2 to 4 JCOM plots (ca. 20 × 30 m) on cliff faces by map and 2 to 4 BTGL plots (ca. 10 × 10 m) on slopes within stakes. Artificial nest boxes were set in part of the RHAU plot. Breeding success and chick growth did not differ between natural burrows and nest boxes (Kuroki et al. 1998).

For RHAU we walked in the plot and checked the presence of eggs or chicks in 10 to 66 nests annually, including nest boxes, every 5 d. As RHAU are sensitive to disturbance during egg laying and incubation, we monitored them primarily after hatching. Chicks that disappeared from the nest after 40 d were considered to have fledged (Takahashi et al. 2001). We monitored the contents of 26 to 62 JCOM nests annually every 5 d from ca. 50 m away using a 20× to 40× telescope due to difficulties in approaching the nests. Chicks that disappeared after 45 d were considered to have fledged (Kato et al. 2001). For BTGL we walked in study plots and marked each nest with a numbered stake when we found newly laid eggs and banded newly hatched chicks. We monitored 30 to 104 nests annually and checked the presence of banded chicks every 5 d. Chicks that disappeared after 30 d or after attaining 500 g were considered to have fledged (Watanuki 1987b).

As the indices of the timing of breeding in each year, we used the mean laying date of the first egg in BTGL nests, and the mean hatching date of RHAU (Fig. 2a). The mean hatching date of the first JCOM chick in nests was used as timing index for this species, as we did not identify egg laying by JCOM in some years. Development period of embryo, i.e. incubation period, is relatively constant in most homoeothermic bird species so both the timing of egg-laying and the timing of hatching can be used as an index for the timing of breeding. As an index of breeding success for RHAU, we used the number of fledglings produced per chick hatched per pair (Fig. 2b). For JCOM and BTGL, we used the number of fledglings produced per pair that had eggs.

Collection and analysis of seabird diet

RHAU bring back food cross-wise in their bills in the evening and night, and JCOM and BTGL, in the stomach during the day. We caught RHAU arriving with prey after sunset and collected 64 to 226 bill-loads each year. Chicks and adults of BTGL and JCOM sometimes vomited food when they were

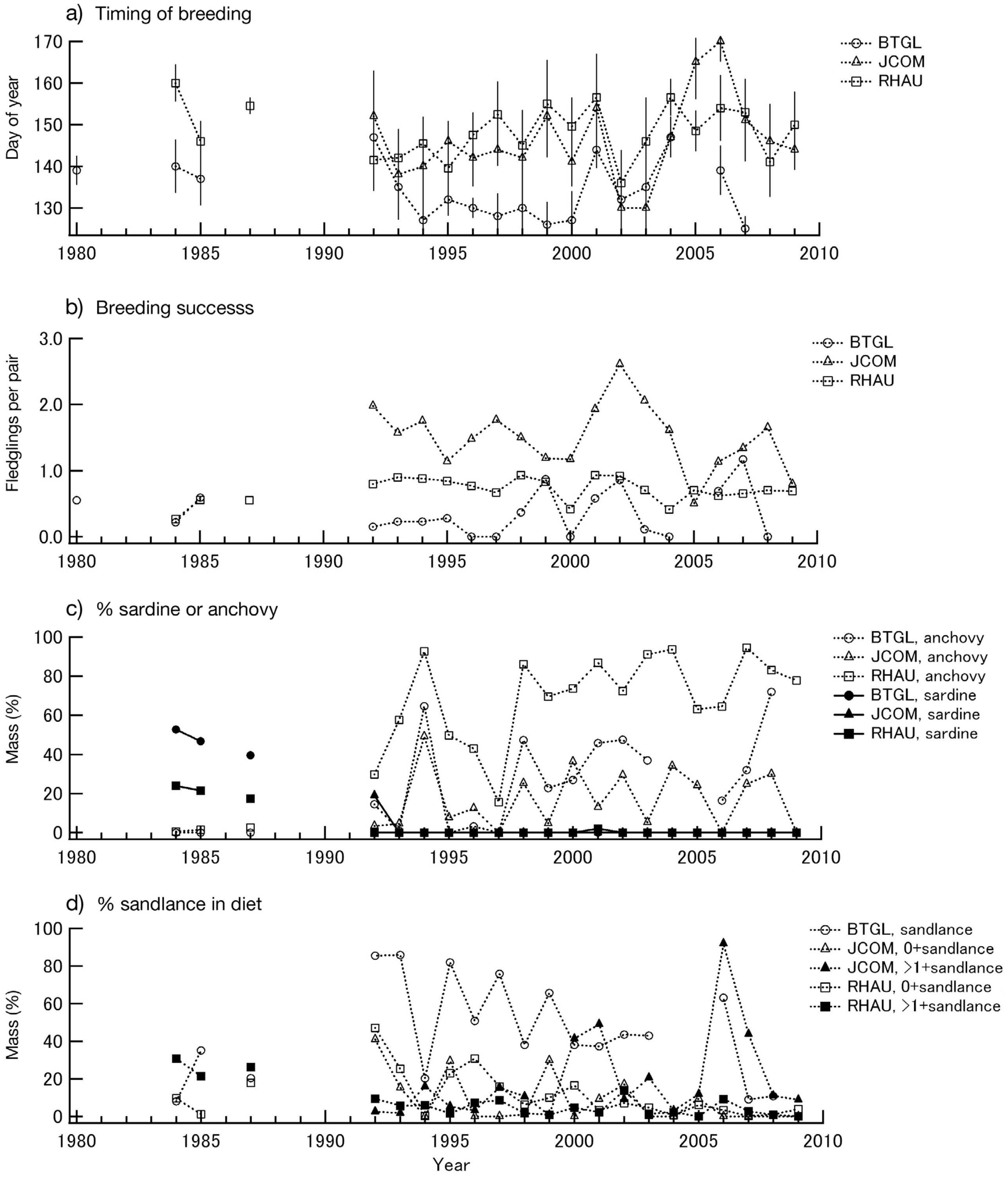

Fig. 2. *Larus crassirostris*, *Cerorhinca monocerata*, *Phalacrocorax filamentosus*. Interannual changes in (a) timing (mean ±1 SD) of breeding, (b) breeding success, and (c,d) dietary composition of black-tailed gulls (BTGL), rhinoceros auklets (RHAU), and Japanese cormorants (JCOM). (a) The timing is represented by egg laying for BTGL and hatching for RHAU and JCOM. (b) Breeding success is shown as the mean number of fledglings per pair. (c) Changes in the mass proportion of sardine and anchovy in the diet. (d) Changes in the mass proportion of 0+ sandlance and >1+ sandlance in the diet of RHAU and JCOM, and of all sandlance in the diet of BTGL

caught, and we collected 19 to 115 regurgitations from BTGL and 21 to 37 from JCOM each year.

Each food sample was weighed, and prey items were sorted and weighed separately. Prey items were identified to the lowest possible taxonomic level. We estimated the length of prey fish from otolith size (Ishikawa & Watanuki 2002) or we measured the total length of undigested fish. The sandlance were categorized into cohorts of 0+ yr (<110 mm total length) and >1+ yr (≥110 mm) (Takahashi et al. 2001), although it was sometimes difficult in food samples of BTGL, since these were degraded. We also calculated the percentage mass of important prey (sardine, anchovy, 0+ and >1+ sandlance) in the total each year (Fig. 2c,d).

Prey abundance

As indices of the availability of major prey in spring (krill, sandlance) and summer (anchovy, sandlance), we used the reported stock size of anchovy, catch per unit effort (CPUE) for krill, and the total annual catch of 0+ sandlance from fisheries (Fig. 3a). Krill and 0+ sandlance are harvested in March to April and May, respectively, around the island. We used the CPUE for krill (KrillCPUE, annual catch per fishing days as reported by fishermen on Yagishiri Island, ~4 km east of Teuri Island, in 1992 to 2007) and the annual catch of 0+ sandlance around Teuri and Yagishiri Islands (CatSL0, published by the Department of Fisheries and Forestry from 1980 to 2005, and on www.pref.hokkaido.lg.jp from 2006). The Tsushima anchovy stock is distributed from the west coast of Kyushu to the Japan Sea coast, and is seasonally available for seabirds breeding on Teuri Island when its distribution extends to the north. Its stock size (ENGstock) has been estimated annually by the Fisheries Agency since 1991, and its trend has been validated by local acoustic surveys (http://abchan.job.affrc.go.jp, in Japanese).

Local climate and broad-scale climate indices

Wind, rain, snow, ice or low air temperatures can cause freezing of the Teuri nesting grounds, metabolic stress, and difficulty in finding food. Changes in ocean temperature (indexed by SST) may influence the distribution and abundance of prey. We used monthly (February to July) average air temperature (Temp.) and monthly rainfall (Rain) recorded on Yagishiri Island, and the total snowfall in March (Snow), when seabirds arrive at the colony, recorded at Haboro weather station (~30 km east of Teuri Island) (www.data.jma.go.jp, in Japanese) to measure local weather conditions. We used monthly mean SST in an area of 60 × 150 km around the island (Area A in Fig. 1, Fig. 3b) to index ocean temperature. Local SST in this sector was reported by Hakodate Kaiyou Kisyodai from 1985 (www.jma-net.go.jp/kahodate/menu/sea.html, in Japanese); it was based on MGDSST (merged satellite and *in situ* data global daily SST) collected by the AVHRR (advanced very high resolution radiometer) sensor on NOAA (US National Oceanic and Atmospheric Administration) satellites and the Japanese multi-functional transport satellite (MTSAT).

Anchovy is harvested from waters with a SST of 12 to 15°C around Hokkaido (Mihara 1998), and seasonally expands its distribution northward during summer. RHAU switches prey from sandlance and juvenile greenling to anchovy when warm water (SST = 13°C) arrives at the southern edge of its maximum foraging range (164 km; Table 1, Area C in Fig. 1) in late April to late June (Watanuki et al. 2009). We used the date of warm water arrival (WWA, www.jma-net.go.jp/kahodate/menu/sea.html, in Japanese) in the region as an index of the seasonal availability of anchovy to breeding seabirds.

We used an index of the flow rate of the TC (area of the water at 100 m depth with temperature >10°C) (www.data.kishou.go.jp/kaiyou/shindan/e_2/maizuru_tsushima/maizuru_tsushima.html, in Japanese; Fig. 3c) to understand the effects of the flow on SST and the timing of the northern expansion of anchovy distribution. Surface chlorophyll *a* concentration (chl *a*) in spring was hypothesized to relate to the timing of breeding through the availability of local prey during the spring (krill and sandlance) and to the chick diets through availability of sandlance in summer. We used monthly (March to May) chl *a* in an area of 81 × 81 km around Teuri Island (Area B in Fig. 1, Fig. 3b) that was obtained from Ocean Color Web (http://oceancolor.gsfc.nasa.gov/) at a spatial resolution of 9 km by the SeaDAS 6.2 data analysis system reported after 1998 (http://oceancolor.gsfc.nasa.gov/seadas/).

Broad-scale climate indices are known to influence local climate and then marine ecosystems in the North Pacific (Chiba & Saino 2003, Minobe et al. 2004, Chiba et al. 2005). We used the Pacific Decadal Oscillation (PDO) index (www.data.kishou.go.jp/shindan/b-1/pdo/pdo.html), which reflects changes in air pressure and SST over the Pacific; the North Pacific Index (NPI; www.data.kishou.go.jp/db/

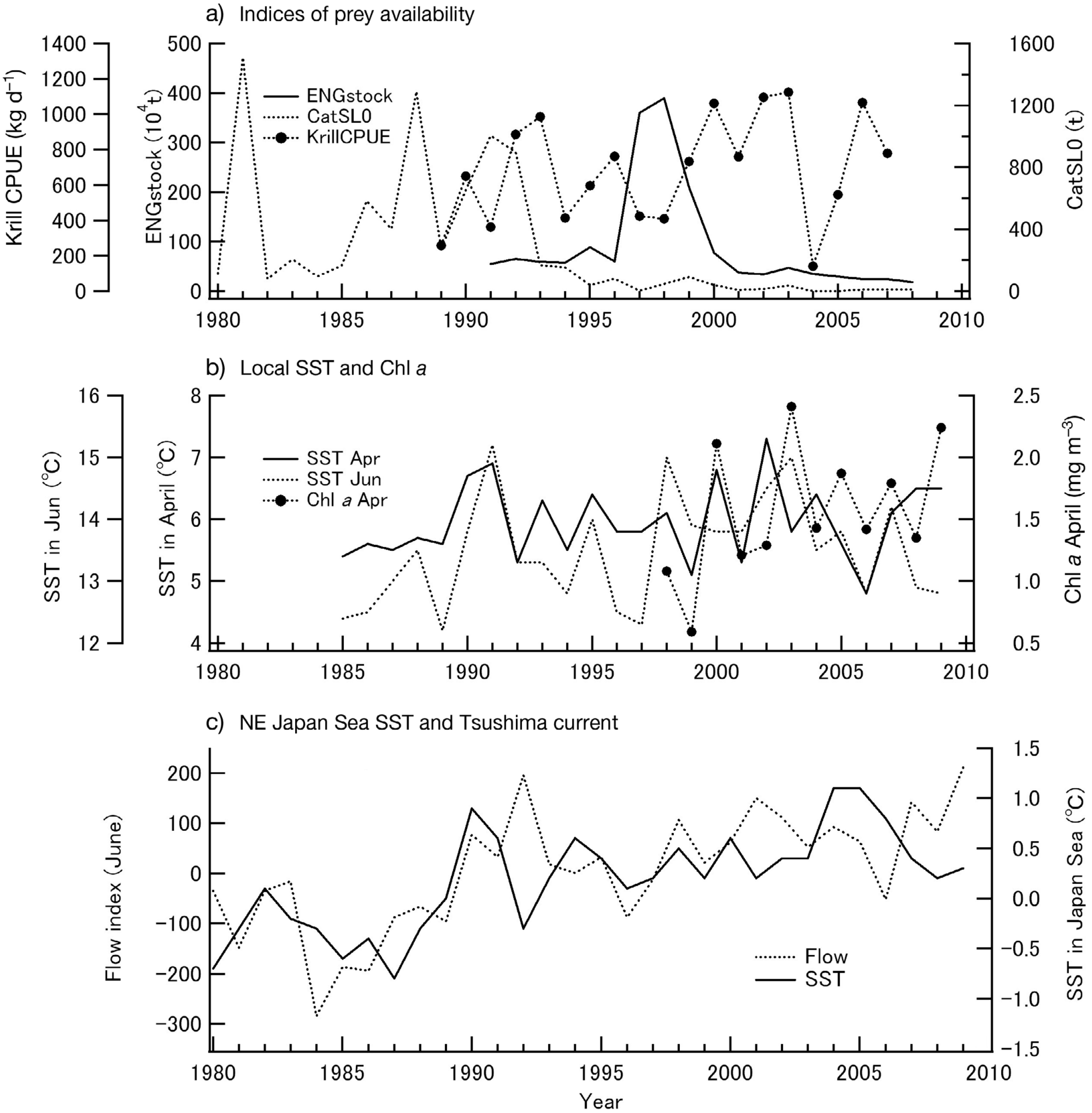

Fig. 3. (a) Estimated Tsushima anchovy *Engraulis japonicus* stock size (ENGstock), annual fishery harvest of 0+ sandlance *Ammodytes personatus* (CatSL0), and catch of krill *Thysanoessa longipes* and *T. inermis* per day (KrillCPUE) around Teuri Island. (b) Sea-surface temperature (SST) in Area A (Fig. 1) in April and June and surface chlorophyll *a* concentration in Area B (Fig. 1) in April. (c) Annual mean SST over the northeastern Japan Sea (www.data.jma.go.jp) and the Tsushima Current flow index in June

climate/pdo/npiwin.txt), which reflects the strength of the Aleutian low pressure; and the Arctic Oscillation (AO) index (www.cpc.ncep.noaa.gov.products/precip/CWlink/daily_ao_index), which reflects the difference in air pressure between the Arctic and mid-latitudinal area of the North Pacific.

Analyses

To test for long-term interannual trends in seabird diet and breeding, we used simple linear regression analyses. To identify effects of local climatic factors and prey availability indices on variation in the timing of breeding, diet, and breeding success (the dependent variables), we used path analysis with Amos V. 6.0 software (Amos Development Corporation). For Temp., Rain, and SST in February to June, we used those in the month in which each had the strongest correlation (largest Pearson's r) with the dependent variables. In addition, we used annual values of Snow in March, CatSL0, KrillCPUE, and WWA. To simplify the analysis, indirect effects such as those of the TC flow on SST were not included in the models but examined separately. If correlation between potential independent variables was significant, co-variance between these was included in the potential path models. Year was included as a potential independent factor to test for trends in seabird diet and breeding performance. The model giving the smallest value of the Akaike Information Criterion (AIC) was selected as the best fitting model, and the top 3 models (ΔAIC < 2.0) were considered as potential models (Burnham & Anderson 1998). Following Frederiksen et al. (2004), we examined whether the slopes of factors were significant using Type III sums of squares, and used the R^2 value (coefficient of determination) as the proportion of variance explained by each model.

The TC flow can indirectly affect the breeding biology and diets of seabirds through changes in SST and WWA (Watanuki et al. 2009). To look at the effects of the flow index on SST and WWA, we performed linear regression analyses using 1985 to 2009 data. To understand how broad-scale climate relates to the local climate factors, we performed path analyses using long-term data (1943 to 2008) in which PDO, NPI, and winter average AO were independent and Temp. in April, Snow, mean February wind speed recorded at Yagishiri Island, and the TC flow index in June were dependent variables.

Chl *a* data were collected from 1998. Because of the small sample size (12 yr), we used simple linear regression analyses to examine the effects of chl *a* on the availability of krill and sandlance that were harvested around the island and the proportion of these species in the diet.

RESULTS

Trends in climate and seabird parameters

We found no significant 1 yr lagged autocorrelations in the timing of breeding or breeding success of any species ($p > 0.05$). No significant inter-annual linear trends were found in the timing of breeding or the breeding success in all 3 seabird species, or in the mass proportion of 0+ sandlance, >1+ sandlance, and sandlance in the diet of RHAU, JCOM, and BTGL, respectively ($p > 0.05$; Fig. 2). There were increasing trends in the mass proportion of anchovy in the diet of RHAU ($r = 0.788$, $n = 21$, $p < 0.01$) and BTGL ($r = 0.614$, $n = 18$, $p < 0.01$), though that for JCOM showed no trend ($p > 0.05$), presumably because no JCOM diet data were available before 1991 (Fig. 2c). Negative trends were found in the mass proportion of 0+ sandlance in the diet of JCOM ($r = -0.510$, $n = 18$, $p < 0.05$) and that of >1+ sandlance in the diet of RHAU ($r = 0.767$, $n = 21$, $p < 0.001$; Fig. 2d).

During the study period, there were increasing linear trends in Temp. ($r = 0.448$ to 0.539, $n = 21$, $p < 0.05$), except in June ($p > 0.05$) and in the TC flow index ($r = 0.477$ to 0.658, $n = 20$, $p < 0.05$). No trends were observed in Rain ($p > 0.05$), except in May ($r = 0.546$, $n = 21$, $p = 0.009$), Snow, SST and WWA ($p > 0.05$). ENGstock and KrillCPUE showed no significant trends ($p > 0.05$), but CatSL0 showed a decreasing trend ($r = 0.492$, $n = 19$, $p = 0.03$).

Timing of breeding

RHAU bred later in years with cold Temp. in April (Fig. 4), heavy Snow, and little Rain in April in the top 3 models, though ΔAIC were small among models (Table 2). JCOM bred later in years with cold air temperature and lower SST in April in the top 3 models, though as was seen for RHAU, ΔAIC were small among models (Fig. 4, Table 2). For the laying date of BTGL, ΔAIC were too small among top models to pick consistently significant factors (Table 2). Chl *a* peaked in April in 10 out of 12 yr and in May in the other years. Simple linear regression analyses indicate that Chl *a* in March to May did not relate to the timing of breeding for any species ($p > 0.05$).

Chick diet

In the 2 top models, RHAU fed more on anchovy in years when WWA was earlier, though ΔAIC were small among models (Table 3). However, surprisingly ENGstock was not included in the top 3 models (Table 3). JCOM fed more on 0+ sandlance in years with high CatSL0 in 3 top models (Table 3). The null model was selected as top model, and no factors explained the proportion of sandlance in the diet of BTGL (Table 3). Chl *a* in March to May did not relate to the spring prey availability indices (KrillCPUE:

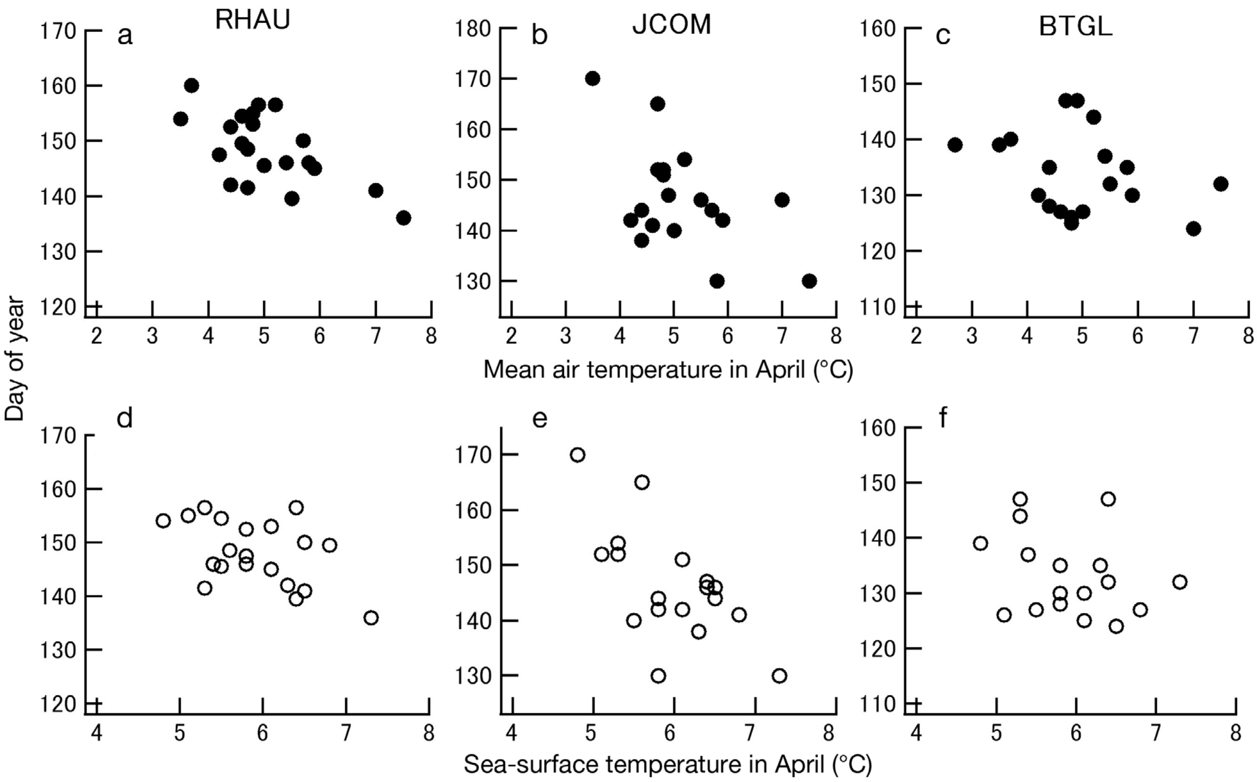

Fig. 4. *Cerorhinca monocerata*, *Phalacrocorax filamentosus*, *Larus crassirostris*. Relationships between the mean air temperature (Temp.) in April (a, b, c; ●) or sea-surface temperature (SST) around the colony in April (d, e, f; ○), the mean egg laying date of black-tailed gulls (BTGL) and the mean hatching dates of rhinoceros auklets (RHAU) and Japanese cormorants (JCOM)

Table 2. *Cerorhinca monocerata*, *Phalacrocorax filamentosus*, *Larus crassirostris*. Fitted path models relating timing of breeding (laying date for black-tailed gulls [BTGL]; hatching date for rhinoceros auklet [RHAU] and Japanese cormorant [JCOM]) to monthly mean air temperature (Temp.) in April, total snowfall (Snow) in March, total rainfall (Rain) in April, local sea-surface temperature (SST) in April, and krill capture per unit effort (CPUE). Year is also included as a factor. Covariance between Temp. in April and SST in April was significant ($r = 0.446$, $p < 0.05$) and included in all models. Models having ΔAIC < 2.0 but up to the third-best models are shown. ΔAIC, parameter estimates (with SE and significance in parentheses), and the coefficient of determination (R^2) are also shown. – = independent variable not selected

Species	ΔAIC	Year	Temp. (Apr)	Snow (Mar)	Rain (Apr)	SST (Apr)	Krill CPUE	R^2
RHAU (hatching)	0.000	–	−3.115 (0.895, <0.001)	0.063 (0.024, 0.008)	−0.119 (0.049, 0.014)	–	–	0.584
	0.529	–	−2.216 (1.122, 0.048)	0.068 (0.023, 0.003)	−0.112 (0.047, 0.017)	−2.217 (1.712, 0.195)	–	0.598
	1.654	–	−3.179 (0.887, <0.001)	0.064 (0.024, 0.007)	−0.103 (0.048, 0.032)	–	−0.002 (0.003, 0.491)	0.560
JCOM (hatching)	0.000	1.007 (0.259, <0.001)	−4.556 (1.815, 0.012)	−0.057 (0.036, 0.108)	–	−7.595 (2.793, 0.007)	–	0.759
	0.122	0.883 (0.276, 0.001)	−3.789 (1.930, 0.050)	–	–	−8.137 (2.971, 0.006)	–	0.699
	1.066	1.026 (0.253, <0.001)	−4.531 (1.770, 0.010)	−0.059 (0.035, 0.092)	–	−7.555 (2.725, 0.006)	−0.005 (0.005, 0.347)	0.773
BTGL (laying)	0.000	–	–	–	–	−0.732 (0.498, 0.141)	–	0.112
	0.085	–	–	–	0.026 (0.018, 0.137)	−0.987 (0.469, 0.035)	–	0.276
	0.276	–	–	–	–	–	–	0.000

$p > 0.05$; CatSL0: $p > 0.05$). Chl *a* in these months did not relate to the proportion of 0+ or >1+ sandlance in the diet of RHAU and BTGL ($p > 0.05$) either. There was significant negative correlation between Chl *a* in April and the proportion of 0+ sandlance in the diet of JCOM ($r = -0.629$, $n = 12$, $p = 0.03$), though its biological significance was unclear.

Breeding success

For RHAU, the top 3 models showed that breeding success was greater in years with earlier onset of breeding and earlier WWA (Table 4). For JCOM, the top 3 models showed that breeding success was greater in years with earlier breeding, lower Temp. and less Rain in June, earlier WWA, and greater CatSL0 (Table 4). The breeding success in BTGL varied widely between years and appeared to be greater in years with earlier WWA.

Interactions of local and large-scale climate

The TC flow index in May and June was negatively related to WWA ($r = -0.588$ to -0.495, $n = 17$, $p = 0.03$ to 0.01), indicating that warm waters arrived later when the flow rate was reduced. June SST increased when the June TC flow was stronger ($r = 0.493$, $n = 17$, $p = 0.027$). Temp. in April was positively associated with the winter AO index in the top 3 models (Table 5). The mean wind speed in February was negatively associated with the winter AO index and positively associated with the NPI in the top 3 models (Table 5). Snow in March was negatively associated with winter AO and increased interannually in the top 2 models. The TC flow index in June was negatively associated with the PDO index and increased interannually (see Fig. 3c also) in the top 3 models. This indicates that anomalously low SST on the western side of the Pacific related to a weak TC in June.

Table 3. *Cerorhinca monocerata*, *Phalacrocorax filamentosus*, *Larus crassirostris*. Fitted path models relating the mass proportion of anchovy (for rhinoceros auklet [RHAU] and Japanese cormorant [JCOM]), 0+ and >1+sandlance (for JCOM) or sandlance (for black-tailed gulls [BTGL]) in bird's diet to local sea-surface temperature (SST) in June, the date of arrival of 13°C water within the RHAU foraging range (WWA), the stock size of anchovy (ENGstock), and the annual catch of 0+ sandlance (CatSL0). Year is also included as a factor. Covariance between WWA and SST in June was significant ($r = -0.664$, $p < 0.05$) and was included in all models. Models having ΔAIC < 2.0 but up to the third-best models are shown. ΔAIC, parameter estimates (with SE and significance in parentheses), and the coefficient of determination (R^2) are shown. – = independent variable not selected

Species	ΔAIC	Year	SST (Jun)	WWA	ENGstock	CatSL0	R^2
RHAU (anchovy)	0.000	3.258 (0.506, 0.001)	–	–1.787 (0.609, 0.003)	–	–	0.722
	1.087	2.988 (0.495, 0.001)	–	–1.874 (0.593, 0.002)	–	–	0.714
	1.203	3.023 (0.519, 0.001)	13.181 (4.765, 0.006)	–	–	–0.019 (0.018, 0.282)	0.679
JCOM (0+sandlance)	0.000	–	–	–	–	0.039 (0.011, <0.001)	0.415
	0.366	–	3.789 (2.884, 0.189)	–	–	0.041 (0.011, <0.001)	0.484
	0.389	–	–	–0.481 (0.370, 0.194)	–	0.037 (0.011, <0.001)	0.442
JCOM (>1+ sandlance)	0.000	1.688 (0.979, 0.085)	–	–	–	–	0.148
	0.743	–	–	–	–	–	0.000
	1.644	–	–	–	–	–0.028 (0.026, 0.289)	0.065
JCOM	0.000	–	–	–	–	–	0.000
(anchovy)	0.918	–	–	–0.585 (0.559, 0.296)	–	–	0.062
BTGL	0.000	–	–	–	–	–	0.000
(sandlance)	0.631	–	–	–	–	0.034 (0.029, 0.249)	0.072
	1.053	–	–	–	0.057 (0.058, 0.330)	–	0.061

Table 4. *Cerorhinca monocerata*, *Phalacrocorax filamentosus*, *Larus crassirostris*. Fitted path models relating the number of fledglings per nest to the timing of breeding (hatching for rhinoceros auklet [RHAU] and Japanese cormorant [JCOM], laying for black-tailed gulls [BTGL]), monthly mean air temperature (Temp.) in June, total rain fall (Rain) in June, local sea-surface temperature (SST) in June, the date of arrival of 13°C water within the RHAU foraging range (WWA), the stock size of anchovy (ENGstock) and the annual catch of 0+ yr sandlance (CatSL0). Year is also included as a factor. Covariance between Temp. in June and SST in June (r = 0.398, $p < 0.05$) and between SST in June and WWA (r = –0.664, $p < 0.05$) were significant and included in all models. Models having ΔAIC < 2.0 but up to the third-best models are shown. ΔAIC, parameter estimates (with SE and significance in parentheses), and the coefficient of determination (R^2) are also shown. – = independent variable not selected

Species	ΔAIC	Year	Timing	Temp. (Jun)	Rain (Jun)	SST (Jun)	WWA	ENGstock	CatSL0	R^2
RHAU	0.000	–	–0.013 (0.005, 0.005)	–	–	–	–0.012 (0.005, 0.015)	–	–	0.423
	0.116	–	–0.013 (0.004, 0.002)	–	–	–	–0.012 (0.005, 0.012)	0.000 (0.000, 0.146)	–	0.490
	0.138	–	–0.013 (0.004, 0.002)	–	–	–0.071 (0.046, 0.128)	–0.018 (0.006, 0.002)	0.000 (0.000, 0.076)	–	0.554
JCOM	0.000	0.052 (0.009, <0.001)	–0.024 (0.005, <0.001)	–0.380 (0.061, <0.001)	–0.004 (0.002, 0.061)	–	–0.031 (0.007, <0.001)	–	0.001 (0.000, <0.001)	0.902
	1.865	0.051 (0.009, <0.001)	–0.025 (0.004, <0.001)	–0.370 (0.060, <0.001)	–0.003 (0.002, 0.077)	–0.039 (0.081, 0.635)	–0.033 (0.010, 0.001)	–	0.001 (0.000, <0.001)	0.914
	1.880	0.049 (0.009, <0.001)	–0.024 (0.005, <0.001)	–0.389 (0.061, <0.001)	–0.004 (0.002, 0.069)	–	–0.031 (0.007, <0.001)	0.000 (0.000, 0.675)	0.001 (0.000, <0.001)	0.909
BTGL	0.000	–	–	–	–	–	–0.024 (0.013, 0.060)	–	–	0.179
	1.144	–	–	–	–	–		–	–	0.000
	1.146	–	–0.048 (0.051, 0.345)	–	–	–	–0.026 (0.012, 0.037)	–	–	0.241

DISCUSSION

We conducted an analysis of seabird–climate relationships for the northern Japan Sea, thereby updating previous long-term studies of this region, prey and seabirds (Takahashi et al. 2001, Deguchi et al. 2004, Ito et al. 2009, Watanuki et al. 2009). In the present paper, we focused on examining trends in climatic factors and seabird parameters as our time series is now of sufficient duration to investigate directional climate change as well as climate variability. The present study is significant, as relatively few long-term seabird studies have been carried out in the western North Pacific (Kitaysky & Golubova 2000, Watanuki et al. 2009). Our approach was to test for trends in large-scale and local climate indices and seabird parameters, and to relate factors using regression and AIC model selection procedures. We first tested the seabird parameters and found no evidence of autocorrelation.

Timing of breeding

Climate factors affected the timing of breeding, but differently between species. RHAU bred earlier in years with a warm and wet spring and little snow, probably because frozen soil and snow prevent them from excavating their burrows (Watanuki 1987a, Watanuki et al. 2009). JCOM bred earlier in years with higher spring SST and air temperature. Catches of adult Japan Sea greenlings in the study region tended to be higher in years with a warmer winter (Hoshino et al. 2009), and flatfish come to shore during early spring and spawn earlier in warmer regions (Nagasawa & Torisawa 1991, Minami 1995). Thus, the abundance and seasonality of these prey species of JCOM in spring (M. Ito unpubl. data) might be related to the timing of JCOM. BTGL laid eggs earlier in years when the spring SST was from 3.0 to 4.9°C (Tomita et al. 2009), since swarms of krill, i.e. the main prey of BTGL in spring, occur at the surface with this range of SSTs in this region (Hanamura et al. 1989). However, we could not find any consistent linear effects of spring SST and krill CPUE on BTGL timing (Fig. 4, Table 2), so that longer term studies including other climate factors and more appropriate prey availability measures should be carried out before conclusions can be drawn.

Table 5. Fitted path models relating local physical factors (air temperature in April at Yagishiri, Temp. [Apr]; average wind speed at Yagishiri in February, Wind [Feb]; total snowfall in March at Haboro, Snow [Mar]; Tsushima current flow index in June, Flow [Jun]; to Pacific Decadal Oscillation [PDO], North Pacific Index [NPI] and average winter Arctic Oscillation [AOav; December to February]) index. Year is also included as a factor. Covariance between Year and PDO ($r = 0.310$, $p < 0.05$), between year and AO (winter) ($r = 0.345$, $p < 0.001$), and between PDO and NPI ($r = -0.531$, $p < 0.01$) were significant and included in all models. Models having ΔAIC < 2.0 but up to the third-best models are shown. ΔAIC, parameter estimates (with SE and significance in parentheses), and the coefficient of determination (R^2) are shown. – = independent variable not selected

	ΔAIC	Year	PDO	NPI	AOav	R^2
Temp. (Apr)	0.000	–	–	–	1.071 (0.335, 0.001)	0.142
	0.924	0.008 (0.007, 0.285)	–	–	0.901 (0.368, 0.014)	0.148
	1.201	–	–	0.144 (0.161, 0.370)	1.014 (0.334, 0.002)	0.142
Wind (Feb)	0.000	–	–	0.312 (0.130, 0.017)	−0.687 (0.288, 0.017)	0.170
	1.639	–	−0.066 (0.154, 0.668)	0.269 (0.154, 0.080)	−0.680 (0.288, 0.018)	0.165
	1.974	0.001 (0.006, 0.849)	–	0.319 (0.308, 0.014)	−0.708 (0.308, 0.022)	0.174
Snow (Mar)	0.000	0.478 (0.211, 0.023)	–	–	−24.739 (10.329, 0.017)	0.124
	1.071	0.543 (0.218, 0.013)	−4.372 (4.521, 0.334)	–	−26.775 (10.295, 0.009)	0.144
Flow (Jun)	0.000	4.383 (0.664, <0.001)	−55.414 (14.794, <0.001)	–	–	0.499
	0.535	4.078 (0.708, <0.001)	−52.700 (14.654, <0.001)	–	40.033 (33.173, 0.228)	0.515
	1.271	4.296 (0.666, <0.001)	−46.814 (16.878, <0.001)	14.138 (15.849, 0.372)	–	0.505

Using path analyses the effect of year on the timing of JCOM was significant (Table 2) presumably because JCOM timing was extraordinary late in 2005 and 2006 (Fig. 2a). Thus, at least between 1992 and 2009, there did not appear to be long-term linear trends in the timing of breeding in seabirds in our region. During the past 30 to 50 yr, the timing of seabird breeding has advanced in the Arctic (Gaston et al. 2009, Moe et al. 2009), but has been delayed in the Antarctic (Barbraud & Weimerskirch 2006). In the temperate zone, results are more variable; laying or hatching occurs later in the western North Sea (Frederiksen et al. 2004, Wanless et al. 2008), where the North Atlantic Oscillation index has been decreasing, but earlier in the Canadian Pacific (Bertram et al. 2001, but see Hipfner at www.dfo-mpo.gc.ca/CSAS/Csas/publications/resdocs-docrech/2010/2010_053_e.pdf), where SST has been increasing. No apparent trends were observed for auklets off the California coast (Thayer & Sydeman 2007, Schroeder et al. 2009), but murres have been observed earlier (W. Sydeman pers. comm.). No change has been observed for Southeast Alaska (Slater & Byrd 2009). Thus, the impact of global warming on the timing of seabird breeding appears to be variable among regions, presumably depending on the local ecosystem and climate system. There could also be age-dependent differences (Pinaud & Weimerskirch 2002) in seabird responses to climate variability and change. We cannot evaluate this hypothesis for our unmarked populations in the Japan Sea, but the variability observed in global patterns of seabird timing in relation to climate certainly may be related to age-specific breeding phenology and the age structure of studied seabird populations.

Chick diet

Decadal and interannual variability of local climate factors and prey availability affected the seabird diet. RHAU and BTGL fed on sardine and sandlance from 1984 to 1987, but RHAU fed on anchovy and BTGL on sandlance after 1992 (see also Deguchi et al. 2004). These decadal changes in chick diet reflected the cold-to-warm regime shift in the late 1980s in the TC region (see also Fig. 3c), with a steep decrease in the catch of cold-water sardine and an increase in the catch of warm-water anchovy (Tian et al. 2008). Anchovy spawn in the western North Pacific at a SST of 15 to 28°C, and sardine, at 13 to 20°C (Takasuka et al. 2008). Cumulative mortality through the early life stages of sardine between 1988 and 1991, when SST was higher, apparently caused the stock to crash (Watanabe et al. 1995).

Interannual variation in the proportion of anchovy in the diet of RHAU was explained by the timing of the arrival of warm water (SST = 13°C) within the bird's foraging range. In years with a strong TC, RHAU switched prey earlier from cold-water species (sandlance and juvenile greenlings; Nagasawa & Torisawa 1991) to anchovy and hence fed more on anchovy in these years (Watanuki et al. 2009). The annual catch of 0+ sandlance was positively related to the proportion of 0+ sandlance in the diet of JCOM, supporting the relationship between the seabird diet and local prey availability. The proportion of sandlance in the diet of BTGL, however, could not be explained by either local climate factors or the catch of 0+ sandlance. This is surprising as BTGL are surface feeders and feed mainly on sandlance (Deguchi et al. 2004; Table 1, Fig. 2d). Possibly because of a narrow foraging habitat, BTGL might not be able to switch to anchovy when they become available.

Breeding success

There were no trends in the breeding success of seabirds on Teuri Island. Breeding success of RHAU was determined by the arrival of warm water in the northern Japan Sea. Increasing breeding success was correlated with earlier arrival dates of the warm TC because anchovy were advected into this region with the warm waters and provided more energy to chicks than other prey (Watanuki et al. 2009). Yet, we found no evidence that breeding success was significantly influenced by the anchovy stock size (Table 4). The seasonal expansion of the anchovy distribution to the Teuri seabird foraging area might be important rather than overall abundance of this Tsushima anchovy stock, which was measured in the southern areas of the Japan Sea. In years when the local availability of epipelagic fish (anchovy and sandlance) was low, JCOM fed on benthic and epibenthic fishes in coastal areas 30 to 40 km from the colony, and, hence, their feeding frequency was reduced (Watanuki et al. 2004), ultimately affecting chick growth and survival (Kato et al. 2001). Similar to RHAU, breeding success of JCOM was greater in years when warm waters arrived earlier, i.e. high local anchovy availability. Anchovy stock size had no significant relationship with this species either. The local annual catch of 0+ sandlance (important prey of JCOM; Table 1) positively affected breeding success, also indicating the importance of the availability of this prey.

Why the breeding success of RHAU and JCOM was higher in years when they bred earlier, as reported in common murre *Uria aalge* in the North Sea (Votier et al. 2009) and cassin's auklet and common murre in California (Schroeder et al. 2009), is unclear. RHAU and JCOM feed on different prey during the pre-laying, laying, and chick-rearing periods (Kato et al. 2001, Ito et al. 2009, M. Ito unpubl. data), yet both species showed an inverse relationship between timing and success. The effects of SST on prey availability could differ between spring (egg laying) and summer (chick rearing). With simple regression analyses, no annual trends were observed in the breeding success of JCOM, though positive effects of year on it (Table 4) could be related to interannual trends in prey availability and timing of breeding.

No climate factors or prey availability indices explained the large interannual variations in the breeding success of BTGL. The gulls fed mostly on sandlance (Fig. 2d). As found in the North Sea (Furness & Tasker 2000), BTGL that feed mainly on sandlance might be sensitive to changes in the availability of sandlance, but the catch of 0+ sandlance was not correlated with their breeding success. The potential impact by feral cats on nesting BTGL (Watanuki 2010) might make it difficult to detect the climate factors and prey availability that are associated with their breeding performance.

In regions where seabirds feed mainly on sandlance, climate factors have affected their breeding success through bottom-up effects (Aebischer et al. 1990, Frederiksen et al. 2006). In our region, however, variability of local chl *a* concentration did not relate to the availability indices of local seabird prey (krill and 0+ sandlance), the proportion of these prey in the diet, or the seabird timing of breeding. Rather, interannual change in the availability of anchovy, an important alternative prey to sandlance, that appeared to be driven by the warm TC seemed to be important in this area. Alternatively, chl *a* could be a poor indicator of the abundance of availability of forage fish prey.

CONCLUSIONS

Interannual variations in broad-scale atmospheric indices, the AO and the Aleutian Low (manifested as the PDO), are linked to winter wind stress and the summer flow rates of the TC (Minobe et al. 2004, present study), respectively. These factors influence the chick diets and breeding performance of 2 species of seabirds in northern Japan Sea, but not a third that may be responding, mainly, to terrestrially based factors (invasive cats). In this area the seasonal range expansion of warm waters and anchovy plays a key role in driving chick diet and breeding performance of seabirds. Our study indicates that the mechanisms of response from climate to seabirds are specific to the regional ecosystem under study as well as variation in the life histories of the seabirds under consideration.

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Contribution to the Theme Section 'Seabirds and climate change'

Little auks buffer the impact of current Arctic climate change

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ABSTRACT: Climate models predict a multi-degree warming of the North Atlantic in the 21st century. A research priority is to understand the effect of such changes upon marine organisms. With 40 to 80 million individuals, planktivorous little auks *Alle alle* are an essential component of pelagic food webs in this region that is potentially highly susceptible to climatic effects. Using an integrative study of their behaviour, physiology and fitness at 3 study sites, we evaluated the effect of ocean warming on little auks across the Greenland Sea in 2005 to 2007. Contrary to our hypothesis, the birds responded to a wide range of sea surface temperatures via plasticity of their foraging behaviour, allowing them to maintain their fitness levels. Predicted effects of climate change are significantly attenuated by such plasticity, confounding attempts to forecast future effects of climate change using envelope models.

KEY WORDS: Behavioural plasticity · Envelope models · Global warming · North Atlantic · Pelagic food web · Zooplankton

INTRODUCTION

The earth's climate is warming, and this trend is amplified in Polar regions (Serreze et al. 2007, Graversen et al. 2008). Recent investigations confirm significant ocean warming in the Arctic sector of the North Atlantic (Polyakov et al. 2005, Walczowski & Piechura 2006, Dmitrenko et al. 2008), and predict further increase of sea surface temperatures (SST) in this region across the 21st century (Karnovsky et al. 2010). One current challenge is to investigate the effect of these rapid changes upon organisms, food webs and biogeochemical cycles (Beaugrand et al. 2010). In this study, we tested the hypothesis that warmer surface water conditions in the North Atlantic influence the morphology, physiology and behaviour of little auks *Alle alle*, as well as their fitness (reproductive output and survival).

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The little auk is a particularly well-suited study species in the context of climate change because it is an important component of the Arctic food web, and is likely to be significantly affected by changing sea temperatures. Little auks are the most numerous seabird in the North Atlantic (with an estimated population of 40 to 80 million individuals, Stempniewicz 2001), and consume up to 24 % of local plankton production (Karnovsky & Hunt 2002). They mainly feed on copepods, which are strongly affected by climate change, with a marked tendency for temperate, smaller-sized species to spread northwards (Beaugrand et al. 2009). Moreover, the little auk field metabolic rate is 70% higher than predicted by body mass, and they have very limited capacity to store fat. Consequently they are predicted to be particularly sensitive to altered feeding conditions (Harding et al. 2009a).

Here we used a natural experiment across the Greenland Sea to mimic forecasted ocean warming of the North Atlantic (see Fig. 1). This framework follows Wernberg et al. (2010), who successfully used synoptic, regional differences in SST to simulate forthcoming ocean warming and test the response of marine organisms to climate change. Such design also allowed further investigations, such as testing the evolutionary response of plants to climate change (Etterson & Shaw 2001), and complies with Brown et al. (2011). In our study system, recent work showed a very strong link between summer SST within the foraging areas of little auks, species composition of local zooplankton communities, and the dietary preferences of the birds (Karnovsky et al. 2010), whereby colder water contained more larger copepods, which were also preferentially fed upon by little auks (Karnovsky et al. 2010). Conversely, birds had to feed on smaller, less profitable copepod species in warmer water. Comparing the ecophysiology of little auks from different colonies subject to contrasting SST regimes at one moment in time therefore allowed us to simulate the effect that increasing water temperatures might have on this Arctic species across the 21st century. Using this rationale we tested the hypothesis that higher summer SST would result in diminished little auk fitness, with the predictions that higher SST would modify little auk diet, foraging effort, provisioning rates, breeding success and adult survival.

MATERIALS AND METHODS

The study took place during the little auk breeding season (July) in 2005, 2006 and 2007 at Kap Höegh, East Greenland (70° 43′ N, 22° 38′ W, hereafter KH), Hornsund, West Spitsbergen (77° 00′ N, 15° 22′ E, hereafter HS), and Kongsfjorden, West Spitsbergen (79° 01′ N, 12° 25′ E, hereafter KF), respectively (Fig. 1). However, not all variables listed below were collected at all sites in all years (see Table 1 for details).

Sea surface temperatures

We estimated mean SST for the month of July (the little auk chick-rearing period) each year for an area of ~4000 km^2 adjacent to each colony, using satellite data provided by the EUMETSAT Ocean and Sea Ice Satellite Application Facility (OSI SAF; see Welcker et al. 2009a). The size of this sampling area was chosen so as to fully enclose little auk core foraging areas at sea, as determined from at-sea direct observations and recordings of foraging trip durations (Karnovsky et al. 2010, Welcker et al. 2009a). Mean July SST was calculated by averaging daily means based on all data points available within the selected areas.

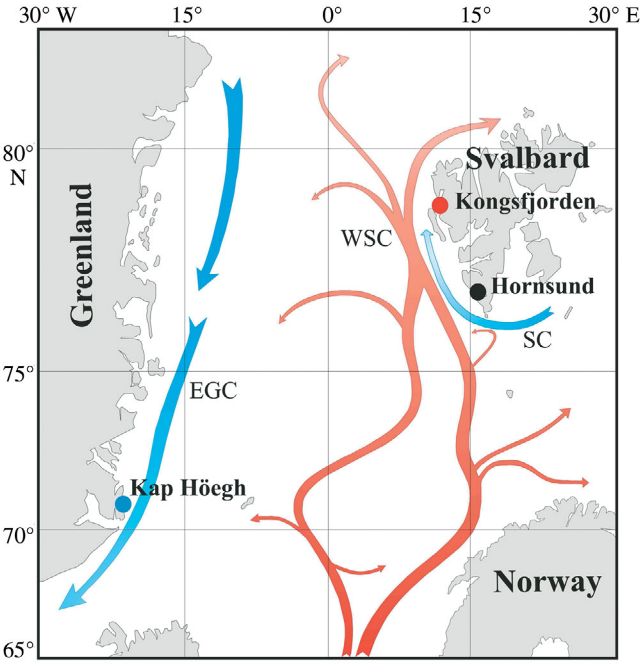

Fig. 1. Position of the 3 study sites in the Greenland Sea. The East Greenland Current (ECG) maintains cold water conditions off Kap Höegh. Off Hornsund, the cold Sørkapp Current (SC) and the warm West Spitsbergen Current (WSC) provide intermediate water temperature conditions, whereas the WSC forces warmer Atlantic water into the Kongsfjorden area. The northernmost study site is therefore the warmest in terms of sea-surface temperature

Diet

Prey items caught by adults breeding at all colonies and brought back to their chicks were collected and identified following Harding et al. (2009a). Briefly, breeding little auks were caught in noose carpets at the colony, and zooplankton that they collected at sea were scooped out of their gular pouch. Individual plankton meals were stored in 4% borax-buffered formaldehyde solution, and examined under a stereomicroscope. Prey items were identified to species level wherever possible, and remaining taxa were identified to the lowest possible taxonomical level. *Calanus* species were identified according to Kwaśniewski et al. (2003). Abundant taxa were enumerated from subsamples while large and rare individuals from different taxa were counted for the whole diet sample.

Foraging effort

We determined foraging parameters of little auks in 2007 at the 3 study sites using time-depth-recorders (TDR). The TDRs used were Cefas G5 Data Storage Tags (CTL) with 8 MB of memory, and were cylindrical in shape with a rounded tip to minimise water resistance. The TDRs weighed 2.7 g in air, or 1.6% of the average initial mass of experimental birds. These devices have no measurable effect on little auk energy consumption (Harding et al. 2009a). We programmed the TDRs to record temperature and pressure every 5 s for up to 5 d. When the birds dived below 1.5 m, temperature and pressure readings were made every 0.2 s for the duration of the dive. TDRs were attached ventrally using Loctite® glue to adult little auks raising 1 to 18 d old chicks. Birds were caught either by hand in accessible nest crevices, or using noose carpets on rock surfaces. Handling lasted <10 min in all cases and data loggers were deployed for a maximum of 5 d. Recorded data were analysed following Harding et al. (2009a) so as to extract (1) foraging trip durations, (2) total flight time per foraging trip, (3) total number of dives per 24 h and (4) the proportion of time (%) spent underwater per 24 h.

Table 1. Sample sizes for measurements conducted at the different study sites in different years. SST: sea surface temperature (number of days for which satellite data were available). Foraging: number of birds equipped with time-depth recorders. Chick feeding: number of birds for which chick feeding rates were determined. FMR: number of birds for which field metabolic rate was estimated. Reproduction: overall number of nests for which breeding parameters were determined, although growth rates and fledging masses were only determined at KH and HS (see 'Materials and methods'). Condition: total number of adult birds weighed and measured. The survival analysis was conducted up to 2009; see 'Materials and methods' for sampling details. –: no data

	Kap Höegh (KH)			Hornsund (HS)			Kongsfjorden (KF)	
	2005	2006	2007	2005	2006	2007	2006	2007
SST	18	18	7	31	30	12	13	13
Diet	20	24	22	33	30	23	22	22
Foraging	–	–	6	–	–	11	–	7
Chick feeding	18	14	15	–	–	13	22	38
FMR	15	12	–	–	–	–	16	27
Reproduction	31	29	32	10	47	41	29	41
Condition	78	140	86	38	36	45	352	296

Chick feeding rates

To estimate chick feeding rates at KH and HS, breeding adults were individually marked with colour rings or picric acid, and their nest sites were observed non-stop for 24 to 48 h periods, allowing exact recording of nest visits. In addition to direct observations, miniature radio-transmitters (Holohil Systems and Biotrack) attached to breeding adults were also used to determine chick feeding rates at KF (see Welcker et al. 2009b for details).

Daily energy expenditure

Daily energy expenditure (DEE in kJ d^{-1}) of little auks breeding at KH and KF was estimated using the doubly labelled water (DLW) technique, following Welcker et al. (2009b) and the single sample method. Breeding adults caught at the nest or on the colony were weighed, given an intraperitoneal injection of DLW, colour-marked and released immediately. A single blood sample was drawn upon recapture, within 24 to 72 h. Isotopic dosages, laboratory analyses and DEE calculations followed Speakman (1997) and were conducted as detailed by Welcker et al. (2009b).

Breeding performance

Little auks raise a single chick in an underground nest crevice. During chick rearing, each studied nest was monitored every 3 d. Chick growth rates and fledging mass were only recorded at KH and HS using a Pesola balance (precision ±2.0 g) because nests were out of reach at KF, and only the presence/absence of the chick was determined using light-scopes (Moritex Europe). Fledging mass was the last measurement taken prior to a chick's departure from the colony, and only chicks that had reached 20 d when they disappeared from the nest were considered fledged (Harding et al. 2004). Fledging age and maximum fledging success (defined as the number of chicks fledged or reaching 20 d per number hatched) were calculated for a subsample of nests at each of the 3 colonies.

Adult body condition and survival

For all adults caught at the 3 colonies, we recorded body mass, headbill length and wing length, and these measurements were used to calculate an index of body condition (body mass corrected for structural size) as detailed in Harding et al. (2011). Adult survival rates of birds from KH and KF were determined using a capture-mark-recapture analysis. Briefly, at KH, breeding adults (n = 147) were caught in 2005 and individually marked with combinations of 3 colour rings and 1 metal ring. At KF, 299 birds were caught in 2006 and an additional 110 individuals in 2007, and marked in a similar way. Subsequent resighting sessions were conducted annually during the breeding season until 2009, with a minimum of 6 d per year and site. We used Cormack-Jolly-Seber (CJS) models implemented in the program MARK (White & Burnham 1999) to estimate yearly survival rates. With our data, we were unable to separate mortality from permanent emigration; therefore, estimated survival rates reflect apparent survival rather than true survival (however, for simplicity, we refer to 'survival rates' in this paper). We fitted 2 sets of CJS models: (1) using the combined data from KH and KF to estimate yearly survival from 2006/07 to 2008/09 and to test for between-colony differences, and (2) using KH data only to estimate yearly survival in 2005/06 for which no data was available for KF.

We assessed the goodness-of-fit of the global model allowing for time and colony-specific survival (denoted as Φ) and resighting probabilities (denoted as p) using the program U-CARE (Choquet et al. 2009). This model clearly did not fit the data (χ^2_4 = 31.55, p < 0.001). Inspection of the component tests revealed that rejection of the CJS model was mainly based on Test 2.CT, indicating strong resighting heterogeneity (trap-happiness), especially in KF birds. We accounted for trap dependence by estimating different resighting probabilities for individuals that were seen versus not seen the previous year (Pradel 1993), denoted as *h* in our models. The resulting model $\{\Phi_{c \cdot t}, p_{c \cdot t \cdot h}\}$, where c is colony and t is time (year), fitted the data well (χ^2_2 = 0.72, p = 0.70) and was used as the starting point for model selection based on Akaike's information criterion adjusted for small sample size (AIC_c; Anderson & Burnham 1999). The goodness-of-fit test for the second dataset (KH only) indicated that the CJS model fitted these data well (χ^2_3 = 2.13, p = 0.55), thus the model $\{\Phi_t, p_t\}$ was used as a starting point for this analysis. All possible models allowing survival probabilities to vary with time and/or colony and/or SST (including additive models) were examined. To account for model selection uncertainty we report survival estimates ±SE based on model averaging (Burnham & Anderson 2002; see Table 3).

Further statistical analyses

Differences in SST between years and sites were assessed using ANOVA. We used least squares linear regressions to test whether variation in our response variables across the different colonies and different years was related to differences in SST (Wernberg et al. 2010). This was done to assess the effect of SST on foraging effort (foraging trip duration, flight time, number of dives and time underwater per foraging trip), chick feeding rates and chick growth (peak mass, fledging mass and fledging age), daily energy expenditure and adult body condition. Data were log-transformed where necessary.

To examine the effect of SST on diet composition we used a 2-pronged approach. To account for the fact that these data contained many zeros (prey item not present in a sample) which cannot be accommodated with simple data transformations, we first fitted a generalised linear model with binomial errors to test whether SST affected the probability of a diet item (*Calanus hyperboreus*, *C. glacialis* and *C. finmarchicus*) to occur in a sample. In a second step, we then tested whether the proportion of these items in the diet was related to SST, excluding all zeros. Data were arcsine-transformed for this analysis.

Similarly, we used a generalised linear model with binomial error to assess the effect of SST on fledging success. All statistical analyses were performed using R 12.2. Means (*X*) are provided ±SD.

RESULTS

We studied birds at 3 different localities in 2005 to 2007 (Fig. 1), where they foraged for zooplankton in surface waters (<40 m). SST in foraging areas off the 3 study sites differed substantially ($F_{2,121} = 96.25$, $p < 0.001$) and this difference was consistent across years ($F_{2,121} = 2.03$, $p = 0.136$). SST was lowest around KH ($X = 0.39 \pm 0.29$°C), intermediate around HS ($X = 1.81 \pm 0.18$°C) and highest around KF ($X = 4.51 \pm 1.06$°C). Cold areas of the Greenland Sea favour large copepod species (*Calanus hyperboreus,* 7 to 8 mm long), while warmer areas favour smaller ones (*C. glacialis,* 3 to 5 mm long and *C. finmarchicus,* 2 to 4 mm long; Karnovsky et al. 2010). Studying food loads brought back to the colonies by breeding parents, we found that little auks fed primarily on copepods (68 to 97 %). Diet was adjusted according to local copepod availability, with birds preferentially feeding on large copepods in the cold water off Greenland (Table 2, Fig. 2A) and on small copepods in warm water off Spitsbergen (Table 2, Fig. 2B,C). Birds also nearly doubled their foraging trip duration for warm compared to colder water, and nearly tripled their foraging flight time (Table 2, Fig. 3AB). However, the number of dives per foraging trip and time spent underwater per foraging trip was not significantly correlated with SST (Table 2, Fig. 3C,D). This indicates that copepod swarms were similarly profitable once the birds were underwater; however, little auks breeding near warm waters had to spend more time on the wing to reach them. Despite enhanced foraging activity over warm water, little auk daily energy expenditures estimated by the DLW method were unaffected by SST (Table 2). We speculate that little auks might buffer higher foraging costs by reducing their energetic investment into other activities, for instance by decreasing patrolling flight over the breeding site outside their actual foraging trips (a common and energetically costly behaviour in this species).

Crucially, plasticity in foraging behaviour allowed birds to balance their energy budgets, and to maintain chick provisioning rates across the SST range (Table 2). Chick growth curves were consequently similar when parents foraged in cold and warm water (Fig. 4). In warmer water, chicks tended to reach higher peak mass and to fledge later (Table 2; but note the very low regression coefficients for both relationships: 0.048 and 0.040, respectively), yet the essential parameters of fledging mass and fledging success were unaffected by SST across the 3 study sites (Table 2). Further, there was no effect of SST on the body condition index of breeding little auks (Table 2, Fig. 5), nor on adult survival (Table 3, Fig. 6). There was nonetheless substantial interannual variability in adult survival especially at KH, strongly suggesting that this variable might also be driven by events occurring outside of the breeding season (Fort et al. 2009).

Table 2. Statistical analyses testing the potential link between sea surface temperature (SST) and different seabird parameters. Statistical tests are based on least squares linear regressions except for diet probabilities (probability of a prey item occurring in a diet sample) and breeding success for which a relationship with SST was assessed by generalised linear models with binomial errors. See 'Materials and methods' for details. Significant p-values ($p < 0.005$) in **bold**. FMR: field metabolic rate. [a]*z*-value

Variable	Estimate ± SE	*t*	df	p	R^2
Diet proportion *Calanus hyperboreus*	−0.085 ± 0.015	−5.841	117	**<0.0001**	0.226
Diet proportion *C. glacialis*	0.087 ± 0.017	5.267	192	**<0.0001**	0.126
Diet proportion *C. finmarchicus*	0.022 ± 0.004	5.093	186	**<0.0001**	0.122
Diet probability *C. hyperboreus*	−1.298 ± 0.229	−5.677[a]	193	**<0.0001**	
Diet probability *C. glacialis*	2.378 ± 0.938	2.536[a]	193	**0.011**	
Diet probability *C. finmarchicus*	0.354 ± 0.107	3.313[a]	193	**<0.0001**	
Foraging trip duration	0.930 ± 0.264	3.520	22	**0.0019**	0.331
Flight time per foraging trip	0.960 ± 0.142	6.775	22	**<0.0001**	0.661
Dives per foraging trip	−0.552 ± 14.145	−0.039	22	0.97	0.045
Time underwater per trip	0.093 ± 0.195	0.477	22	0.638	0.035
FMR	−4.072 ± 9.657	−0.422	68	0.675	0.003
Chick feeding	−0.004 ± 0.017	0.258	118	0.797	0.0006
Chick peak mass	0.028 ± 0.011	2.454	120	**0.0155**	0.048
Chick fledging age	0.008 ± 0.003	2.873	197	**0.0045**	0.040
Chick fledging mass	0.440 ± 1.160	0.380	120	0.705	0.001
Fledging success	−0.026 ± 0.087	−0.304[a]	339	0.761	
Condition	0.278 ± 0.146	1.908	1041	0.057	0.003

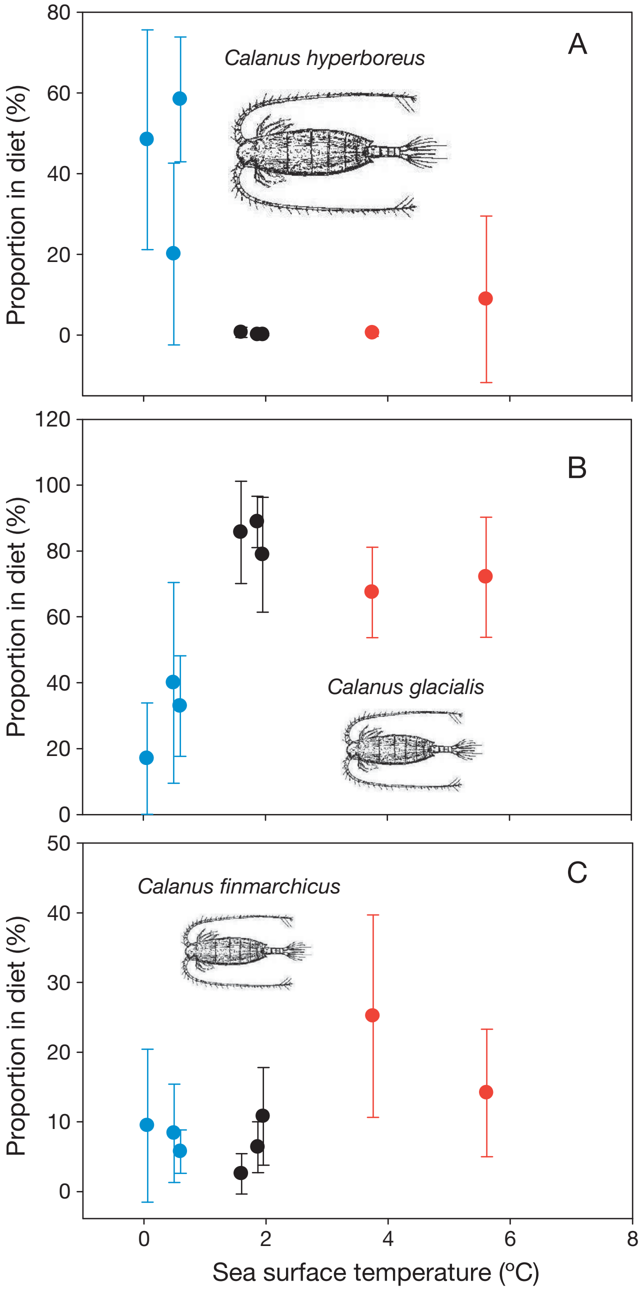

Fig. 2. *Alle alle*. Feeding preferences on different copepods, means ± SE. (A) *Calanus hyperboreus* (7 to 8 mm long), (B) *C. glacialis* (3 to 5 mm long), (C) *C. finmarchicus* (2 to 4 mm long). Blue: Kap Höegh; black: Hornsund; red: Kongsfjorden. See Table 2 for detailed statistics

DISCUSSION

Using our comparative framework across the Greenland Sea, we reject the hypothesis of a general influence of current Arctic Ocean warming on the fitness of the highly abundant, ecologically important little auk. During our study, the overall SST differential measured across study sites was >5°C. In oceanographic terms, this is a major difference, which is predicted to cause vast changes in zooplankton community composition (Beaugrand et al. 2009). Such a ΔSST is close to the maximum change of 7°C predicted for the North Atlantic in the 21st century (Karnovsky et al. 2010). We therefore consider this ΔSST and our study design adequate to test the effect of ocean warming on little auk ecophysiology.

One potential limitation of our study design is that we studied birds of the same species exposed to contrasted environmental conditions which, however, attended breeding colonies hundreds of km apart. There is therefore the possibility that observed patterns are not due to species-specific plasticity, but to micro-evolution of distinct groups within a metapopulation. However, a study of North Atlantic Alcidae (the seabird family including little auks) demonstrated that distant breeding populations of the same species are genetically highly homogeneous, strongly suggesting intense genetic mixing, even between the most distant breeding sites (Riffaut et al. 2005). Furthermore, recent population genetic analyses of little auks breeding across the North Atlantic also show very high genetic mixing among populations (K. Wojczulanis-Jakubas et al. unpubl.). It is, therefore, reasonable to assume that birds from our 3 study sites belong to the same population, with similar potential for ecophysiological plasticity.

Moreover, our analyses focused on the effect of ocean surface warming, which is in line with the major research objectives of the inter-governmental panel on the effect of climate change (IPCC, working group II) for their forthcoming 2014 assessment report. However, a series of other biotic and abiotic environmental variables may potentially affect the ecophysiology and fitness of seabirds such as little auks (e.g. wind and air temperature, competition, see Fort et al. 2009), and might explain the wide numerical range recorded for some variables, such as breeding success (61 to 98%) or annual adult survival (61 to 92%; Fig. 6). Furthermore, some results specific to the HS site, which deviate from the general, significant trends presented in Fig. 3C,D, suggest the existence of locally different functional relationships between SST and seabird foraging parameters. These aspects deserve further investigation, yet there is compelling evidence that water temperature is the single most important environmental parameter within oceanic ecosystems, and that its rapid increase is currently triggering a complete reorganisation of the plankton community upon which little auks feed in the North Atlantic (Beaugrand et al. 2009, 2010).

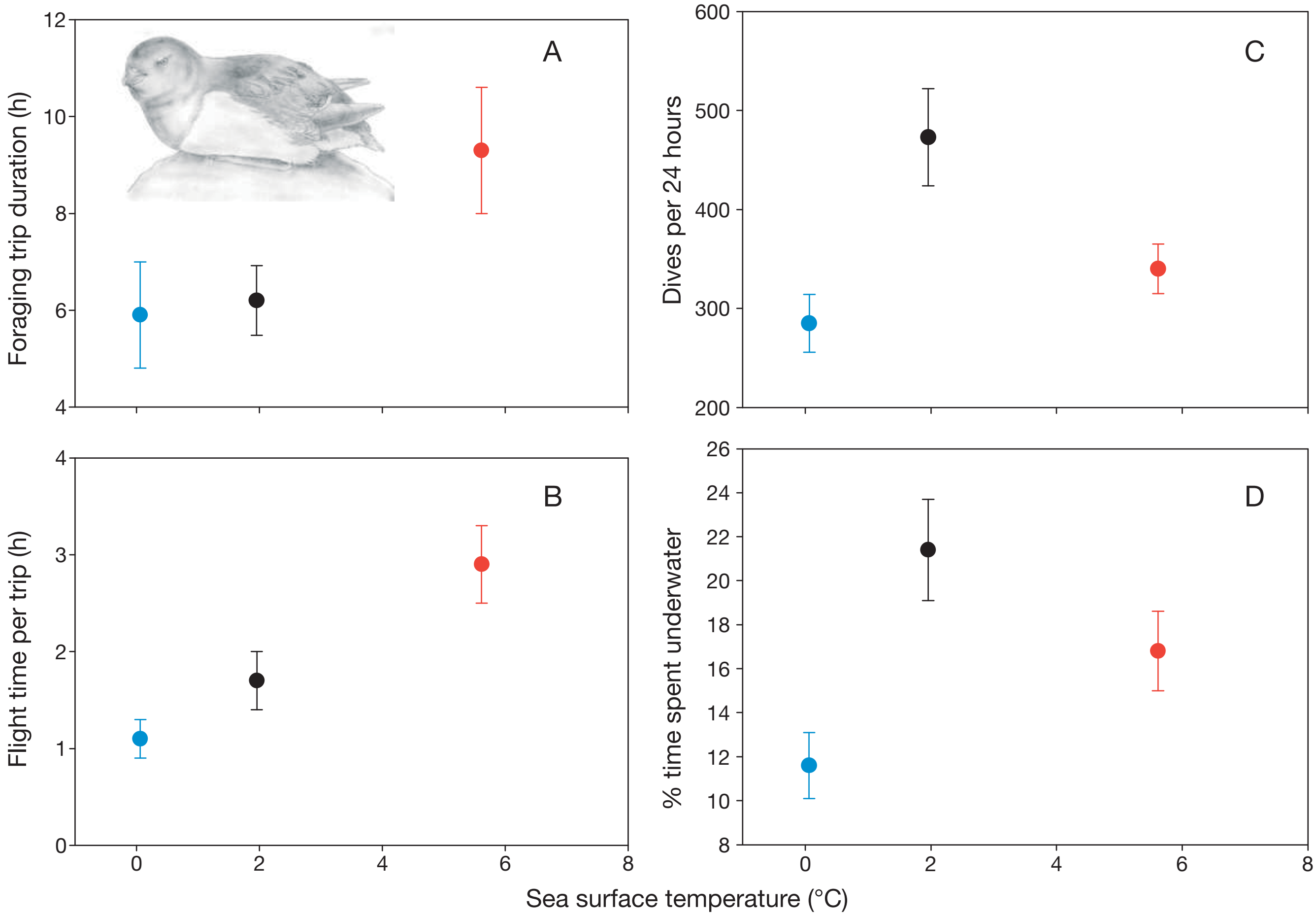

Fig. 3. *Alle alle*. Influence of sea surface temperature (SST) upon (A) foraging trip duration, (B) flight time per foraging trip, (C) total number of dives per 24 h and (D) proportion of time spent underwater (see Table 2 for statistical details). Data were recorded in 2007 (blue: Kap Höegh, black: Hornsund, and red: Kongsfjorden) using time-depth recorders deployed between 1.3 and 4.7 d ($\bar{X}$ = 3 ± 1), recording between 2 and 14 foraging trips ($\bar{X}$ = 7 ± 3) for each bird

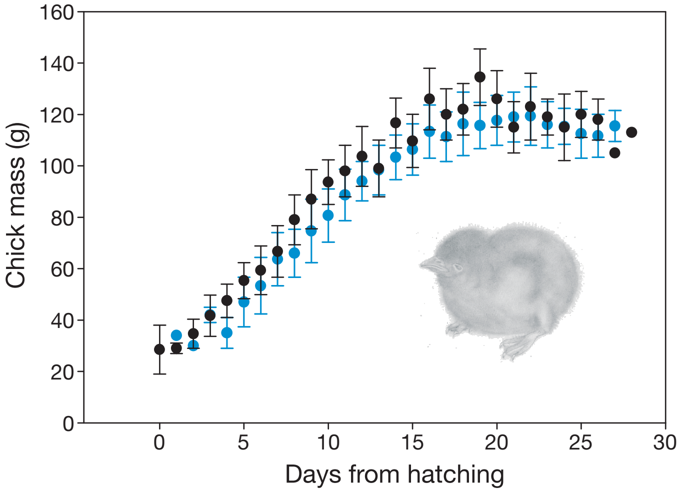

Fig. 4. *Alle alle*. Average growth curves of chicks in 2005 to 2007 at (blue) Kap Höegh (cold water) and (black) Hornsund (warm water). See Table 2 for detailed statistics

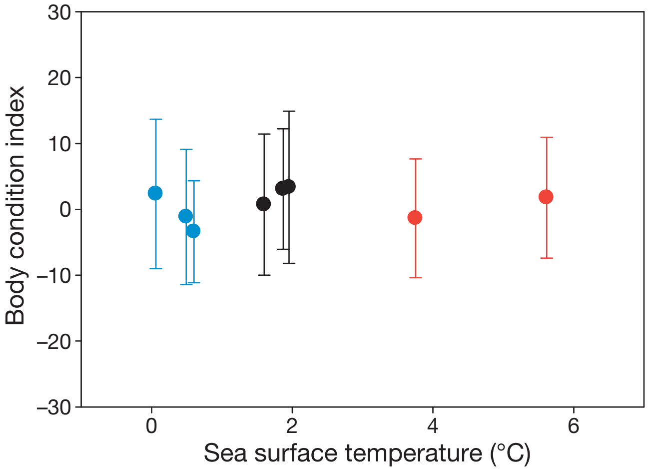

Fig. 5. *Alle alle*. No effect of water temperature on the body condition index of adults breeding at 3 Greenland Sea colonies (blue: Kap Höegh, black: Hornsund, and red: Kongsfjorden) in 2005 to 2007. See Table 2 for detailed statistics

Table 3. Survival modelling for adult little auks from Kap Höegh (KH) and Kongsfjorden (KF) in 2006 to 2009. The 5 most parsimonious models according to AIC_c are given out of the possible models allowing survival probabilities to vary with time and/or colony and/or sea surface temperature (SST) that were tested. Φ = apparent (yearly) survival; p = resighting probability; c = colony (KH vs. KF); t = time; h = resighting heterogeneity (h1 extending 1 yr, h2 extending 2 yr)

Φ	p	Deviance	No. parameter	ΔAIC_c	AIC_c weight	Model likelihood
c × t	h2	856.71	9	0	0.424	1
c × t	c + h2	855.59	10	0.909	0.269	0.635
c × t	h1	860.21	8	1.461	0.204	0.482
c × t	c + h1	859.57	9	2.860	0.102	0.239
c × SST	h2	878.70	7	17.93	0.00005	0.0001

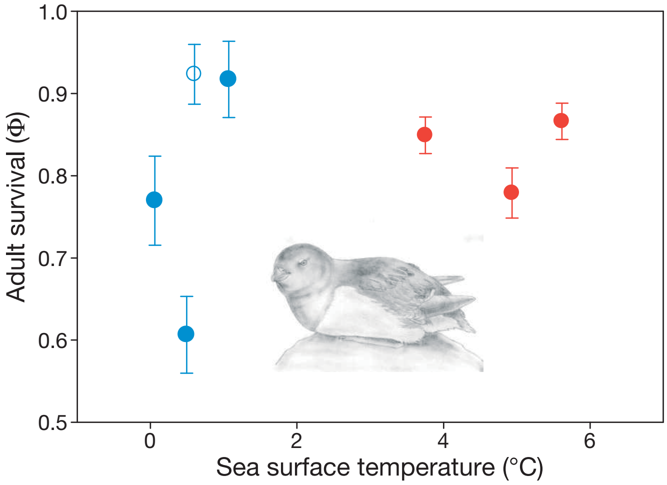

Fig. 6. *Alle alle*. No effect of water temperature on the survival rate of adults breeding at 2 Greenland Sea colonies (blue: Kap Höegh, red: Kongsfjorden) in 2006 to 2009. The best model including sea surface temperature (SST) was 17.9 AICc units less well supported than the best model without an effect of SST. Note substantial annual variation in adult survival at Kap Höegh (open symbol: 2005 data point). See Table 3 for detailed statistics

Beyond these caveats, our findings are important for a better understanding of the short-term plastic responses of marine polar organisms to rapid ocean warming, for studies modelling the ecological influence of current and future Arctic climate change, and for the design of ecological monitoring of a warming Arctic (Grémillet & Charmantier 2010). In particular, our study is among the first to assess the capacity of a marine predator to buffer the consequences of climate change. Our conclusions are coherent with those of recent investigations which stress that behavioural plasticity is the primary mechanism by which animals deal with the consequences of climate change (Bradshaw & Holzapfel 2006, Charmantier et al. 2008, Kearney et al. 2009). A wide range of studies have identified correlations between climate variables and the distribution, phenology, and dynamics of wild populations (Parmesan & Yohe 2003). Such evidence has played a key role in demonstrating the ecological consequences of ongoing climate change, and these correlations have been used to design climate envelope models to forecast future trends (Sommer et al. 2010). Behavioural plasticity demonstrated here significantly attenuates the effect of anticipated climatic effects, undermining the ability of envelope models to realistically mirror future trends. Our data, therefore, underline recent criticism of such models (Morin & Thuiller 2009), and support the proposed development of mechanistic models as an alternative (Buckley et al. 2010). These novel tools are powerful and can be better validated, yet they require vast amounts of information relative to the functional ecology of the species concerned. In this context, our detailed study of the ecophysiology of little auks facing the consequences of climate change is a crucial step towards developing mechanistic models of the effect of climate change upon marine organisms (Fort et al. 2009).

During the study period, little auks maintained their fitness despite contrasting ocean surface temperatures and copepod availability across the Greenland Sea. This indicates that they are successful at dealing with the influence of current climate change in the Arctic. However, recent experiments and modelling strongly suggest that little auks function close to their maximum foraging capabilities, and will not cope with further degradation of their feeding conditions (Karnovsky et al. 2010). Indeed, breeding little auks for which flight costs had been artificially augmented had significantly lower body masses, and fledged considerably lighter chicks (Harding et al. 2009b). Consequently, we argue that even if little auks seem currently able to buffer the consequences of climate change in the North Atlantic, such abilities will not extend indefinitely. Following rapid North Atlantic warming, the 5°C isotherm will soon reach the East Greenland coast at 70° N and West Spitsbergen at 80° N. This will not only exclude large *Calanus hyperboreus* copepods whose thermal preferendum lies between −2 and +4°C (Karnovsky et al. 2010), but may also favour 'southern invaders,' such as *Metridia lucens*, which are currently absent from the area. It remains to be tested whether little auks will manage to efficiently feed upon these organisms, an adaptation which will require morphological (bill shape), physiological (digestion) and behavioural plasticity. Understanding the limits of such plasticity is essential for the mechanistic modelling of climate effects on little auks and other organisms to achieve its potential.

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Contribution to the Theme Section 'Seabirds and climate change'

Climate affects food availability to planktivorous least auklets *Aethia pusilla* through physical processes in the southeastern Bering Sea

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ABSTRACT: Climate change might affect marine top predators by altering availability and nutritional quality of their prey. Climate effects vary on a regional basis, and our understanding of the relationships between fluctuations in climate and food resources in sub-arctic regions with seasonal ice cover is limited. We studied the effects of inter-annual climate variability (as reflected in the Pacific Decadal Oscillation, PDO, and the timing of the winter ice retreat) on zooplankton–planktivorous predator linkages in one of the most productive regions of the southeastern Bering Sea, the 'Green Belt'. We examined changes in diets (species composition of chick meals and stable isotope signatures of adult blood) and relative food availability (as reflected in blood plasma concentrations of the stress hormone corticosterone) of planktivorous least auklets *Aethia pusilla* breeding on St. George I. (shelf-break) and St. Paul I. (shelf) during 2003 to 2005 and 2008 to 2009. We found that isotopic signatures of blood and composition of chick meals differed between the colonies. The proportion of energy-rich oceanic copepods *Neocalanus* spp. in the diet declined during warm years (high PDO and early ice retreat) on St. Paul but not on St. George. However, inter-annual and seasonal dynamics of corticosterone were similar between the colonies, and auklets experienced higher nutritional stress during warm compared to cold years. Our results suggest that the influx of prey-bearing water masses from the ocean basin and the retention time of oceanic copepods on the shelf are the main factors affecting composition of prey and its availability to auklets. We conclude that anticipated climate warming will negatively affect food availability of planktivorous predators in the Green Belt region of the southeastern Bering Sea.

KEY WORDS: Climate impacts · Nutritional stress · Oceanic shelf-system · Seabirds · Stable isotopes · Corticosterone

INTRODUCTION

Understanding the impacts of climate change on biota is a major current challenge in ecology and conservation. In marine ecosystems, climate warming affects trophic linkages between producers and primary consumers (Mackas et al. 2007, Ji et al. 2010, Coyle et al. 2011), which in turn alter availability of food resources to top predators (Hunt et al. 2002). During reproduction, marine predators such as seabirds rely on predictable seasonal peaks in the availability of prey to meet their energy demands (e.g. Hipfner 2008, Shultz et al. 2009). Climate-induced environmental changes may influence the timing and magnitude of these peaks (Mackas et al. 2007, Hunt et al. 2008). However, specific effects of environmental changes

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on seabirds vary across regions (Irons et al. 2008). In particular, the mechanisms underlying physical forcing are thought to be fundamentally different in marine ecosystems with seasonal ice cover (Hunt et al. 2008). Yet there is a lack of general predictions regarding the impacts of climate on top predators breeding in regions with seasonal ice cover (but see Kitaysky & Golubova 2000).

Predictions about consequences of anticipated climate warming on the Bering Sea food web have been advanced in the mechanistic Oscillating Control Hypothesis (OCH) (Hunt et al. 2008). The OCH predicts that regulation of the Bering Sea shelf ecosystem is different between cold and warm climate regimes with a close coupling of zooplankton productivity to the timing of winter ice retreat. Cold regimes with late ice retreat and low water temperatures favor an early phytoplankton bloom and higher probability of secondary blooms (if there is sufficient mixing) in the middle shelf domain, which can sustain a strong production of energy-rich large shelf copepods *Calanus marshallae*. In contrast, warm regimes with early ice retreat and high water temperatures result in a late phytoplankton bloom and increased stratification of the water column that prevents mixing later in the season and cannot sustain larger species of zooplankton (Hunt et al. 2008, 2011). These predictions have been generally supported by field observations made in the middle shelf domain regions of the Bering Sea (Baier & Napp 2003, Coyle et al. 2008, 2011), but the implications for top predators have not been directly investigated.

The Green Belt (see Fig. 1) is a vast region and one of the most productive areas of the Bering Sea (Springer et al. 1996). The Green Belt is characterized by large influx of oceanic water masses into a (seasonally ice covered) shelf ecosystem (Springer et al. 1996). Thus the Green Belt is a more heterogeneous environment than the ocean basin and middle shelf domains situated farther away from the shelf edge, with zooplankton communities originating from both the ocean basin and the shelf (Coyle et al. 2008, Stabeno et al. 2008). The OCH does not address potential effects of the influx of oceanic water masses and energy-rich oceanic copepods *Neocalanus* spp. into the shelf regions (Coyle et al. 2008), and the applicability of the OCH to food web structuring in the Green Belt regions has not been previously tested.

Seabirds integrate processes at low trophic levels and changes in their food availability indicate potential changes in prey communities and abundances (e.g. Furness & Camphuysen 1997, Piatt et al. 2007). In the Bering Sea, planktivorous auklets have been used as indicators of environmental variability and ecosystem response to physical forcing (Springer & Roseneau 1985, Springer et al. 2007, Benowitz-Fredericks et al. 2008, Bond et al. 2011). Least auklets preferentially feed on large energy-rich calanoid copepods originating either from the ocean basin (*Neocalanus cristatus*, *N. plumchrus* and *N. flemingeri*) or from the shelf (*Calanus marshallae*), which they replace with lower-quality prey such as euphausiids, decapods and amphipods when copepods are scarce (Bédard 1969, Springer & Roseneau 1985, Roby & Brink 1986, Springer et al. 2007).

We assessed inter-annual and seasonal changes in environmental conditions on the availability of food to least auklets *Aethia pusilla*, one of the most numerous planktivorous seabirds breeding in the Pribilof Domain, which is located in the southeastern part of the Green Belt. We used a 2-pronged approach to examine the effects of climate variability on food resources of least auklets breeding on the 2 largest colonies of St. Paul I. (continental shelf region) and St.

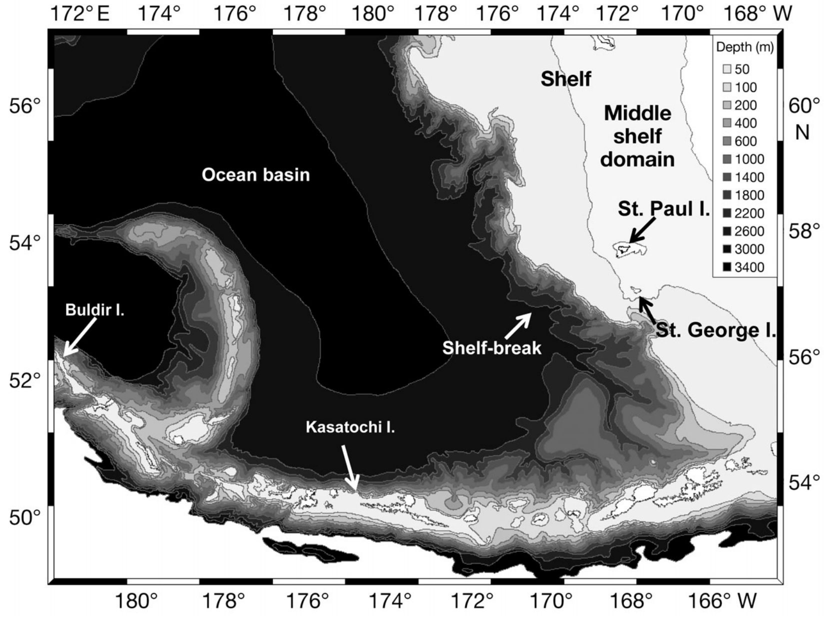

Fig. 1. Southeastern Bering Sea showing the location of the Pribilof Islands, St. Paul I. (shelf) and St. George I. (shelf-break), and the Aleutian Islands, Buldir I. and Kasatochi I. (ocean basin). The Green Belt runs along the edge of the continental shelf (shelf-break). For a detailed description on the location of the Green Belt and the major currents see Springer et al. (1996; their Figs. 1 & 2)

George I. (shelf-break region), Pribilof Islands (Fig. 1). First, we used species composition of chick meals and stable isotope signatures in red blood cells of adults to characterize the type of prey species and its origin (relative distance from shelf), respectively. Inter-annual changes in diet composition are suggested to be indicative of climate-driven phenological mismatches between prey and seabirds (Springer et al. 2007, Hipfner 2008), and stable isotope signatures of carbon (δ^{13}C) of birds' tissues are frequently used to assess the origin of the prey (i.e. Quillfeldt et al. 2005). δ^{13}C signatures decline along the continental shelf-ocean basin gradient (Hobson et al. 1994) and hence can be used to distinguish between foraging locations in the shelf and oceanic regions of the Bering Sea (Schell et al. 1998, Smith et al. 2002). Second, since direct quantification of temporal changes in food availability in marine ecosystems is often logistically impossible, we used blood plasma levels of the stress hormone corticosterone in adults as a proxy for changes in their food availability (Kitaysky et al. 2007, 2010, Benowitz-Fredericks et al. 2008). Concentrations of this hormone increases predictably in response to declines in food availability (Kitaysky et al. 1999a,b, 2001, 2007, Wingfield & Kitaysky 2002). This technique has been successfully applied in ecological studies of several species of seabirds (Buck et al. 2007, Williams et al. 2007, Doody et al. 2008, Welcker et al. 2009), including least auklets (Benowitz-Fredericks et al. 2008).

The goals of the present study were (1) to examine foraging responses to inter-annual climate variability of planktivorous seabirds breeding at locations with different oceanographic properties in the Green Belt of the southeastern Bering Sea; and (2) to understand the underlying mechanism(s) driving climate-induced variations in food availability to planktivores at the Green Belt. The specific objective was to compare the inter-annual and seasonal dynamics of species compositions and stable isotope values of diets and corticosterone levels of breeding least auklets in 2 locations between the relatively warm years of 2003 to 2005 and the cold years of 2008 to 2009. Based on the OCH and previous studies in the southeastern Bering Sea (Hunt et al. 2002, 2008, Springer et al. 2007, Benowitz-Fredericks et al. 2008, Coyle et al. 2008, Stabeno et al. 2008), we made the following predictions: (1) Diet composition differs between birds breeding on St. Paul I. and St. George I., with the diet composition of birds on St. George I. containing a larger proportion of oceanic prey. This difference should be most strongly pronounced during warm years when oceanic copepods are scarce in the shelf regions (Coyle et al. 2008). (2) Stable isotope signatures of δ^{13}C should be higher in birds breeding on St. Paul I. compared to birds breeding on St. George I., reflecting the colony's proximity to the shelf-break. We expect the difference in δ^{13}C between the islands to be larger during warm years, when birds breeding on St. Paul I. do not have access to oceanic *Neocalanus* copepods, compared to cold years when oceanic copepods are present in the diet of birds on both islands (Springer et al. 2007). (3) Levels of corticosterone should be higher during warm years when food availability is low. We expect the inter-annual and seasonal dynamics of corticosterone to be similar between islands (Benowitz-Fredericks et al. 2008) since climate-induced changes in physical forcing have been observed to affect the entire region (Stabeno et al. 2008).

MATERIALS AND METHODS

Study site and climate variables

The study was conducted at the 2 major Pribilof Islands, St. George I. (56° 36′ 20″ N, 169° 33′ 35″ W, located near the shelf-break, and St. Paul I. (57° 7′ 30″ N, 170° 17′ 3″ W), located on the continental shelf in the southeastern Bering Sea (Fig. 1), during the relatively warm years 2003 to 2005 and the cold years 2008 to 2009. St. Paul and St. George Islands are situated approx. 90 km from each other and are located in the Pribilof Domain.

Inter-annual climate variability was characterized by the Pacific Decadal Oscillation (PDO) and by the Ice Retreat Indices (IRI) (Table 1). We chose these pa-

Table 1. Climate variables. The Pacific Decadal Oscillation (PDO) index is the leading principal component of the monthly North Pacific sea surface temperature variability. The summer PDO is the average PDO from June, July and August. In the eastern Bering Sea, positive PDO values correspond to warm conditions, whereas negative values correspond to cold conditions. The Ice Retreat Index (IRI) is defined as the number of days after March 15 when the average ice concentration is more than 10 % of a specified area on the continental shelf of the eastern Bering Sea (www.beringclimate.noaa.gov/data)

Year	Summer PDO	IRI
2003	0.84	0
2004	0.44	23
2005	0.69	0
2008	−1.57	35
2009	−0.25	46

rameters based on the mechanistic predictions of the OCH, which focuses on the roles of timing of ice retreat and summer water temperatures in regulation of zooplankton productivity (Hunt et al. 2008). The PDO index is the leading principal component of the monthly North Pacific sea surface temperature variability (Mantua et al. 1997). In the eastern Bering Sea, positive PDO values correspond to warm conditions, whereas negative values correspond with cold conditions. The summer PDO is the average PDO from June, July and August. The IRI is defined as the number of days after March 15 when the average ice concentration is more than 10% of a specified area on the continental shelf of the eastern Bering Sea (for more details see www.beringclimate.noaa.gov/data).

Capture and blood sampling of study species

We studied least auklets during the breeding season from June to August each year. Least auklets incubate for approx. 30 d followed by a chick-rearing period of about 26 to 31 d (Roby & Brink 1986), and both sexes share parental duties equally (Jones 1993). During 2003 to 2005, our aim was to sample 10 birds during 3 breeding stages: incubation (2 June to 21 June), early chick-rearing (28 June to 15 July), and late chick-rearing (26 July to 2 Aug). In 2008 and 2009, we sampled 10 birds every week on St. Paul I. and every second week on St. George I. starting in early July until mid-August. In 2008, due to extensive snow cover at the colonies, egg-laying was delayed (Konyukhov 2008), which allowed us to sample chick-rearing adults later in the season compared to previous years. We also collected blood from auklets nesting at 2 Aleutian Islands, Buldir I. (52° 21′ 17″ N, 175° 55′ 13″ E; 2003: n = 8; 2004: n = 7) and Kasatochi I. (52° 10′ 39″ N, 175° 30′ 30″ W; 2005: n = 7) (Fig. 1), to characterize isotope values of least auklets foraging only in oceanic water masses.

Auklets were captured at their colonies during daylight hours, using mist nets and noose carpets (Benowitz-Fredericks et al. 2008). Birds were sampled for blood from the brachial vein of the wing using a hypodermic needle and heparinized capillary tubes. All blood samples were taken within 3 min after capture. Unlike catecholamine hormones, such as adrenaline, which are stored and released into circulation almost immediately in response to a stressor, such as being captured, corticosterone must be synthesized in response to the stressor and is not manifest in the bloodstream for several minutes (reviewed in Sapolsky et al. 2000). Therefore, blood samples obtained within 3 min of initial capture reliably reflect baseline (pre-capture) levels in birds (reviewed in Romero & Reed 2005). Blood samples were stored on ice and centrifuged on the same day to separate plasma from red blood cells. After separation, plasma and red blood cells (RBC) were frozen until corticosterone and stable isotope analyses. Least auklets provision their chick by delivering whole zooplankton prey items that they store in a gular pouch (Bédard 1969). Auklets voluntarily regurgitate chick meals upon capture, and those were collected and stored in a preservative until further analyses. Active breeding was verified by the presence of chick meals in a gular pouch and/or brood patch status. An overview of sample sizes is given in Table 2.

Identification of prey

Chick meals were analyzed for prey species composition by identifying individual specimens to the lowest taxonomic level possible. Morphological similarities prevented us from distinguishing between the 2 closely-related species *Neoclananus plumchrus* and *N. flemingeri*, and the data for those 2 species were pooled for analyses. Following Springer & Roseneau (1985) and Springer et al. (2007), we calculated the percentage biomass for each category. Since we were interested in the proportion of copepods in the diets and the location from which they originated, we divided the diet contents into 3 major categories: oceanic *Neocalanus* copepods (*N. cristatus* and *N. plumchrus/flemingeri*), shelf copepods (*Calanus marshallae*), and other zooplankton originating mainly from the shelf.

Stable isotope analyses

Turnover time of isotopes in the tissue is critical when using stable isotopes as dietary tracers since it determines whether the isotopes reflect past or current diet (Hobson & Clark 1992, 1993). We used red blood cells which turn over every 15 to 17 d, so that the carbon they contain came from diets during the previous 2 to 3 wk (Carleton & del Rio 2005), to gain information about the origin of auklet diet before the onset of sampling, which was especially important for 2008 to 2009 when sampling started at late incubation. Red blood cells were freeze-dried and analyzed with continuous flow isotope ratio mass spectrometry (CF-IRMS) using a Costech Elemental Analyzer (Model ECS 4010), a Thermo Finnigan

Table 2. *Aethia pusilla.* Sampling dates and sample sizes for the regurgitations of chick meals, stable isotope values of $\delta^{13}C$ in red blood cells, and baseline corticosterone levels in the blood plasma of adult least auklets breeding on St. Paul I. (shelf) and St. George I. (shelf-break), Pribilof Islands, in 2003 to 2005 and 2008 to 2009

Year	St. Paul				St. George			
	2 Jun to 21 Jun	28 Jun to 11 Jul	12 Jul to 2 Aug	3 Aug to 12 Aug	2 Jun to 21Jun	28 Jun to 11 Jul	12 Jul to 2 Aug	3 Aug to 12 Aug
Chick meals								
2003		13	13			25	11	
2004		60	41			11	8	
2005		31	19				20	27
2008			31	22			33	
2009		1	39				33	
$\delta^{13}C$								
2003	14		8		7	7	7	
2004	21	20	6		7	7	7	
2005	7	7	6		7	7	7	
2008		7	7	7		8	7	5
2009		10	20			10	20	
Corticosterone								
2003	14		12		10	24	14	
2004	22	20	7		18	20	10	
2005	12	9	6		10	20	20	
2008		35	32	18		11	15	5
2009		12	39			10	16	1

MAT ConFlo III interface and a Delta Plus IRMS, at the Alaska Stable Isotope Facilities of the University of Alaska Fairbanks (Williams et al. 2007). Isotope results are presented in δ notation according to:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}} - 1)] \times 1000‰$$

where X is either ^{15}N or ^{13}C and R is the ratio of heavy to light isotope ($^{15}N/^{14}N$ and $^{13}C/^{12}C$). Atmospheric air and Vienna PD belemnite were used as standards for nitrogen and carbon, respectively. Measurement precision (SD) based on replicate measurements of the laboratory standard (peptone) was ±0.11‰ for $\delta^{13}C$.

Corticosterone assay

Total corticosterone (free and bound fractions) was measured using a radioimmunoassay at the University of Alaska Fairbanks, according to established protocols (Benowitz-Fredericks et al. 2008). Briefly, for each sample, 20 µl of plasma was equilibrated with 2000 cpm of tritiated corticosterone prior to extraction with 4 ml of re-distilled dichloromethane. After extraction, percent tritiated hormone recovered from each individual sample was assessed and used to correct final values. Samples were reconstituted in PBSG buffer and combined with antibody and radiolabel in a radioimmunoassay (Wingfield & Farner 1975, Wingfield et al. 1991). Dextran-coated charcoal was used to separate antibody-bound hormone from unbound hormone. Inter- and intra-assay CVs were less than 9% and 2%, respectively.

Statistical analyses

All data were analyzed using the 'R' statistical packages. Data on corticosterone levels were log-transformed to meet the assumptions of normality and heterogeneity of variances for parametric tests (Zar 1999). All inter-annual comparisons were performed on data obtained between July 12 and August 2 during chick-rearing.

To test the relationship between foraging locations and stable isotope values of auklets blood, we examined a change in the isotopic signatures between the ocean basin and the continental shelf regions of the Bering Sea. We compared the isotope values of red blood cells of birds breeding on the 2 Aleutian Islands (Buldir I. and Kasatochi I., ocean basin), with St. George I. (shelf-break) and St. Paul I. (shelf) using 2-way ANOVA with Location and Year as fixed factors.

To examine how inter-annual climate variability affects the composition, origin, and availability of prey, we ran a linear model with Island as fixed factor and summer PDO and IRI as continuous predictor variables for responses in the proportion of *Neocalanus* copepods in the diet, δ^{13}C, and corticosterone. The interaction terms island by summer PDO and island by IRI were included to test whether the islands respond to climate variability similarly. We only used the percentage oceanic *Neocalanus* copepods in the diet, since they are the main copepods in auklet diets. Since the data on diet composition were not normally distributed and could not be transformed to meet the requirements of parametric tests, we performed the analyses on ranks. To investigate significant interaction terms, we used correlation analyses (Spearman's rank correlation test for the proportion of *Neocalanus* in the diet).

For seasonal comparisons of δ^{13}C and corticosterone, we were primarily interested in how seasonal changes in response variables were affected by the environmental parameters (IRI and PDO) and between the islands. As our test of homogeneity of slopes indicated significant Year × Date × Island interaction terms (δ^{13}C: $F_{4,245} = 2.58$, p = 0.038; corticosterone: $F_{4,406} = 5.59$, p < 0.001), the interpretation of results of a full ANCOVA model would be difficult. Thus we conducted separate ANCOVAs with colony as factor and date as covariate for each year, with δ^{13}C and corticosterone as response variables. To examine the relationships between colony-year-specific seasonal enrichment of δ^{13}C and summer PDO and IRI we used regression analyses.

RESULTS

Spatial comparisons of stable isotopes

As expected from the colony locations, stable isotope values of δ^{13}C in red blood cells of auklets were low for birds breeding in the ocean basin (Aleutian Islands) compared to birds breeding on the shelf (St. Paul I.); birds breeding close to the shelf-break (St. George I.) had intermediate values (island effect δ^{13}C: $F_{2,64} = 465.88$, p < 0.001) (Fig. 2).

We also observed a large difference in δ^{15}N between birds on the Pribilof Is. and the Aleutian Is. (Fig. 2). Nitrogen stable isotopes provide information about the trophic level of the birds' diet (Hobson et al. 1994); however, interpreting differences in trophic levels is beyond the scope of this study. Therefore, we include the data for comparison to other studies/species, but will not discuss the differences in δ^{15}N signatures, focussing only on differences in δ^{13}C signatures that indicate the origin of the prey source.

Inter-annual comparisons

Diet species composition differed markedly between the islands (Table 3, Fig. 3): while oceanic *Neocalanus* copepods dominated the diets of auklets on St. George I. (except in 2003), they were entirely absent or occurred in small amounts in the diets of birds on St. Paul I. during 2003 to 2005. There was a significant negative relationship between summer PDO and the proportion of *Neocalanus* in the diet, but there was no overall effect of IRI (Table 3). However, the effects of summer PDO and IRI on the proportion of *Neocalanus* in the diet differed between the islands (Table 3). The proportion of *Neocalanus* copepods in the diet decreased in warmer years only for birds breeding on St. Paul I. (summer PDO, St. Paul: $r_S = -0.82$, p < 0.001; St. George: $r_S = -0.11$, p = 0.252, Fig. 3). The proportion of *Neocalanus* copepods in the diet of least auklets breeding on St. Paul also increased with later timing of ice retreat (IRI: $r_S = 0.75$, p < 0.001). However, an opposite, albeit weak, trend was observed on St. George, with a decrease in the proportion of *Neocalanus* copepods in the diet with later timing of ice retreat (IRI: $r_S = -0.20$, p = 0.027).

During the 5 study years, δ^{13}C values were consistently higher in birds breeding on St. Paul I. than those on St. George I. (Table 3, Fig. 2). There was no overall relationship between climate variability (as reflected in summer PDO and IRI) and δ^{13}C of auklets on the Pribilof Islands. However, the relationship between IRI and δ^{13}C was different between the islands (Table 3): a decrease in δ^{13}C with later timing of ice

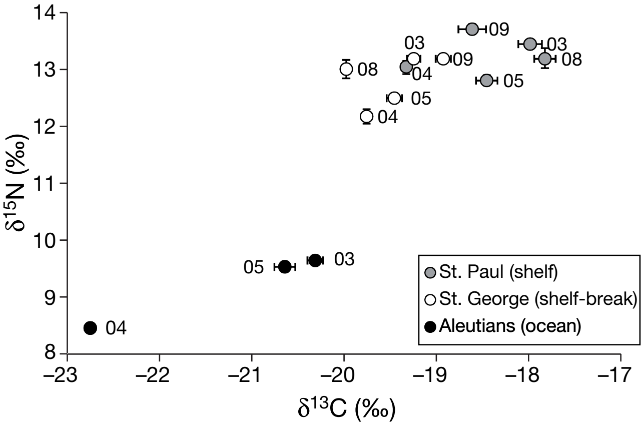

Fig. 2. *Aethia pusilla*. Inter-annual and inter-island variation in δ^{13}C and δ^{15}N signatures (mean ± SE) in red blood cells of least auklets breeding on the Pribilof Islands, St. Paul I. (shelf) and St. George I. (shelf-break), in 2003 to 2005 and 2008 to 2009; and the Aleutian Islands (ocean basin), Buldir I. and Kasatochi I., in 2003 to 2005. As predicted, δ^{13}C signatures were enriched in birds breeding on the shelf compared to birds breeding in the ocean basin and shelf-break

retreat was observed on St. Paul I. ($r = -0.27$, $p = 0.044$) whereas an increase was observed on St. George I. ($r = -0.31$, $p = 0.032$).

There was no inter-island difference in corticosterone (Table 3, Fig. 3), and there was a significant positive relationship between corticosterone and the summer PDO index (Table 3, Fig. 3), indicating that on both islands, corticosterone levels were higher during years with warmer sea-surface temperatures. There was no overall effect of IRI on corticosterone, but birds breeding on St. Paul I. and St. George I. were affected differently (Table 3). Birds on St. Paul I. had highest corticosterone levels during years with early ice retreat ($r = -0.44$, $p < 0.001$); birds on St. George I. were not affected by ice conditions ($r = -0.08$, $p = 0.485$).

Table 3. *Aethia pusilla.* The effects of the island, Ice Retreat Index (IRI) and summer Pacific Decadal Oscillation (PDO) on average annual proportion of *Neocalanus* in the diet, baseline corticosterone levels in the blood plasma, and δ^{13}C in red blood cells of least auklets breeding on St. Paul I. (shelf) and St. George I. (shelf-break), Pribilof Islands, in 2003 to 2005 and 2008 to 2009. Statistically significant relationships ($p < 0.05$) are in bold

	Effect df	*F*	Error df	p	Parameter estimate (95% CI)
Neocalanus					
Island	1	37.61	237	**<0.001**	−132.36 (−160.79, −103.93)
Summer PDO	1	91.24	237	**<0.001**	−26.66 (−40.35, −12.97)
IRI	1	0.97	237	0.326	−1.29 (−1.95, −0.64)
Island × Summer PDO	1	61.12	237	**<0.001**	−20.05 (−38.73, −1.37)
Island × IRI	1	39.15	237	**<0.001**	3.16 (2.16, 4.15)
δ^{13}C					
Island	1	89.15	99	**<0.001**	2.09 (1.67, 2.51)
Summer PDO	1	0.22	99	0.637	0.49 (0.23, 0.75)
IRI	1	0.31	99	0.582	0.02 (0.01, 0.03)
Island × Summer PDO	1	2.13	99	0.148	−1.01 (−1.38, −0.64)
Island × IRI	1	37.51	99	**<0.001**	−0.04 (−0.06, −0.03)
Corticosterone					
Island	1	1.75	168	0.188	0.21 (0.04, 0.38)
Summer PDO	1	36.36	168	**<0.001**	0.15 (0.05, 0.25)
IRI	1	<0.01	168	0.994	<0.01 (<0.01, 0.01)
Island × Summer PDO	1	3.53	168	0.062	−0.01 (−0.14, 0.11)
Island × IRI	1	6.38	168	**0.012**	−0.01 (−0.01, <−0.01)

Seasonal comparisons

Seasonal shifts in the diet composition were more pronounced during the warm compared to cold years (Table 4). A shift from calanoid copepods to other zooplankton species in the diet occurred in the warm years during mid-July of 2004 and 2005 on St. Paul I., and in late July of 2003 on St. George I. Oceanic *Neocalanus* copepods were present in the diets of birds on St. George I. during all years but were only present in the diets of birds on St. Paul I. during years with late ice retreat, and they remained the dominant prey species during the cold years 2008 and 2009 but not in the warm year 2004.

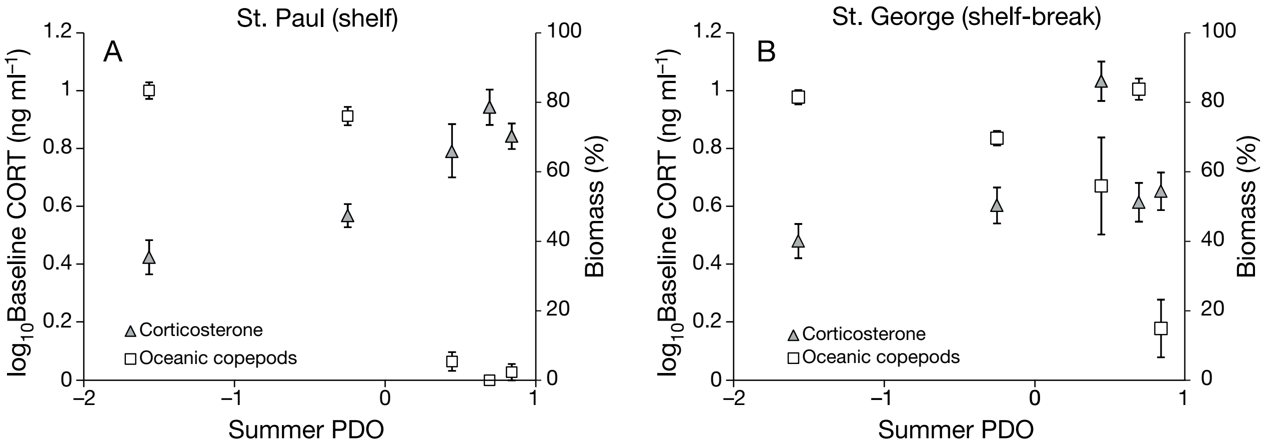

Fig. 3. *Aethia pusilla*. Relationship between summer Pacific Decadal Oscillation (PDO) and annual baseline corticosterone levels (CORT; mean ± SE) in the blood plasma and the proportion of oceanic copepods *Neocalanus* spp. (mean ± SE) in the diets of least auklets breeding on (A) St. Paul I. (shelf) and (B) St. George I. (shelf-break), Pribilof Islands, in 2003 to 2005 and 2008 to 2009. Corticosterone levels were similar between the islands and were higher during warm years (positive PDO)

Table 4. *Aethia pusilla.* Percentage biomass (mean ± SE) of oceanic copepods *Neocalanus* spp., shelf copepod *Calanus marshallae* and other zooplankton prey in regurgitated chick meals of least auklets breeding on St. Paul I. (shelf) and St. George I. (shelf-break), Pribilof Islands, in 2003 to 2005 and 2008 to 2009

Year	Species	St. Paul				St. George			
		29 Jun to 10 Jul	11 Jul to 18 Jul	19 Jul to 27 Jul	28 Jul to 12 Aug	29 Jun to 10 Jul	11 Jul to 18 Jul	19 Jul Jul to 27 Jul	28 Jul to 12 Aug
2003	Oceanic copepods	10.3 ± 5.9		3.4 ± 3.4	0	93.0 ± 2.0	84.2 ± 9.6		14.9 ± 8.3
	Shelf copepods	4.2 ± 4.0		0.5 ± 0.5	0	0	0		3.7 ± 3.0
	Other zooplankton	85.5 ± 7.2		96.1 ± 3.4	100	7.0 ± 2.0	15.8 ± 9.6		81.4 ± 9.1
2004	Oceanic copepods	81.4 ± 2.2		6.2 ± 3.0	0	67.7 ± 6.5		55.9 ± 14.0	
	Shelf copepods	0		1.8 ± 1.5	0	0		0	
	Other zooplankton	18.6 ± 2.2		92.1 ± 3.7	100	32.3 ± 6.5		44.1 ± 14.0	
2005	Oceanic copepods	0		0		84.3 ± 3.0	88.4 ± 2.3	76.4 ± 6.7	89.4 ± 2.9
	Shelf copepods	59.5 ± 16.0		0.6 ± 0.6		0.4 ± 0.2	0	0	0
	Other zooplankton	40.5 ± 16.0		99.4 ± 0.6		15.3 ± 3.0	11.6 ± 2.3	23.6 ± 6.7	10.6 ± 2.9
2008	Oceanic copepods		82.0 ± 5.3	81.1 ± 4.5	87.6 ± 1.6		84.6 ± 2.0	72.4 ± 4.1	88.1 ± 1.5
	Shelf copepods		3.7 ± 1.9	4.2 ± 3.1	3.3 ± 1.2		0.6 ± 0.3	0.3 ± 0.1	0.4 ± 0.1
	Other zooplankton		14.2 ± 3.6	14.6 ± 2.8	9.2 ± 1.2		14.9 ± 2.0	27.2 ± 4.1	11.4 ± 1.5
2009	Oceanic copepods		74.4 ± 4.2	72.1 ± 3.6	91.0 ± 4.0		68.2 ± 2.5		70.9 ± 3.3
	Shelf copepods		5.3 ± 1.7	6.8 ± 1.6	0.2 ± 0.1		13.2 ± 2.2		16.6 ± 3.4
	Other zooplankton		20.3 ± 4.1	21.1 ± 3.6	8.8 ± 3.9		18.6 ± 2.9		12.4 ± 1.3

Table 5. *Aethia pusilla.* Seasonal changes in δ^{13}C values (mean ± SE) in red blood cells of least auklets breeding on St. Paul I. (shelf) and St. George I. (shelf-break), Pribilof Islands, in 2003 to 2005 and 2008 to 2009. r: Pearson correlation coefficient between isotope and day of year; statistically significant relationships ($p < 0.05$) are indicated in **bold**

Year	δ^{13}C				Slope	r (95% CI)
	2 Jun to 21 Jun	28 Jun to 14 Jul	19 Jul to 30 Jul	2 Aug to 12 Aug		
St. Paul						
2003	−19.5 ± 0.11	−18.0 ± 0.13			0.042	**0.85 (0.73, 0.93)**
2004	−18.9 ± 0.09	−19.2 ± 0.07	−19.3 ± 0.03		−0.008	**−0.39 (−0.12, −0.61)**
2005	−19.4 ± 0.20	−18.3 ± 0.11	−18.5 ± 0.12		0.027	**0.65 (0.29, 0.85)**
2008		−17.5 ± 0.12	−17.8 ± 0.12	−18.5 ± 0.05	−0.024	**−0.83 (−0.93, −0.62)**
2009		−17.6 ± 0.07	−18.0 ± 0.12	−19.2 ± 0.07	−0.058	**−0.91 (−0.95, −0.81)**
	2 Jun to 21 Jun	3 Jul	13 Jul to 14 Jul	2 Aug to 12 Aug		
St. George						
2003		−21.3 ± 0.10	−21.3 ± 0.08	−19.3 ± 0.07	0.055	**0.92 (0.81, 0.97)**
2004	−20.1 ± 0.05	−19.5 ± 0.11	−19.8 ± 0.04		0.007	**0.39 (−0.05, 0.71)**
2005	−20.4 ± 0.08	−19.3 ± 0.05	−19.5 ± 0.08		0.022	0.82 (0.60, 0.92)
2008		−19.7 ± 0.09	−20.0 ± 0.04	−20.0 ± 0.08	−0.010	**−0.59 (−0.82, −0.20)**
2009		−18.3 ± 0.13	−18.6 ± 0.07	−19.2 ± 0.07	−0.031	**−0.82 (−0.91, −0.65)**

Seasonal dynamics of δ^{13}C were similar between auklets on the 2 islands in 2003 and 2005 (Island × Date interaction term: 2003: $F_{1,51} = 3.11$, $p = 0.084$; 2005: $F_{1,37} = 0.33$, $p = 0.567$) but not in 2004, 2008 and 2009 (Island × Date interaction term: 2004: $F_{1,64} = 9.15$, $p = 0.004$; 2008: $F_{1,37} = 7.16$, $p = 0.011$; 2009: $F_{1,56} = 17.27$, $p < 0.001$). However, the relationships between δ^{13}C were similar between the islands and were strongly influenced by summer PDO and IRI (Table 5, Fig. 4). During warm years (positive PDO and early ice retreat), δ^{13}C values generally increased or remained stable over the season, while they decreased during the cold years (negative PDO and late ice retreat).

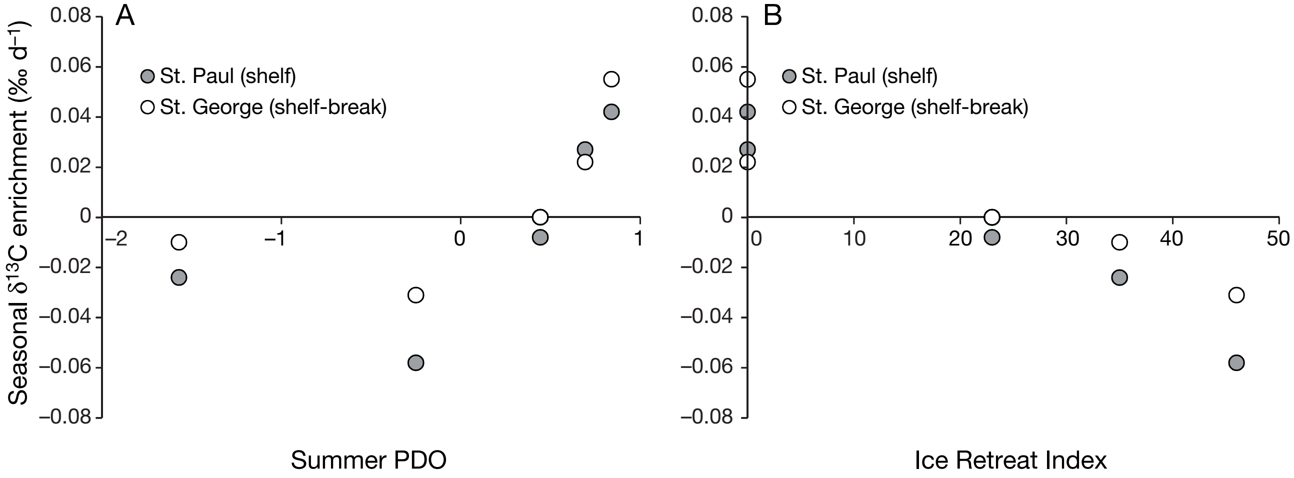

Fig. 4. *Aethia pusilla*. Relationship between the summer (A) Pacific Decadal Oscillation (PDO) and (B) Ice Retreat Index and the seasonal changes in δ^{13}C values in red blood cells of least auklets breeding on St. Paul I. (shelf) and St. George I. (shelf-break), Pribilof Islands, in 2003 to 2005 and 2008 to 2009. Seasonal changes in the δ^{13}C values are indicated by the slope (seasonal isotope enrichment) of the regression between the δ^{13}C and sampling date for each island and for each year

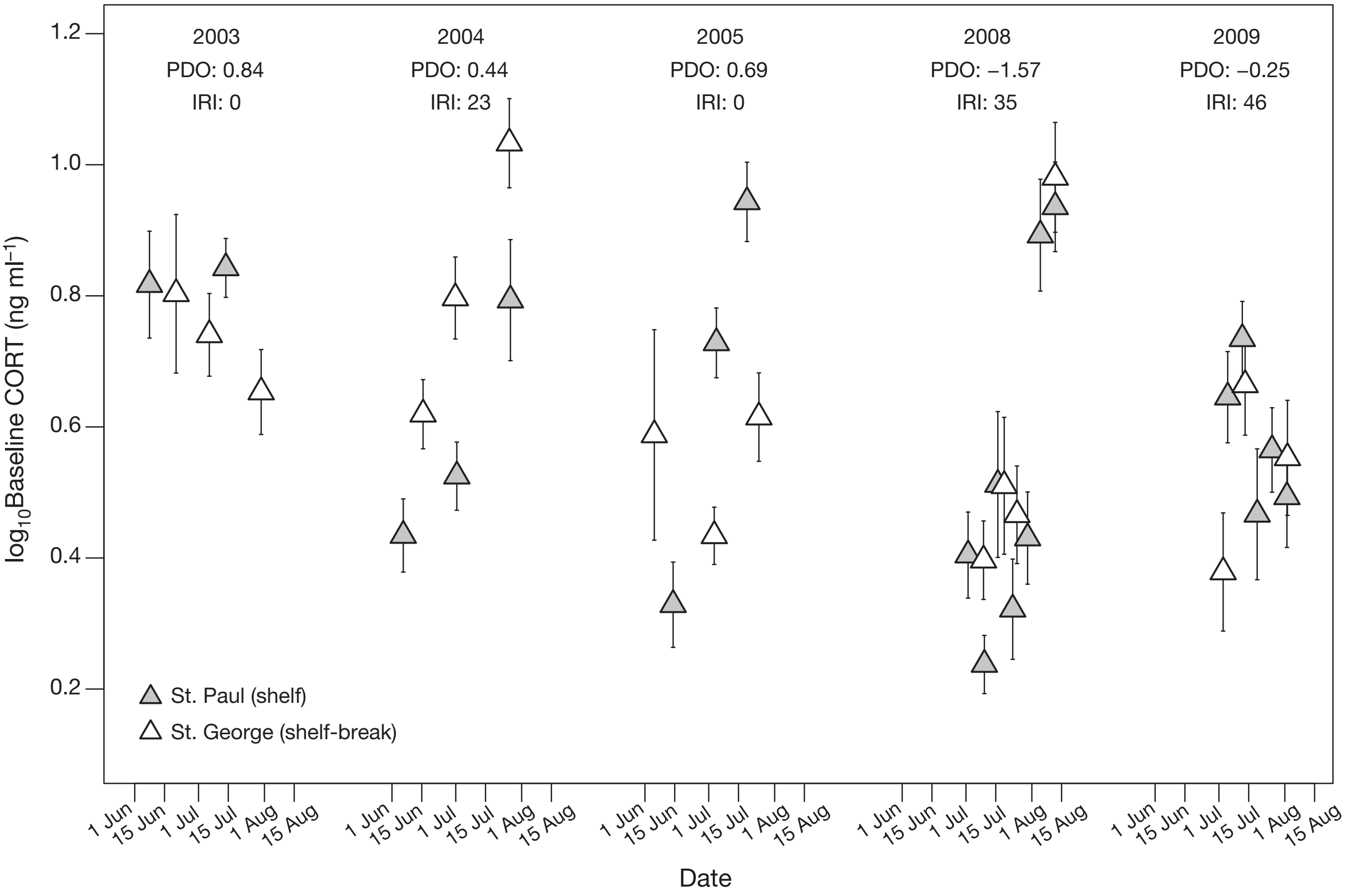

Fig. 5. *Aethia pusilla*. Seasonal changes of baseline corticosterone levels (CORT; mean ± SE) in the blood plasma of least auklets breeding on St. Paul I. (shelf) and St. George I. (shelf-break), Pribilof Islands, in 2003 to 2005 and 2008 to 2009. The summer Pacific Decadal Oscillation (PDO) and Ice Retreat Index (IRI) values are shown for each year. Seasonal dynamics of corticosterone varied among years, but was similar between the islands in 2003, 2004 and 2008

Corticosterone levels increased during the breeding season, with the exception of 2003 and 2009. Seasonal dynamics in baseline levels of corticosterone were similar between auklets on the 2 islands in 2003, 2004 and 2008 (Island × Date interaction term: 2003: $F_{1,70} = 1.07$, $p = 0.304$; 2004: $F_{1,83} = 1.81$, $p = 0.182$; 2008: $F_{1,102} = 0.14$, $p = 0.710$; Fig. 5) but not in 2005 and 2009 (Island × Date interaction term: 2005: $F_{1,73} = 14.39$, $p < 0.001$; 2009: $F_{1,78} = 4.16$, $p = 0.045$; Fig. 5).

DISCUSSION

Inter-annual climate variability affects temporal dynamics in food availability

In this study we used a 2-pronged approach to examine the effects of climate variability on the food availability to planktivores in one of the most productive marine areas, the Green Belt in the southeastern Bering Sea. Diet compositions and stable-isotope signatures of auklets' red blood cells indicated differences in zooplankton prey and foraging areas between birds breeding on St. Paul and St. George Islands. Despite these differences, inter-annual dynamics of corticosterone levels in the blood plasma were similar between the islands. Similar to long-term observations in other seabird species (Buck et al. 2007, Kitaysky et al. 2007, 2010, Shultz & Kitaysky 2008, we did not observe a consistent pattern (increase or decrease) in corticosterone levels between incubation and chick-rearing. Thus, variations in corticosterone levels in least auklets do not reflect changes of the energetic demands of the birds between reproductive stages, but rather reflect changes in food availability.

As we predicted, we found that food availability (as reflected in corticosterone values) was lower during the warm (positive PDO) compared to cold (negative PDO) years on both St. Paul I. and St. George I. However, the timing of ice-retreat only had a large effect on auklets breeding on St. Paul I., with higher food availability (as reflected in corticosterone values) during years with late ice retreat. This inconsistency of auklet responses to the timing of ice retreat between the islands might be explained by the fact that summer PDO and IRI were changing in parallel during all years except from 2004. Birds on St. George I. had their highest levels of corticosterone levels in 2004, which had a late timing of ice retreat but later developed into a warm year with a high summer PDO. This illustrates that for a cold regime to support high levels of food resources to planktivores, both a late ice retreat and sustained cold water temperatures throughout the summer are needed.

The observed difference in corticosterone levels between cold and warm regimes is likely to affect the birds differently. High levels of nutritional stress reduce reproductive success and survival of adult seabirds, which might have immediate impact on population dynamics (Buck et al. 2007, Kitaysky et al. 2007, 2010). Disappearance of lipid-rich oceanic copepods from the diets can also impose severe nutritional limitations on growing auklet chicks (Springer et al. 1986, Roby 1991, Gall et al. 2006), which could increase their post-fledging mortality (Kitaysky et al. 2003, 2006). Thus, mediated by the physiological effects of nutritional stress, a warming climate is likely to have a negative impact on planktivores in the productive Green Belt area of the southeastern Bering Sea, as observed in other areas of the North Pacific (Kitaysky & Golubova 2000, Sydeman et al. 2006, Hipfner 2008, Bond et al. 2011).

Spatial and temporal heterogeneity of zooplankton communities

The differences in diet composition and use of foraging areas (indicated in carbon stable isotope signatures of their blood) between least auklets breeding on St. Paul I. and St. George I. supported our predictions and reflected the proximity of the respective colony to the continental shelf break. Our findings on the effects of climate on diet composition were also in line with our predictions. During the warm years, 2003 to 2005, birds breeding on St. Paul I. (shelf area) switched diets from lipid-rich copepods to zooplankton with lower lipid content (Springer et al. 2007), whereas oceanic copepods dominated the diets of birds breeding on St. George I. (shelf-break area). In contrast, *Neocalanus* copepods dominated the diets on both islands during cold years. As we expected, red blood cells of birds breeding on St. Paul I. (situated in the continental shelf region) were enriched in $\delta^{13}C$ values compared to birds breeding on St. George I. (shelf-break) and on the Aleutian Islands (ocean basin) (Fig. 2). The enriched $\delta^{13}C$ values observed in birds breeding on St. Paul I. reflect a diet originating in the shelf ecosystem (Hobson et al. 1994, Schell et al. 1998) and hereafter will be referred to as $\delta^{13}C$ shelf signatures.

Contrary to our predictions, the inter-island difference in $\delta^{13}C$ signatures was not more pronounced during warm years, and we did not find a clear interannual effect of climate on $\delta^{13}C$. However, interestingly we found that the $\delta^{13}C$ shelf signatures were still evident in the red blood cells of birds breeding on St. Paul I. in 2008 and 2009 when oceanic *Neocalanus* copepods dominated their diets. The mismatch between oceanic *Neocalanus* copepods in least auklet chick meals and the $\delta^{13}C$ shelf signature in the red blood cells of adults could have resulted from a change in the location, and therefore isotope signatures, of *Neocalanus* copepods. Oceanic *Neocalanus* copepods, though originating in the ocean basin, would have obtained enriched $\delta^{13}C$ signatures typical of the shelf ecosystem if they relied on the shelf foodweb for foraging (Schell et al. 1998). The $\delta^{13}C$ signatures of *Neocalanus* copepods collected in different regions of the southeastern Bering Sea in mid-July of 2008 suggest that this is likely. For example, the $\delta^{13}C$ signatures of *Neocalanus* copepods sampled in close proximity to St. Paul I. ($\delta^{13}C$ = −18.16‰ and −18.30‰ for *N. cristatus* and *N. flemingerei*, respectively) were higher compared to *Neocalanus* spp. collected in shelf-break areas ($\delta^{13}C$ = −20.33‰ and −21.16‰ for *N. cristatus* and *N. flemingerei*, respectively), which resembled isotope signatures of open-ocean foraging auklets (Fig. 1) (A. Pinchuk unpubl. data). Least auklets were observed to be foraging in close proximity to the respective islands in 2008 (K. Kuletz pers. comm.) and in previous years (Obst et al. 1995). Alternatively, the mismatch between oceanic *Neocalanus* copepods in least auklet chick meals and the enriched $\delta^{13}C$ signature in the red blood cells of adults could reflect a difference between adult and chick diets. For example, common guillemots *Uria aalge* that carry a single prey item to their chicks have been observed to feed on low quality prey themselves while feeding their chick with high quality prey (Wilson et al. 2004). However, Bédard (1969) found no differences between adult and chick diets in the least auklet. Therefore, it seems more likely that oceanic copepods near St. Paul I. were part of the shelf food web, and during cold years they obtained stronger shelf $\delta^{13}C$ signatures by having a longer retention time on the shelf, either by an earlier advection on the shelf or by having a longer lifespan on the shelf compared to warm years.

Possible mechanisms driving temporal dynamics in food availability

Our results on auklet responses to climate variability in the Green Belt are in line with the OCH; during warm years zooplankton availability to planktivorous predators is lower compared to cold years. The OCH predicts that during cold years with late ice retreat, an early ice-associated phytoplankton bloom sustains a high abundance of meso-zooplankton, the food source of planktivorous predators. In contrast, during warm years with early ice retreat, a delayed open-water phytoplankton bloom is not sufficient to sustain a high biomass of meso-zooplankton and, in turn, determines a low availability of prey to planktivorous predators (Hunt et al. 2008, 2011, Coyle et al. 2011). However, these predictions of the OCH are specific for meso-zooplankton species originating in the middle shelf domain (such as *Calanus marshallae*), while for the least auklets and most likely other planktivorous predators in the Green Belt, the summer biomass of oceanic *Neocalanus* copepods advected onto the continental shelf is probably more critical. Additionally, the OCH predicts enhanced phytoplankton production on the shelf during cold years and the possibility of a secondary bloom when mixing is sufficient; whereas during warm years, higher water temperatures increase stratification of the water column and prevent any mixing, leading to nutrient depletion (Hunt et al. 2002, 2008). During cold years, the *Neocalanus* copepods advected on the shelf are well supported by an enhanced productivity of the shelf ecosystem; whereas during warm years, the *Neocalanus* copepods advected on the shelf are probably severely food-limited and may experience high mortality due to starvation (Coyle et al. 2008). Thus *Neocalanus* copepods are dependent on the shelf productivity. Nevertheless, the proportion of large oceanic copepods in least auklet diets was only positively related to the timing of sea ice retreat and negatively related to the summer PDO for birds breeding on St. Paul I., and not on St. George I. Although this difference between colonies is to be expected, with zooplankton on the shelf being more reliant on the processes occurring on the shelf compared to zooplankton at the shelf-break, the effects of summer PDO on food availability (as reflected in corticosterone levels) were similar between St. Paul I. and St. George I. Thus, although the OCH is still applicable for predicting the effects of climate variability on the Green Belt ecosystem, the timing of winter ice retreat and summer sea surface temperatures alone are insufficient to explain changes of prey availability to planktivorous predators in the region.

Two scenarios have been proposed to affect copepod abundance during ‘warm’ and ‘cold’ years: (1)

In the North Pacific, increased sea-surface temperatures are associated with earlier ontogenetic migration of *Neocalanus plumchrus* to depth and/or increased mortality of later cohorts (Mackas et al. 1998, 2007), making them unavailable to planktivorous seabirds (Hipfner 2008). For auklets, which rely on a predictable copepod biomass peak for feeding their young, timing of the different stages of the *Neocalanus* life cycle determines the temporal overlap between copepod biomass peak and the energetic demands of the breeding season (Hipfner 2008). A recent shift towards an earlier occurrence of CV-copepodite stages in *Neocalanus* spp. was also observed in the Bering Sea shelf in the late 1990s, as compared to the early 1980s (Napp et al. 2002), and Coyle et al. (2008) suggested that increased mortality due to food limitation may have caused a decline in the abundance of shelf copepods on the shelf during warm years. However, the disappearance of *Neocalanus* copepods from the diets on St. Paul I. during the warm years of 2003 to 2005 cannot be fully explained by their early ontogenetic migration or increased mortality during warm years. *Neocalanus* were still available to auklets on St. George I. and yet birds on both colonies experienced similar high stress levels during these warm years. Thus, changes in the timing of *Neocalanus* life cycle and increased *Neocalanus* mortality cannot be the only mechanism affecting availability of food to planktivores in the Green Belt.

(2) In the Pribilof Domain, changes in the physical oceanographic conditions might affect *Neocalanus* copepod distribution, displacing them outside the foraging realm of least auklets (Springer et al. 2007). In the warm year of 2004, food availability declined on St. Paul I. in response to the movement of copepod-depleted shelf water into the Pribilof Domain (Coyle et al. 2008, Hunt et al. 2008, Stabeno et al. 2008), and a concurrent food shortage was observed in birds on St. George I. (Benowitz-Fredericks et al. 2008). These observations suggest a parallel response of auklets breeding on both islands to a major change in physical oceanography that affected the entire Pribilof Domain. The arrival of copepod-depleted shelf waters into the Pribilof Domain probably occurs on a regular basis during warm years, as evidenced in the seasonal enrichment of birds' $\delta^{13}C$ signatures in 2003 and 2005 indicative of foraging in shelf waters. In contrast, during the cold years of 2008 to 2009, $\delta^{13}C$ values gradually declined during the season, suggesting that there was a continuous influx of oceanic water into the Pribilof Domain. It has been suggested that the direction of major currents may change between warm and cold years on the middle shelf domain, however, little is known about how it would affect inflow of oceanic water masses into the Pribilof Domain and other parts of the Green Belt (Stabeno et al. 2008). Our results suggest that the inflow of oceanic water masses is stronger during cold years and that during warm years the inflow might be prevented by the expansion of shelf water increasing the strength of the front between oceanic and shelf water masses. Thus, besides the effects of climate on phytoplankton productivity on the shelf and its subsequent effect on *Neocalanus* mortality, the dynamic interactions of the oceanic and shelf water masses on the continental shelf are likely to be the main factors governing availability of zooplankton to planktivores in the Green Belt.

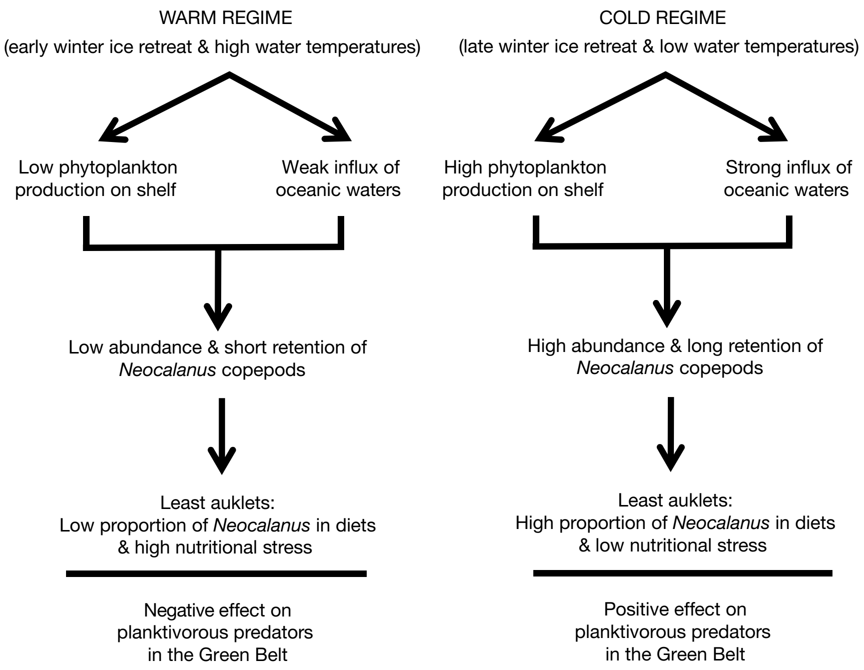

Fig. 6. Flow diagram showing our predictions about how climate affects planktivorous predators in the Green Belt of the Bering Sea. Climate-induced changes in physical forcing will negatively affect planktivores by altering the availability of their main food source, *Neocalanus* copepods, during warm years (see 'Conclusions' for details)

CONCLUSIONS

The present study adds to the growing understanding of seabird responses to climate variability and change. We can use our data to generate basic predictions about the effects of warming climate on planktivorous predators in the Green Belt of the Bering Sea through bottom-up processes, which might be applicable to other continental shelf regions with seasonal ice cover (Fig. 6). During a warm regime the phytoplankton bloom on the shelf is limited, and the influx of oceanic water onto the shelf is weak. This results in low abundance and short retention time of oceanic *Neocalanus* copepods on the shelf. Decreasing availability of *Neocalanus* copepods increases nutritional stress in planktivorous predators and will thus negatively affect them. In contrast, during cold regimes the phytoplankton bloom on the shelf is strong, and retention time of *Neocalanus* copepods on the shelf is long. High abundance of *Neocalanus* copepods results in low nutritional stress levels of planktivorous predators and more favorable conditions. Testing this hypothesis will require an integrated study of seasonal water movements in the region while simultaneously monitoring changes in zooplankton communities and food availability of planktivorous predators.

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Contribution to the Theme Section 'Seabirds and climate change'

Linking climate variability, productivity and stress to demography in a long-lived seabird

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ABSTRACT: We examined the reproductive ecology of black-legged kittiwakes *Rissa tridactyla* in several breeding colonies in the North Pacific to test if inter-annual changes in the Pacific Decadal Oscillation (PDO), Winter Ice Cover (ICI), or local sea-surface temperature (SST) predict changes in productivity (fledglings per nest) or nutritional stress (corticosterone). We explored the implications of the observed variation in productivity and stress for projected population dynamics based on a previously demonstrated corticosterone–survival relationship. Although productivity was highly variable (0 to 0.9 fledglings nest^{-1}), the relationships between productivity and environmental indices were weak, with local SST providing slightly more explanatory power than PDO or ICI, suggesting that local factors rather than large-scale climate variability may determine variation in productivity. The relationships between stress and environmental indices were stronger than the relationship between productivity and environment. The measured response of stress to environment showed opposite signs between the southern and northern colonies, and typically implied annual mortality rates varying from 11 to 17%. The observed relationships between climate and stress indicate that anticipated warming might bring at least short-term demographic benefits for kittiwakes in the Bering shelf region, while having negative impacts on birds breeding in the Gulf of Alaska and western Aleutians. We predict decline (without immigration) for colonies with the lowest productivity and conclude that climate variability is likely to affect survival of North Pacific kittiwakes on a region-specific basis. Longevity of these birds may not always be sufficient to buffer their populations from low reproductive performance.

KEY WORDS: Demographic consequence · Corticosterone · Kittiwake · Survival · Food availability · Colony

INTRODUCTION

Predicting the effects of changing climate on populations of marine top predators is a major challenge in ecology. Despite substantial work linking seabird demography to climate variability (Jenouvrier et al. 2005, Frederiksen et al. 2007, Sandvik & Erikstad 2008, Wolf et al. 2009, Oro et al. 2010, Barbraud et al. 2011), we are still very limited in our ability to make generalizations. Seabird responses vary on a location-specific basis (i.e. Gaston et al. 2005, Irons et al. 2008, Shultz et al. 2009), which may reflect different tradeoffs between survival and reproduction being favored in different locations (Coulson 2002). However, characterizing the regional variability of demographic responses to changing environments is difficult because of the intensive, long-term study typically needed to characterize demography and, in particular, adult survival.

The most comprehensive and conclusive studies of seabird demography at the colony level must involve long-term collection of information on both fecundity

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and survival of individuals. However, such study is logistically feasible at only a small number of colonies. In addition, the representativeness of small-scale studies for assessing the regional effects of climate on a seabird population is unclear. Long-term information on survival is lacking for many regions of great economic or ecological importance, and limited resources make it unlikely that intensive, long-term studies will be initiated. The dual requirements for intensive, long-term study (generally requiring focusing on 1 or a few sites) to estimate demographic rates and for integrating information on the localized responses of multiple colonies spread out over space thus present a major challenge to overcome (Brown et al. 2011), and an alternate approach that does not require such intensive demographic study may be needed to develop an understanding at the regional scale.

Physiological measurements, and in particular stress hormones with known correlations with food supply and survival (e.g. Romero & Wikelski 2001, Brown et al. 2005, Blas et al. 2007, Kitaysky et al. 2010, Satterthwaite et al. 2010), provide a practical alternative for assessing likely population dynamics in data-limited systems. Using black-legged kittiwakes *Rissa tridactyla* in the North Pacific as a model system, we examined the relationship between climate variability and demographic performance by leveraging recent advances in measuring seabird nutritional stress (as reflected in secretion of corticosterone, hereafter CORT) and its relation to demographic rates (Kitaysky et al. 2010, Satterthwaite et al. 2010).

Major climate changes have been observed in the northern Pacific over the last few decades (Springer 1998, Anderson & Piatt 1999, Hunt et al. 2002, 2008). Coincident with these changes, piscivorous seabirds declined in the continental shelf areas of the central and southeastern Bering Sea (Springer 1998, Hunt & Byrd 1999, Hunt et al. 2002, Byrd et al. 2008a). On the other hand, several colonies in the Aleutian Archipelago increased in size (e.g. Renner & Williams 2005), suggesting that climate variability might have differential effects on birds breeding in different regions of the North Pacific. This set of colonies allows the examination of relationships between environmental changes and population processes (reproduction and survival) to understand how seabird populations respond to climate change. Survival has not been directly measured in most of these colonies (except Cook Inlet in the late 1990s; Piatt 2004), but long-term measures of nutritional stress are available (Kitaysky et al. 2010, their appendix), and a link between corticosterone and mortality has been established (Kitaysky et al. 2010, Satterthwaite et al. 2010).

In the present paper, we tested the hypothesis that major climatic indices and local measures of sea-surface temperature (SST) can predict productivity and CORT levels (and thus inferred food stress and adult mortality risk) for multiple black-legged kittiwake colonies in the Gulf of Alaska (GOA), Aleutian Archipelago, and southeastern Bering Sea regions. Seabird reproductive performance, survival, and CORT levels have previously been linked to local variation in food availability and SST (Kitaysky et al. 2007, 2010, Shultz et al. 2009), but our study addressed these links on a larger geographic scale (i.e. Aleutians and Bering Sea) and incorporated large-scale climatic indices in addition to local variation in SST. In the northern Pacific, broad-scale indices of climate such as the Pacific Decadal Oscillation (Mantua et al. 1997) and the extent of winter ice cover in the Bering Sea (Overland & Stabeno 2004) encompass ocean–atmospheric patterns of short-term (interannual) and long-term (decadal) climate variability. These indices provide a measure of whether years are relatively warm or cold, and are strong predictors of ecological processes (Hare & Mantua 2000, Hunt et al. 2002, Mueter & Litzow 2008). Knape & de Valpine (2011) suggested that local rather than regional climate measures could provide better predictions, and Shultz et al. (2009) linked highly localized measures of SST to lay dates and resultant reproductive success in Cook Inlet; thus, we explored the predictive power of local SST as well.

To explore the potential for location-dependence of climate effects, we investigated whether linkages between environmental indices and bird performance are similar across regions. Location-specific responses to climate (e.g. Gaston et al. 2005, Frederiksen et al. 2007) have the potential to complicate predicting effects of climate change (Brown et al. 2011), so we explored relationships between the environment and demographic performance for multiple colonies separated by as much as 2000 km.

We also assessed the relative impacts of predicted changes in productivity and stress in the different colonies by building demographic models based on measured productivity and inferred (from CORT) survival in the different colonies to project colony performance in the future. As with other demographic models, we emphasized relative over absolute predictions (Beissinger & Westphal 1998, Brook et al. 2000). Unifying productivity and survival measurements into a single demographic model provides important insight into the importance of observed variation in fecundity and stress for population performance. Although the sensitivity of the population growth rate to adult survival is well appreciated for long-lived species (Morris et al. 2008), it is known that the demographic parameters with the highest sensitivities are often the least variable (Pfister 1998). In long-lived seabirds, 'prudent parent' behavior (Cam et al. 1998) may result in little observed variation in adult survival. Since the impacts of changing vital rates on demography depend on their sensitivity and magnitude of variation (Wisdom et al. 2000), the realized importance of variation in productivity may be higher than expected.

Thus, our study provides a unified framework for assessing the impacts of local and regional environmental variability on both predicted survival and reproduction in multiple seabird colonies. By analyzing multiple colonies, we could assess the generality of relationships identified in specific locations. By incorporating estimates of reproduction and survival into a unified demographic model, we were able to assess the likely effects of observed variation on colony performance and long-term viability. This allows inferences to be made about the projected performance of each colony, and the likely response of colonies in each region to projected climate change.

MATERIALS AND METHODS

Study system

Black-legged kittiwakes *Rissa tridactyla* are long-lived (Hatch et al. 1993, Golet et al. 1998, Piatt 2004) and generally lay 2 eggs clutch^{-1}. Data were collected on population sizes, productivity, and stress hormone levels for black-legged kittiwakes breeding in 6 colonies in the North Pacific region (Fig. 1). Duck Island and Gull Island are located in Cook Inlet in the GOA, ~100 km apart, with Duck Island surrounded by warm estuarine waters, and Gull Island by cooler oceanic water (Piatt et al. 2002, Kitaysky et al. 2010). Saint Paul and Saint George (Pribilof Islands) are located in the Bering Sea; the distance between the islands is ~60 km, with St. George near (25 km) the edge of the Bering Sea shelf (Byrd et al. 2008a). Bogoslof Island is in the central Aleutians, and Buldir Island is in the western Aleutians; both are surrounded by deep ocean water (Shultz & Kitaysky 2008).

Environmental metrics

We used environmental metrics describing SST and the extent of winter sea ice cover to predict variation in seabird productivity and stress. Data were obtained from the National Oceanic and Atmospheric Administration (NOAA; detailed descriptions of the parameters can be found at www.beringclimate.noaa.gov/). For a basin-scale summary of SSTs, we obtained summer Pacific Decadal Oscillation values (PDOs, which integrate SSTs in the North Pacific in June, July and August; Mantua et al. 1997) from www.beringclimate.noaa.gov/. We obtained Ice Cover Index values (ICI, which represent the ice concentration from January 1 to May 31 over the area between 56°N, 163°W and 58°N, 165°W; Overland & Stabeno 2004) from the National Snow and Ice Data Center (NSIDC), available at www.beringclimate.noaa.gov/. We obtained estimates of SST from the Extended Reconstructed Sea-Surface Temperature dataset (ERSST 3b; Smith et al. 2008) at www.ncdc.noaa.gov/ersst/, using ERSST for the 2° block including each colony, with data available through December 2008. Measuring temperature over 2° of latitude and longitude results in an area of approximately 200 km on each side, which is similar to the foraging range of kittiwakes (e.g. 59 km range and 165 km trip length reported by Kotzerka et al. [2010], foraging trips from the Pribilofs may be even longer, Paredes et al. [unpubl. data]). We averaged together March to May SSTs for a spring estimate representative of pre-laying conditions and from June to August for a summer estimate representative of the rearing season. We selected each of these indices on the basis of an *a priori* mechanistic hypothesis (e.g. Hunt et al. 2002, 2011). For example, SST during the breeding season provides a measure of current environmental conditions (e.g. stratification of the water column during the summer, which might affect vertical fish distribution), on either a local (SST) or regional

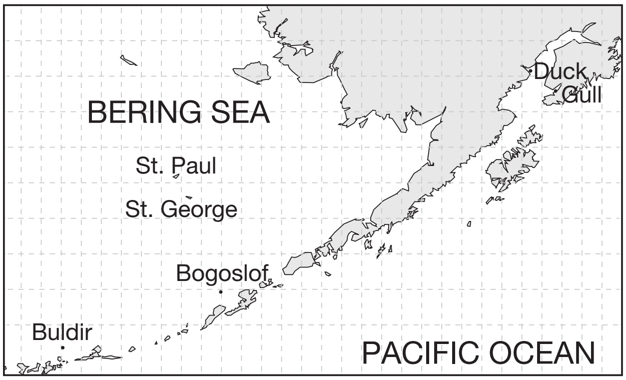

Fig. 1. Study region. This map was generated using a rectangular projection, grid lines equal 1° of latitude or longitude. Each degree of latitude corresponds to ~111 km, while each degree of longitude corresponds to ~71 km at the southern border of the map or 52 km at the northern border

(PDOs) scale. The extent of winter sea ice cover is related to the formation of a cold pool and associated effects on biogeography and the transition between arctic and subarctic community characteristics (Mueter & Litzow 2008). The Oscillating Control Hypothesis (Hunt et al. 2002, 2011) proposes that the timing of phytoplankton production is affected by the timing of ice retreat, and the timing of bloom affects phytoplankton availability to zooplankton and thus food availability for fish and competition between seabirds and other piscivores.

Productivity and count data

We estimated productivity and relative population size based on counts made in reference plots reported in United States Fish and Wildlife Service (USFWS) refuge reports and other data sources (McClintock et al. 2010 for Saint Paul; Shannon et al. 2010 for Saint George [productivity data were collected as described in Kitaysky et al. 2010 for Duck and Gull Island, with counts for both islands and productivity for Gull Island from Piatt et al. 2002]; Renner & Williams 2005 for Bogoslof [with an update for 2008 productivity from J. Williams pers. comm.]; Freeman et al. 2010 for Buldir). We standardized these reference counts (but not productivity values) relative to the maximum reference count observed for each colony. For all colonies except Bogoslof, the productivity index used was chicks fledged per nest. For Bogoslof, the productivity index was calculated from the number of chicks per nest late in the rearing season, but before actual fledging. This may slightly overestimate how many chicks actually fledged. For the Pribilof islands, we excluded data from before 1984 due to changes in sampling methods, a break in the data, and a lack of ICI data for the earliest years.

Measures of stress

We collected measurements of baseline CORT from a variable number of birds in each colony each year (Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m454p221_supp.pdf; not every colony was sampled every year). Collection and measurement of CORT in all colonies followed the same procedures as previously reported by Kitaysky et al. (2010). We used baseline CORT since it reflects current food availability (Kitaysky et al. 2010) and is a predictor of apparent survival of kittiwakes (Satterthwaite et al. 2010).

Statistical analyses

We examined the relationship between each environmental index and mean productivity and mean CORT at each location for each year. We used information theoretic techniques to distinguish whether it was better supported statistically to estimate parameters for all colonies independently or to estimate shared parameters for colonies within one or more regions (see 'Colony-scale versus regional responses'). When analyzing time series data, temporal autocorrelation leads to non-independence of samples (Pyper & Peterman 1998, Brown et al. 2011). Thus, we performed generalized least squares models (GLS; Pinheiro & Bates 2000) assuming autoregressive order 1 errors within each location, implemented via the 'nlme' package in R (R Development Core Team 2009, Pinheiro et al. 2010). We modeled each performance metric (productivity and CORT) as a function of location, environmental metric, and their interaction. We used Akaike's information criterion (AIC; Burnham & Anderson 2002) to compare model formulations where location was the set of individual colonies or to compare various combinations where colonies within regions were combined. To summarize patterns of common or divergent responses, we also calculated correlations among islands in productivity and CORT, using the techniques of Pyper & Peterman (1998) to account for autocorrelation when assessing significance.

We transformed all environmental metrics to *z*-scores (so they had a mean of 0 and a SD of 1) to directly compare the sensitivity of performance metrics (productivity, stress) to the observed range of variation in each environmental measure. To obtain normally distributed error values, we performed the empirical logit transform (Warton & Hui 2011) on productivity and log-transformed CORT. Because the performance metrics are measured on different scales with different transformations, their sensitivities cannot be directly compared.

We explored the extent to which CORT can predict productivity by running a GLS model with logit productivity as the response variable and location, log CORT, and their interaction as independent variables, defining locations as in the best model for productivity as identified above.

Estimating adult survival from stress data

We estimated overall survival for colonies or years as the means of the survival predicted for each individual sampled in that colony or year using the model of Satterthwaite et al. (2010). This is an empirically derived relationship between CORT and mortality based on long-term resighting data of birds first marked and sampled for CORT in 1996 to 1999 on Duck and Gull Islands in Cook Inlet, GOA. Specifically, the estimated probability of mortality over the next year for a bird with a baseline CORT measurement of x (ng ml^{-1}) is:

$$m(x) = \frac{e^{-2.399 + 0.0803x}}{1 + e^{-2.399 + 0.0803x}}$$

Demographic model

We generated estimates of expected lifetime reproductive success for each colony under mean conditions as follows. We estimated reproductive lifespan as the inverse of adult mortality rate (Bókony et al. 2009), yielding the expected number of reproductive events in an individual's lifetime. We estimated annual mortality based on the expected value corresponding to the mean of annual mean CORT measures in each colony. Since our estimates of survival varied across years, we explored the range of lifespans implied by the lowest and highest annual survival estimates. To calculate expected lifetime reproductive output (chicks fledged), we multiplied this expected number of reproductive events by mean productivity. To yield an estimate of the population growth rate, we multiplied expected lifetime reproductive output by 0.5 times the expected survival from a fledged chick to first reproduction (to account for only females laying eggs), inferred from the literature as 0.57 (Suryan et al. 2000). If the resulting value (R_0) is <1, we predict populations will decline if conditions remain similar through time, $R_0 = 1$ implies stability and $R_0 > 1$ implies population growth. This is equivalent to a lifetable analysis defining l_x (survival from newborn [fledging] to age x and m_x (fecundity at age x, in terms of newborn females where newborn is defined as a fledged chick) estimating R_0 as $\Sigma l_x m_x$.

Uncertainty in demographic projections

There are 4 major sources of uncertainty in our demographic projections. (1) The first source of uncertainty is whether the relationship between CORT and survival in the multiple colonies in the present study is the same as in the Cook Inlet colonies used to parameterize the survival probability in Satterthwaite et al. (2010) or whether survival from fledging to first reproduction is the same as that Suryan et al. (2000) reported for a colony in Prince William Sound, GOA, eastern North Pacific. In the absence of long-term mark-recapture studies in all of the colonies under consideration, we cannot directly quantify our uncertainty for how consistent the CORT–survival relationship is across colonies. However, Satterthwaite et al. (2010) present support for a consistent relative, if not absolute, effect of CORT on survival at multiple locations. This was based on the 2 Cook Inlet colonies, which are separated by ~100 km. We might expect more variation in the relationship at larger scales; however, the surrounding oceanography is quite different for Duck Island (warm estuarine waters) and Gull Island (colder oceanic waters), and they differ substantially in productivity (Kitaysky et al. 2010), so the CORT–survival relationship appears robust to differences in geography and biology.

(2) The effect of annual variability, which typically decreases realized long-term demographic performance relative to that expected from the mean value (Morris & Doak 2002). Adequately characterizing the effects of yearly variability on demographic performance requires many years of data on the full life cycle (Morris & Doak 2002); however, unless the strength of stochastic effects vary substantially among colonies, this should not greatly affect comparisons of relative performance.

(3) The bias in estimates of survival. We might overestimate mortality due to negative effects of blood draw to measure CORT (Brown & Brown 2009). We have only limited data to directly assess the effects of blood draw; however, in 1998, 114 birds had blood drawn, 15 of which were never resighted, while 42 birds were banded but had no blood drawn, 3 of which were never resighted (J. F. Piatt et al. unpubl. data for the Cook Inlet colonies). While a higher fraction of birds with blood drawn were never resighted, this difference is not statistically significant ($\chi^2 = 1.09$, $p = 0.30$). Thus, we cannot rule out a small deleterious effect of blood draw, but do not see strong evidence for it. We drew a maximum of 1 ml of blood (often less), or 0.25% by mass for a typical 400 g kittiwake. This is unlikely to have major effects on survival (Sheldon et al. 2008). In addition, Satterthwaite et al. (2010) assumed that most failures to detect a bird that was still alive reflected skipped reproduction rather than failing to detect a bird present in the colony. Mortality was therefore estimated as the probability of dying before returning to the colony rather than on a strictly annual basis, which may overestimate

the annual mortality rate (see Satterthwaite et al. 2010 for fuller discussion of this issue and the rationale behind the approach chosen).

(4) Limited sample size creates uncertainty about mean productivity, mean CORT, and the parameterization of the CORT–survival relationship. In Supplement 2 at www.int-res.com/articles/suppl/m454p221_supp.pdf, we present a calculation of Bayesian credible intervals on our estimates of R_0 that incorporates uncertainty due to sample size. However, as we cannot directly quantify our other sources of uncertainty, we emphasize that the estimated R_0 values are more useful for making comparisons among colonies than predictions of absolute performance. These credible intervals were calculated via Markov Chain Monte Carlo sampling implemented using the MCMCpack library (Martin et al. 2011) of R (R Development Core Team 2009).

RESULTS

Colony-scale versus regional responses

The relationship between CORT and any environmental metric was best described at the regional scale for Cook Inlet and Pribilof colonies of *Rissa tridactyla*, while it was best described for the Buldir and Bogoslof colonies independently (Table 1a). CORT was strongly, significantly, and positively correlated between the 2 Pribilof colonies and the 2 Cook Inlet colonies. Correlations between more distant colonies were generally weak or negative (Table 2). Productivity was best described at the individual-colony level for Bogoslof, Buldir, Duck, and Gull Islands separately, but together for both Pribilof colonies (Table 1b). Productivities on the Pribilofs (St. Paul and St. George) were highly and significantly correlated (Table 3). Productivities among other colonies showed some signs of synchrony, but no other correlations were significant after accounting for autocorrelation.

Productivity

Using the best-supported location set of Bogoslof, Buldir, Duck, Gull, and Pribilofs, a GLS model of logit productivity as a function of PDOs (*z*-score), location, and their interaction revealed a significant effect of location ($p < 0.001$), but, despite the high variation in productivity (0 to 0.9; Fig. 2), there was no significant effect of PDOs or its interaction with location ($p > 0.86$). Results were similarly non-significant for ICI ($p > 0.18$) and summer SST ($p > 0.10$) and marginally significant for spring SST (p =

Table 1. *Rissa tridactyla*. ΔAIC (Akaike's information criterion) scores for different resolutions of location effects (colony versus regional groupings) for generalized least squares (GLS) models of performance metrics: (a) log CORT (corticosterone) and (b) logit productivity) as functions of location, environmental index, and their interactions. The best model for a particular response variable has ΔAIC = 0, models with ΔAIC < 2 receive comparable support, and models with ΔAIC > 4 receive considerably less support. PDO: Pacific Decadal Oscillation; ICI: ice cover index; SST: sea-surface temperature

Location groupings	PDOs	ICI	SST spring	SST summer
(a) Log CORT response to environmental metrics				
All colonies independently	15.50	11.21	6.91	6.64
Pribilofs + remaining colonies	7.50	5.23	3.31	4.16
Cook Inlet + remaining colonies	7.94	6.64	4.12	3.23
Aleutians + remaining colonies	16.61	15.58	12.06	13.53
Cook Inlet + Pribilofs + remaining colonies	**0.00**	**0.00**	**0.00**	**0.00**
Cook Inlet + Aleutians + remaining colonies	9.14	10.77	9.16	9.96
Pribilofs + Aleutians + remaining colonies	8.62	9.47	8.50	10.90
Pribilofs + Cook Inlet + Aleutians	1.20	4.14	5.17	6.86
(b) Logit productivity response to environmental metrics				
All colonies independently	3.52	3.15	1.33	3.52
Pribilofs + remaining colonies	**0.00**	**0.00**	**0.00**	**0.00**
Cook Inlet + remaining colonies	20.97	23.37	21.59	20.97
Aleutians + remaining colonies	23.20	26.06	22.60	23.20
Cook Inlet + Pribilofs + remaining colonies	18.22	21.05	20.86	18.22
Cook Inlet + Aleutians + remaining colonies	31.55	34.73	33.51	31.55
Pribilofs + Aleutians + remaining colonies	20.70	24.06	21.95	20.70
Pribilofs + Cook Inlet + Aleutians	29.49	33.26	33.29	29.49

0.051 for effect of spring SST, interaction with location non-significant at p = 0.80). Examination of model parameter estimates (Table 4) shows that productivities were especially high on Bogoslof and especially low on Buldir, Duck, and (to a lesser extent) the Pribilofs. Warmer temperatures appeared to increase productivity on Bogoslof and the Pribilofs, while decreasing it on Buldir and Duck, although the SEs associated with these estimates were high, and thus inferences about environmental effects are uncertain.

Table 2. *Rissa tridactyla*. (a) Correlations and (b) significance after correcting for autocorrelation (n values in parentheses) between annual mean CORT on pairs of colonies. na: too few years in common to estimate correlation after accounting for autocorrelation; **bold**: statistically significant correlations

	Buldir	St. George	St. Paul	Duck	Gull
(a) Correlation					
Bogoslof	na	−0.557	−0.499	0.113	na
Buldir	1.000	na	na	na	na
St. George		1.000	**0.954**	na	na
St. Paul			1.000	0.127	na
Duck				1.000	**0.943**
Gull					1.000
(b) p-values					
Bogoslof	na (1)	0.329 (5)	0.254 (7)	0.928 (3)	na (2)
Buldir		na (2)	na (2)	na (0)	na (0)
St. George			**0.029 (6)**	na (1)	na (1)
St. Paul				0.954 (7)	na (2)
Duck					**0.007 (6)**

Table 3. *Rissa tridactyla*. (a) Correlations and (b) significance after correcting for autocorrelation (n values given in parentheses, along with sample sizes) between annual productivity on pairs of colonies. na: too few years in common to estimate correlation after accounting for autocorrelation; **bold**: statistically significant correlations

	Buldir	St. George	St. Paul	Duck	Gull
(a) Correlation					
Bogoslof	0.469	0.324	0.414	na	na
Buldir	1.000	0.439	0.328	−0.213	0.438
St. George		1.000	**0.896**	−0.375	0.498
St. Paul			1.000	−0.364	0.564
Duck				1.000	−0.810
Gull					1.000
(b) p-values					
Bogoslof	0.178 (11)	0.379 (11)	0.275 (10)	na (3)	na (3)
Buldir		0.093 (22)	0.216 (21)	0.686 (6)	0.385 (6)
St. George			**0.001 (25)**	0.464 (6)	0.315 (6)
St. Paul				0.479 (6)	0.244 (6)
Duck					0.131 (6)

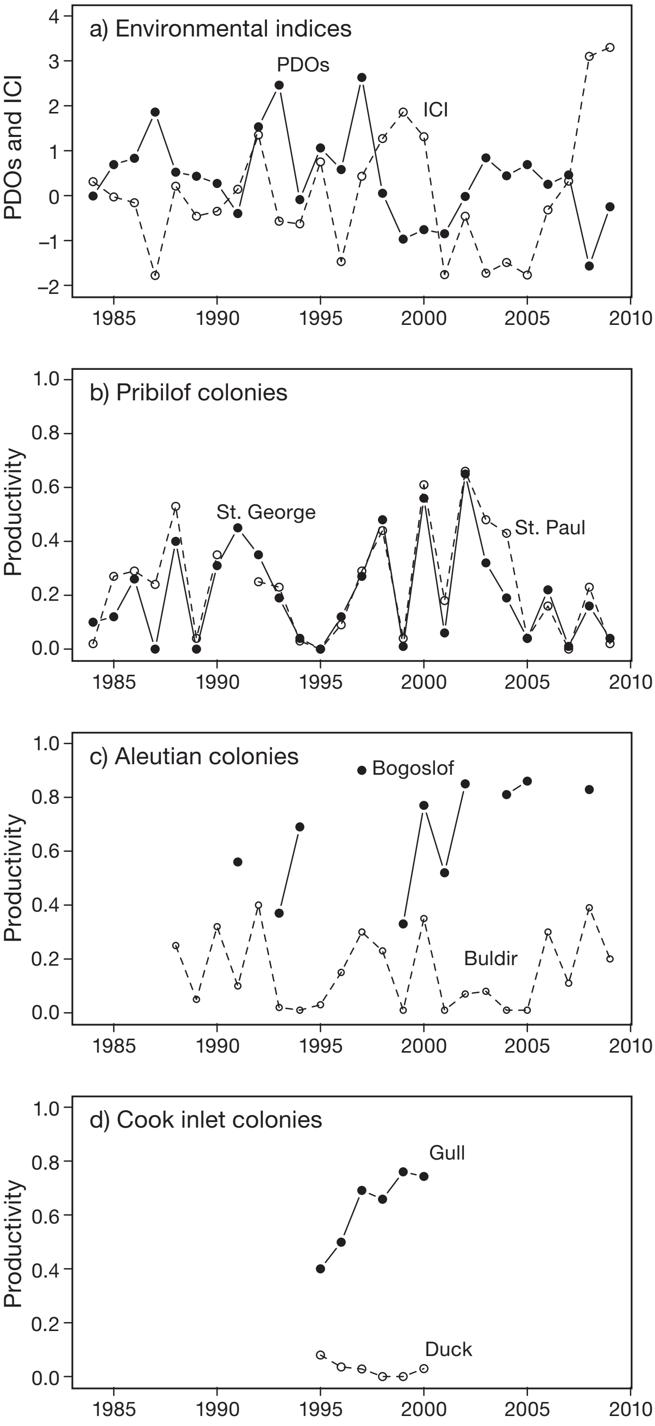

Fig. 2. *Rissa tridactyla*. Environmental conditions (a) as measured by PDO values (Pacific Decadal Oscillation; summer sea-surface temperature, more positive is warmer; solid line) and ICI (ice cover index; extent of winter ice cover, more positive means more ice; dashed line) matched up with productivity for (b) Pribilof colonies (●, St. George; ○, St. Paul), (c) Aleutian colonies (●, Bogoslof; ○, Buldir), and (d) Cook Inlet colonies (●, Gull; ○, Duck). For simplicity, sea-surface temperature is not shown as separate trajectories would be required for each location and season

Table 4. *Rissa tridactyla*. Parameter estimates for the GLS model of productivity as a function of location, spring sea-surface temperature (SST), and their interaction. Reported intercept values are the predicted means ± SE (logit scale) of productivity at the mean value of SST spring, while the reported slope values are the slope of the relationship between logit productivity and *z*-score-transformed SST spring. The last column gives colony means (at mean SST spring) back-transformed to the linear scale for intercept parameters or the back-transformed range predicted when the environmental index is 1 SD below or above its long-term mean for slope parameters

	Mean ± SE (logit)	Mean or range (linear)
Bogoslof at mean SST spring	0.933 ± 0.395	0.708
Buldir at mean SST spring	−2.140 ± 0.534	0.095
Duck at mean SST spring	−2.871 ± 1.540	0.044
Gull at mean SST spring	0.542 ± 1.540	0.622
Pribilofs at mean SST spring	−0.730 ± 0.756	0.315
Bogoslof response to SST spring	0.549 ± 1.289	0.585–0.805
Buldir response to SST spring	−0.365 ± 1.855	0.135–0.065
Duck response to SST spring	−0.612 ± 1.849	0.085–0.020
Gull response to SST spring	0.052 ± 1.849	0.610–0.634
Pribilofs response to SST spring	0.858 ± 1.407	0.160–0.522

Stress

For the best-supported location set of Cook Inlet, Pribilofs, Buldir, and Bogoslof, GLS models of CORT as a function of location, environmental index, and their interactions revealed significant difference among locations and significant location-dependent effects for PDOs (location: $p < 0.0001$; PDOs: $p = 0.0001$; interaction: $p = 0.0005$) and a location-dependent effect of ICI (ICI: $p = 0.65$; interaction: $p = 0.013$), but revealed no significant effect of spring SST (spring SST: $p = 0.18$; interaction: $p = 0.19$) and only a marginally significant effect of summer SST (summer SST: $p = 0.28$; interaction: $p = 0.09$). Stress was highest in Buldir and the Cook Inlet colonies. In general, warmer conditions decreased stress in the Pribilofs and increased stress in Bogoslof and Cook Inlet (Table 5, Fig. 3). The more frequent occurrence of statistically significant relationships for CORT as opposed to productivity arose despite larger sample sizes for productivity.

Relationship between stress and productivity

Productivity appeared to decrease with increasing log CORT (linear regression $R^2 = 0.10$, $p = 0.04$; Fig. 4); however, CORT also varied by colony, making it unclear whether location or CORT was driving variation in productivity. Logit productivity varied significantly among locations ($p = 0.025$ in GLS, treating Pribilof colonies as a single region), but the effects of log CORT ($p = 0.18$) and its interaction with location ($p = 0.80$) were not significant.

Counts and population trends

Byrd et al. (2008a) analyzed population trends on the Pribilofs from 1975 to 2005, finding evidence for stable populations

Table 5. *Rissa tridactyla*. Parameter estimates for the GLS model of corticosterone (CORT) as a function of location, (a) Pacific Decadal Oscillations (PDOs) or (b) ice cover index (ICI), and their interactions. Reported intercept values are the predicted means (logit scale) of productivity at the mean value of environmental state, while the reported slope values are the slope of the relationship between logit productivity and *z*-score-transformed environmental condition. The second-to-last column gives colony means (at mean environmental condition) of CORT back-transformed to the linear scale for intercept parameters or the back-transformed range predicted when the environmental index is 1 SD below or above its long-term mean for slope parameters. The last column gives estimated mortality probabilities corresponding to those CORT values. Note: Buldir had data from only 2 yr, both of which were warmer than average, so we do not present its estimated parameters

	Mean ± SE (log)	Mean or range (linear)	Corresponding mortality
(a) PDOs			
Bogoslof at mean PDOs	1.562 ± 0.122	4.77	0.12
Cook at mean PDOs	2.146 ± 0.135	8.55	0.15
Pribilofs at mean PDOs	1.558 ± 0.140	4.75	0.12
Bogoslof response to PDOs	0.254 ± 0.353	3.70–6.14	0.11–0.13
Cook response to PDOs	0.227 ± 0.136	6.82–10.73	0.14–0.18
Pribilofs response to PDOs	−0.204 ± 0.149	5.82–3.87	0.13–0.11
(b) ICI			
Bogoslof at mean ICI	1.406 ± 0.196	4.08	0.11
Cook at mean ICI	2.154 ± 0.237	8.62	0.15
Pribilofs at mean ICI	1.637 ± 0.237	5.14	0.12
Bogoslof response to ICI	−0.075 ± 0.085	4.40–3.79	0.11–0.11
Cook response to ICI	−0.153 ± 0.119	10.05–7.40	0.17–0.14
Pribilofs response to ICI	0.124 ± 0.102	4.54–5.82	0.12–0.13

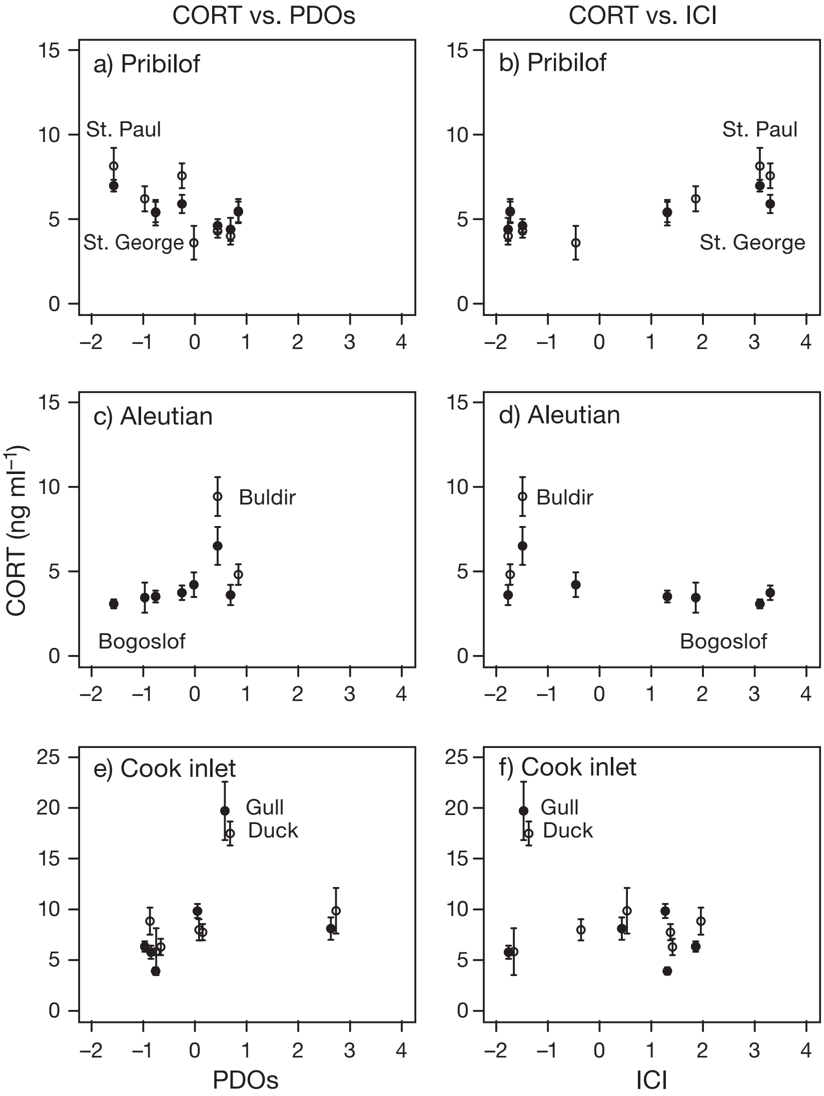

Fig. 3. *Rissa tridactyla*. The relationship between environmental conditions as measured by (a,c,e) PDO values (Pacific Decadal Oscillation; summer sea-surface temperature, more positive is warmer) and (b,d,f) ICI (ice cover index; extent of winter ice cover, more positive means more ice) matched up with mean baseline values of corticosterone (CORT) for (a,b) Pribilof colonies (●, St. George; ○, St. Paul), (c,d) Aleutian colonies (●, Bogoslof; ○, Buldir), and (e,f) Cook Inlet colonies (●, Gull; ○, Duck). Note that for (e) and (f) the *y*-axis scale is different, and Duck Island environmental index values are dithered slightly to the right to avoid overlap. Error bars represent ±1 SE. For simplicity, sea-surface temperature is not shown since separate trajectories would be required for each location and season

on St. George and a decrease followed by a slow increase on St. Paul. Both colonies had slightly higher numbers in 2008 compared to 2005 (Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m454p221_supp.pdf). Although only 3 counts are available for Bogoslof, numbers appear to have more than doubled between 2000 and 2005. No recent counts were available for Duck or Gull Island, but black-legged kittiwakes have declined from the mid-1970s through 2000 on Duck Island, while populations on Gull Island were stable through the 1990s, following an earlier increase (Piatt 2004, his Fig. 14.9; see also Fig. S1 in Supplement 1). Counts on Buldir show a significant downward trend (log abundance decreasing by 0.027 yr^{-1}, linear regression of logged counts, $R^2 = 0.63$, $p = 0.001$).

Population projections

Table 6 summarizes the estimated mean annual adult mortality, the corresponding expected number of reproductive bouts, mean productivity, and resultant calculation of R_0, along with 95 % credible intervals for each colony. Note that these are colony-specific means, with means taken over all years for which data were available; thus, they do not always match the predicted value at mean environmental state for the full time series over which environmental data are available (cf. Tables 4 & 5). Estimated survival values were similar (within 1 %), as were most productivity values, but the productivity predicted at mean SST is higher than the observed mean for the Pribilofs (0.315 versus 0.206 or 0.237) despite nearly complete data (Fig. 2b) due to non-linearity introduced by the logit transformation. We therefore calculated R_0 based on observed means. Credible intervals on R_0 are entirely >1.0, corresponding to growing populations, for Bogoslof and Gull Islands. Credible intervals on R_0 are entirely <1.0, predicting declining populations, for Buldir, St. George, and Duck Island. Fig. 5 illustrates the contributions of varying mortality and varying productivity to the observed range of variation in R_0. Changes in mortality from 11 to 17 % are not trivial, corresponding to the minimum required productivity for a stable population increasing from 0.39 to 0.60 as mortality increases. However, even the upper range of observed mean mortalities can be compensated for with productivity well within the observed range of varia-

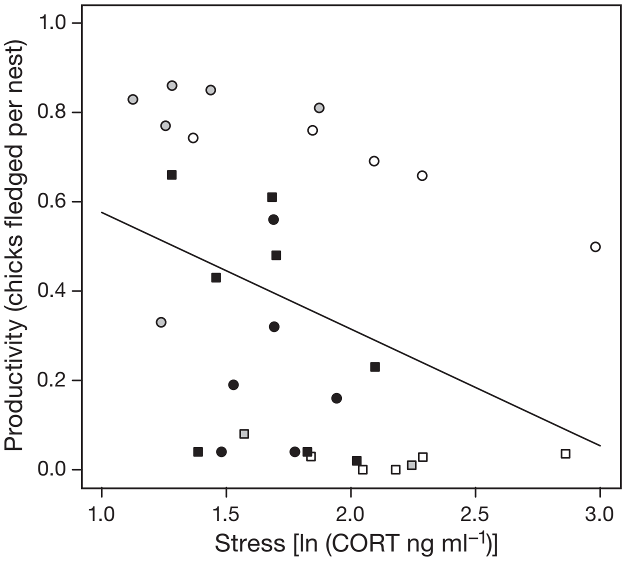

Fig. 4. *Rissa tridactyla*. Relationship between stress (natural log of corticosterone [CORT], ng ml^{-1}) and productivity (chicks fledged nest^{-1}). Black symbols = Pribilof colonies (●, St. George; ■, St. Paul); grey symbols = Aleutian colonies (◉, Bogoslof; ▣, Buldir); and open symbols = Cook Inlet (Gulf of Alaska) colonies (○, Gull; □, Duck). The best fit linear regression (pooling colonies) is indicated by a continuous line

tion, and indeed the 2 colonies with the highest calculated R_0 include both the highest (Gull Island) and lowest (Bogoslof) predicted mortality. In contrast, the worst performing colonies are characterized by low productivities, with means at or below 0.2. As Fig. 5 illustrates, a productivity of 0.2 could only be sustained by an annual mortality <6%, while a productivity of 0.1 could only be sustained by annual mortality <3%.

Table 6. *Rissa tridactyla*. Demographic parameters and projected performance of each colony. Vital rates are annual means calculated for each colony. Calculations of R_0 assume a 1:1 sex ratio and survival from fledging to first reproduction of 0.57 (see 'Materials and methods—Demographic model'); 95% credible intervals (CI) on R_0 were calculated as described in Supplement 2 at www.int-res.com/articles/suppl/m454p221_supp.pdf

Colony	Mortality (%)	Reproductive events	Productivity	R_0	95% CI
Bogoslof	11.3	8.98	0.681	1.74	1.01–3.50
Buldir	13.9	7.22	0.155	0.32	0.18–0.65
St. George	12.3	8.11	0.206	0.48	0.24–0.97
St. Paul	12.4	8.03	0.237	0.54	0.28–1.08
Duck	15.9	6.28	0.029	0.05	0.02–0.36
Gull	15.7	6.37	0.625	1.13	1.03–5.30

DISCUSSION

Adequately characterizing links between environmental conditions and the performance of organisms is a challenging task. Thus, it is perhaps not surprising that even though productivity of *Rissa tridactyla* was highly variable, we found weak relations between productivity and large-scale climate indices or local SSTs. Multiple factors may have competing effects that vary in strength across years, the response to any given factor may not be linear (Piatt et al. 2007, Wolf & Mangel 2008), and responses may be in different directions in different locations. Local SST did not provide a better predictor of stress than did regional environmental indices, and only provided marginally better predictors of productivity. This may reflect the large foraging range of kittiwakes, the importance of regional processes in driving local food availability, and/or complex associations of multiple fine-scale variables that, if not directly identifiable, can be better captured by regional indices (Hallett et al. 2004). More localized measures of SST may provide increased predictive power (Shultz et al. 2009).

Nevertheless, patterns emerged from our analysis. (1) Overall relationships between environmental conditions and nutritional stress (as reflected in CORT) were stronger than relationships between environmental conditions and productivity. This is evidenced by both more significant relationships identified in GLS models and through correlations between adjacent islands in CORT being higher than correlations in productivity (Table 2 vs. Table 3). This suggests that large-scale climate variability is associated with variation in the physiological stress levels kittiwakes incur during reproduction. The southern colonies (western Aleutians and Cook Inlet) incurred less physiological stress during cold years (low PDO and high ICI), while the opposite was observed for the Pribilofs. Because CORT secretion is a reliable proxy for food in seabirds (Kitaysky et al. 2010), this suggests climate change may affect their food resources in opposite ways in different regions of the North Pacific.

(2) We see that climate variability (and future climate change) does not affect all locations equally, based on the lack of strong relationships between climate indices and productivity or stress for the GOA colonies and differential responses between Aleutian and Pribilof colonies

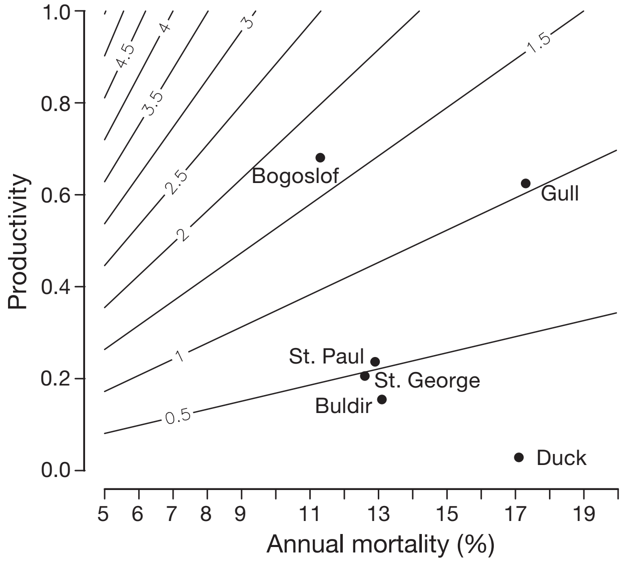

Fig. 5. *Rissa tridactyla*. R_0 predicted for various combinations of annual adult mortality (%) and productivity (chicks fledged per year). ● = annual mean mortality and productivity of each colony; contours = predicted population growth

within the Bering Sea. Similar location-specific relationships between climate and seabird performance have been observed in other systems (Gaston et al. 2005, Frederiksen et al. 2007). The differential response of different regions to climate change complicates the interpretation of which colonies are doing well and which are doing poorly. For example, overall Bogoslof hosts a higher performing colony than the Pribilofs, but in some years the Pribilof colonies may do better. In 2004 both Pribilof colonies had a lower mean CORT than Bogoslof, counter to the usual pattern.

(3) In addition, we often found correlations between performance metrics on adjacent islands (stress in the Pribilofs and Cook Inlet colonies were highly correlated between adjacent islands but not across regions, as were productivities in the Pribilofs). Correlations were lower among the Aleutian colonies, but they are much more widely separated (~1000 km) than those among the colonies at the Pribilofs (60 km) or Duck and Gull Islands (100 km). This suggests that large-scale climate variability affects food resources on a regional basis, but does not explain variation in productivity of kittiwakes. Colony-specific drivers are not clear: potential drivers include factors as diverse as predation pressure, the quality or age of breeding individuals and their ability or willingness to buffer chicks from food shortages, and small-scale variations in prey community composition.

Effects of warming

A correlative study such as ours is unable to pinpoint explicit mechanisms, but it does identify the heterogeneity of the kittiwake responses to environmental variability in the North Pacific regions, and makes testable predictions on how different colonies may respond to warming. Warm years for the Bering Sea (increased PDOs, decreased ICI) are associated with decreased CORT in the Pribilofs. Decreased CORT corresponds to less food stress (Kitaysky et al. 2010) and an increased probability of adult survival (Satterthwaite et al. 2010). For example, estimated mortality rates (ranging between 11 and 17 %) on the Pribilofs were lowest during warm (high PDO and low ICI) compared to those during cold (low PDO and high ICI) years. Therefore, we suggest that, at least short term, warming could benefit kittiwakes in the Pribilofs as long as it does not negatively affect productivity. Of course, long-term warming may lead to complicated feedbacks throughout the food web and potentially to radically different results (Hunt et al. 2002). In addition, strengths and even signs of correlations between demography and putative environmental drivers may change over time and in different climatic regimes (Springer 1998). Indeed, Byrd et al. (2008b) reported a positive relationship between ice cover and productivity of Pribilof kittiwakes, suggesting warming could have a negative effect on productivity. We estimate a negative relationship between winter ice cover and productivity on the Pribilofs. This might partially reflect the use of different metrics for winter ice conditions, but our dataset included more recent years (especially 2008 and 2009) of both high ice cover and low productivity, whereas we excluded data before 1984, which included years of late ice retreat and high productivity.

Demographic projections

Our analyses suggest likely declines for Buldir and Duck Island and potential declines of both Pribilof colonies if current environmental conditions persist (noting, as per Fig. 2, that conditions in the North Pacific have been cold lately) and immigrants do not compensate for low survival and productivity. Given the potential biases in our survival estimates, it is not clear whether immigration is necessary to explain near-stability of the colonies (Fig. S1 in Supplement 1). Our predictions of the worst performance for Buldir and Duck and the best performance for Bogoslof and Gull are borne out by recent population trends (Fig. S1).

Our calculations of R_0 rely on the assumption that the CORT–mortality relationship derived for kittiwakes in Cook Inlet (Satterthwaite et al. 2010) applies to other colonies and that the survival to first reproduction measured by Suryan et al. (2000) in the GOA applies to other parts of Alaska. It may be that the CORT–survival relationship varies among colonies; however, Satterthwaite et al. (2010) found little support for an interaction between CORT and colony in predicting survival, suggesting a similar form to the relationship across islands. We have no data on how survival from fledging to first reproduction varies among colonies, but, if anything, we suspect it should be lower for colonies where chick survival is lower, suggesting young are in worse condition before departing the colony. Quantitative estimates of R_0 should thus be interpreted with caution, but our conclusions about how survival tracks environmental variation are likely more robust, and the large differences in R_0 between colonies from different regions are likely good measures of their relative health and are corroborated by other evidence (e.g. increase in the Bogoslof and declines in the Buldir and Duck colonies). Thus, a demographic modeling approach based on measures of CORT and productivity may not suffice to make precise predictions of population growth rate, but does appear able to successfully predict relative performance. This is a realistic and valuable goal for applied demographic models (Beissinger & Westphal 1998, Brook et al. 2000).

Life-history considerations

None of our population projections incorporate the effects of skipping reproduction entirely in times of poor environmental conditions. While skipped reproduction would *a priori* be expected to reduce population growth rates, it may not if skipping is adaptive behavior (Cam et al. 1998). Then we would expect birds to skip only when skipping carries a survival benefit (relative to breeding) such that lifetime reproductive output is expected to increase as a result. Indeed, Lanctot et al. (2003) found that kittiwakes with high CORT failed to lay eggs, and Goutte et al. (2010) found that female kittiwakes with higher CORT were more likely to skip, suggesting the most stressed birds are the most likely to skip reproduction and by doing so reducing their realized stress and mortality risk. Thus, overall survival may be higher than that estimated just for the subset of birds persisting in breeding despite harsh conditions (and sampled for CORT in our study), representing better long-term prospects for apparently declining colonies. Potential adaptive skipping might also explain the mismatch between demographic projections and recent stability in numbers in the Pribilof colonies.

Despite the importance of survival to the demography of long-lived birds, it appears to be higher productivity that is fueling the higher growth rate of the Bogoslof versus Pribilof colonies and Gull versus Duck. Our estimates of survival based on CORT varied from 68 to 89%, although most values were at the high end of this range, with estimated survival always >80%, except for the Cook Inlet colonies in 1996. Other studies of Pacific black-legged kittiwakes have typically reported lower mortality (10 to 17% on Gull Island and 1 to 7% on Chisik [Duck] [Piatt 2004]; 6 to 9% on Middleton Island [Hatch et al. 1993]; 10.2% with chicks or 4.7% without in Shoup Bay [Golet et al. 1998]), so we may be underestimating adult survival. However, adult survival would have to be quite high to compensate for the low productivity on Buldir and the Pribilofs, and even higher for the near-zero productivities observed at Duck Island. At just 0.11 female chicks fledged per reproductive attempt (long-term mean for the Pribilofs), even if birds experienced 81% survival from fledging to first reproduction (much higher than the 57% estimated by Suryan et al. [2000] and corresponding to 95% annual survival for 4 yr as a juvenile), over 11 reproductive attempts would be required for an expected R_0 of 1.0. This corresponds to an adult survival of 91% annually. Using Suryan et al.'s (2000) estimate of 57% survival from fledging to first reproduction, stability would require almost 16 reproductive events or almost 94% annual survival. For Duck Island, Piatt (2004) reported near 99% survival from 1997 to 1998; however, with 95% confidence intervals for that year extending down to almost 70% that estimate seems unreliable. Estimated survival for the remaining years was near 93%, corresponding to an R_0 of 0.12 given 14.3 reproductive events, 0.57 survival from chick to fledging, and mean reproductive output of 0.0145 female chicks per bout.

Conclusions

Our results reinforce the conclusion that predicting seabird response to climate variability and change is a difficult task that requires close attention to local as well as regional patterns. We predict that warming will have region-specific effects on stress, increasing predicted survival for the northern colonies and decreasing it for southern colonies. Based on our analysis, we expect productivity will be better predicted by local changes in conditions, with local spring SST offering moderate explanatory power, which is consistent with previous findings for Cook Inlet (Shultz et al. 2009).

We conclude that longevity alone may not be enough to buffer against environmental variability and, in particular, that differences between islands in productivity may have important demographic consequences even for long-lived birds. Our results suggest that self-sustaining populations in low-productivity colonies are unlikely, even given optimistic estimates of survival. Thus, we suggest that managers do not accept low productivity on these islands as the *status quo* and that they do focus on identifying drivers of variation in productivity and measures to increase productivity. The apparent mismatch between a calculated R_0 below self-replacement and near-stability or even slight increases in the recent past for St. Paul and the past 30 yr for St. George suggest that migration or skipping of reproduction may be important additional factors in determining colony dynamics; thus, collecting data and building models to describe these processes should be a high priority. Similarly, the concordant predictions of a high R_0 and recent growth of the Bogoslof colony suggest that skipping and migration may be less of a factor there. Our current study identified testable hypotheses awaiting future investigations, while suggesting a tool for combining data on productivity and stress as a proxy for full demographic studies in the face of limited resources and climate change.

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Contribution to the Theme Section 'Seabirds and climate change'

Environmental variation and the demography and diet of thick-billed murres

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ABSTRACT: Conditions in arctic marine environments are changing rapidly, and understanding the link between environmental and demographic parameters could help to predict the consequences of future change for arctic seabirds. Over 20 yr (1988 to 2007), we studied colony attendance, adult survival and reproductive success of thick-billed murres, as well as the departure masses and diets of their chicks at Coats Island, Nunavut, Canada (62.95° N, 82.00° W). We evaluated how each parameter responded to climatic conditions near the colony during the breeding season, and in the winter range during the non-breeding period (delineated using geolocation). We used the Arctic Oscillation (AO) and North Atlantic Oscillation indices, as well as local variables to describe ice, oceanographic and weather conditions. We demonstrate that adult survival varied little among years but was higher after winters with lower AO indices, more ice in the south-western part of the winter range in spring, and cooler sea surface temperatures (SST). By comparison, interannual variation in breeding parameters (breeding success, chick mass and diet) was pronounced and responded to SST and ice conditions near the colony. Counts of birds attending the colony, influenced heavily by pre-breeders, were most strongly related to the conditions that influenced adult survival; counts were positively related to ice concentration in the southwest of the winter range. Relationships between climatic conditions and demographic parameters were often lagged, suggesting effects mediated through the food web. The trend towards higher SST and less ice in the vicinity of the colony has not yet reduced reproductive success. However, a significant, ongoing decline in the rate of energy delivery to nestlings suggests that a critical threshold may eventually be crossed.

KEY WORDS: Demography · Survival · Reproduction · Climate · Thick-billed murre · *Uria lomvia*

INTRODUCTION

Climate variation can affect wildlife populations profoundly, and as concern grows over anthropogenic climate change the urgency of predicting these impacts increases. Past effects of the changing global climate on wildlife are already evident (Hughes 2000, Parmesan & Yohe 2003), and may be more pronounced at high latitudes (Post et al. 2009, Wassmann et al. 2011). However, prediction of future effects requires an understanding of the link between population processes and environmental variables.

For seabirds, understanding the effects of changing climate is complicated by the fact that they range widely across inaccessible oceanic habitats for much of the year. Changes observed in their breeding behaviour, diet and demography are linked to conditions in the marine environment, and can signal environmental change at a variety of spatial and temporal scales (Cairns 1992, Montevecchi & Myers 1997). While the link between prey availability and reproduction is probably direct, the effects of environmental variation on demographic processes such as adult survival may be more subtle and may operate outside of the breeding season and away from the colony.

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Many polar seabirds spend 6 mo or more away from their colonies, and because day length and food availability tend to be lowest in winter, we may expect survival to be influenced primarily by conditions in the wintering range (Gaston 2003, Frederiksen et al. 2008). However, until recently, the wintering ranges of many marine birds were poorly documented. With the advent of solar geolocation, knowledge of seabird winter range has expanded rapidly and dramatically (e.g. Phillips et al. 2004, Egevang et al. 2010). The consequent new knowledge of ranges allows us to examine the relationships between environmental conditions and demographic parameters in ways that were not possible previously.

Non-breeding ranges may be hemispheric in scale and habitat use can vary widely among individuals. As population dynamics for marine birds can be influenced by environmental conditions across large portions of the globe and throughout the year, identifying key environmental parameters poses a challenge. Teleconnection indices, such as the North Atlantic Oscillation (NAO) index, are a major source of interannual variability in atmospheric circulation and have been shown to be important predictors of demographic parameters. The NAO, the pressure differential between Iceland and the Azores, can have profound effects on conditions in the marine environment, altering circulation patterns, precipitation regimes, nutrient transport and upwelling (e.g. Déry & Wood 2004, 2005, Kuzyk et al. 2010). Its influence on food webs is also well documented, including effects on phytoplankton (Edwards et al. 2001), zooplankton (Planque & Taylor 1998) and fish (Arnott & Ruxton 2002). Due to the far-reaching effects, NAO values have been correlated with survival and breeding parameters for a variety of seabirds in the North Atlantic (e.g. Grosbois & Thompson 2005, Sandvik et al. 2008).

The Arctic Oscillation (AO) index describes pressure differences between the polar region and mid-latitudes. It is generally highly correlated with the NAO index and the potential effects are analogous to those of the NAO (Stenseth et al. 2003). However, it may capture more of the variation related to recent climatic change in Arctic regions (Aanes et al. 2002). The link between indices based on barometric pressure and the survival of seabirds is necessarily indirect (Forchhammer & Post 2004), so identifying mechanistic links requires careful model selection and interpretation.

Here, we use 20 yr of observations of thick-billed murres *Uria lomvia* in the eastern Canadian Arctic and ask how survival and breeding are influenced by conditions in different portions of the range. Wintering areas for this population have been recently described (Gaston et al. 2011). We predicted that conditions at the wintering grounds would have the greatest influence on adult survival and numbers of birds attending the colony, while conditions near the colony would have the greatest influence on parameters related to breeding success and the condition and diet of nestlings. We further predicted that lag effects would be important in models explaining chick diet and growth (where climate effects are mediated through food webs) but less important in models explaining survival, which we predicted to be influenced by contemporary weather or stochastic events. As the climate is changing, particularly in northern regions, we used methods that account for temporal trends in climatic variables. Building on the findings of past studies, we evaluated both large-scale climate indices (NAO and AO indices) and environmental variables with finer spatial or temporal resolution (sea surface temperature [SST], ice conditions and extreme weather) to investigate the environmental drivers of demography for this seabird population.

MATERIALS AND METHODS

Study area and species

Thick-billed murres *Uria lomvia* nest on sea cliffs across the circumpolar Arctic and Subarctic. They dive to depths of up to 150 m to forage on small fish, squid and large zooplankton. Nestlings are fed by both parents for 15 to 30 d before departing from the breeding site with the male parent (Gaston & Hipfner 2000).

Field observations were made at a breeding colony of approximately 30 000 pairs at Coats Island, Nunavut, Canada (62.95° N 82.00° W; Gaston et al. 1994), where egg laying begins in mid- to late June and most chicks have left the colony by mid-August. Waters surrounding the colony are classified as low Arctic, and form a part of the Hudson Complex ecoregion which includes Hudson Bay to the south and Foxe Basin to the north (Powles et al. 2004).

Non-breeding range

Timing of colony departure, routes of migration and wintering locations were determined as part of another study using solar geolocation (Gaston et al. 2011). Locations were available for a sample of 7

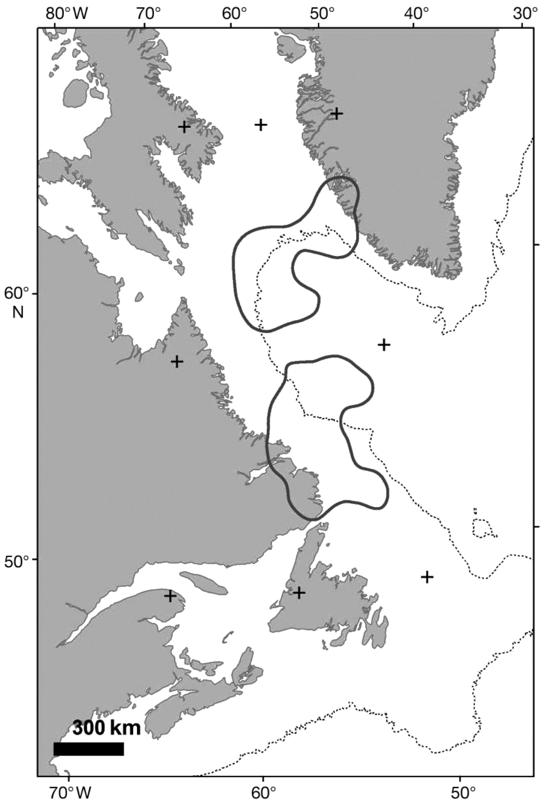

Fig. 1. *Uria lomvia.* The 8 crosses denote the boundaries within which we evaluated ice conditions and sea surface temperatures; this area encloses the winter range of 17 thick-billed murres followed with light-level geolocators by Gaston et al. (2011). The area was further divided into 4 equal quadrants (centre lines denoted by crosses). Dashed line denotes the 2500 m depth contour; solid line encircle 2 foci of murres distribution in April (50% kernel volume contours)

female and 10 male breeders, from August 2007 until July 2008. All birds remained in Hudson Bay until at least mid-November, after which they moved rapidly through Hudson Strait to winter primarily in the southern Davis Strait and northern Labrador Sea. Most birds remained north of 55° N, many in areas of heavy ice cover. To summarise the ocean conditions experienced by birds in winter, we defined the wintering area as bounded by 49.0° to 67.0° N and 50.0° to 65.0° W (Fig. 1). This area, measuring 1.8 million km^2, encloses the core of the winter area, defined using 50% kernel volume contours of the complete set of locations, for January to April, for all individuals.

Band resighting

Chicks and breeding-age adults have been banded at the colony with uniquely coded, field-readable, metal bands since 1985. Adults were captured with noose poles and nestlings were captured by hand at breeding sites during July and August of each year. The band-resighting data used here for estimates of survival are from an intensively monitored portion of the colony (Q-plot), where daily efforts to read bands were carried out during July and August 1990 to 2006. Breeding sites in this area of the colony are very visible, and the sites analysed were selected as the most visible sites. Consequently, the bands of most birds attending this portion of the colony were successfully read each year.

Breeding success

For this same portion of the colony, we made daily observations to determine the breeding status of individuals, during 1990 to 2007. For each active site, we determined the date of hatch and monitored chicks throughout the nestling period. Chicks that disappeared after 14 or more days of brooding were considered to have departed successfully. Any losses of chicks or eggs that resulted from our research activities were excluded from analyses.

Nestling diet

We determined the diet fed to nestling thick-billed murres by conducting observations from a blind at Q-plot. Complete methods have been described by Elliott et al. (2008). In brief, observations were made between 04:00 and 22:00 h during late July and early August of each year from 1993 to 2007 for the 46 sites most clearly visible from the blind. For each observation we determined the taxa and size of the prey item(s), and converted this to a caloric value using the methods described by Elliott & Gaston (2008).

We calculated annual means for the energy value per diet item, the mean number of prey deliveries per active site and the total quantity of energy delivered per chick per hour. We also determined the annual contribution of each of 7 diet categories (Arctic cod, capelin, crustaceans, sandlance, sculpins, other benthic fishes, unidentified/ rare prey) to the total energy delivered to chicks. For some analyses, we reduced the number of parameters for chick diet through a principal component (PC) analysis. We retained components with eigenvalues >1, and generated PC scores for use in subsequent analyses.

Chick mass at departure

We monitored chick growth for a sample of 50 chicks >50 m from plot Q by measuring mass ± 1 g every 2 to 3 d, in 1988 to 2007 (see Hipfner & Gaston 1999 or Gaston et al. 2005 for additional details). We used mass at the final observation prior to departure to generate an annual mean mass at departure. We excluded data from 1989, 2002, 2004 and 2007, because in those years we left the field site too early to obtain a representative sample of departure masses.

Colony attendance

Indices of colony attendance are frequently used as a measure of population size for seabirds (e.g. Birkhead & Nettleship 1980, Gaston 2003). At Coats Island, the numbers present on 10 plots containing 100 to 500 birds each were counted daily between 17:00 and 18:00 h, during 1990 to 2006. Here, we use the mean daily total count for the period from 25 July to 10 August (see Gaston 2002 for additional details). Most breeding sites were occupied continuously by at least 1 member of the pair during those dates (Gaston & Nettleship 1982).

Climatic covariates

We obtained annual and winter (December to March) station-based values for NAO from the Climate Analysis Section, NCAR, Boulder, USA (Hurrell 1995). Monthly mean AO values were obtained from the NOAA Climate Prediction Center (www.cpc.ncep.noaa.gov), and used to generate an AO index for the non-breeding period (September to April). Effects of these indices may be mediated through changes at lower trophic levels (e.g. Stenseth et al. 2004), and adult murres provision their chicks mainly with fish up to 3 yr old (Gaston & Hipfner 2000). Consequently, we considered lag effects of up to 3 yr in these variables (Table 1).

Ice cover and SST data for the wintering area were obtained from the Hadley Centre of the UK Meteorological Office (badc.nerc.ac.uk/data/hadisst/). Monthly mean values were obtained for the period 1990 to 2006 for the area between 49° and 67° N and 50° and 65° W. Grid cells over land were excluded, and a mean value for each month generated. These values were used to generate mean measures of ice concentration and SST for January to March and for April, a time when birds disperse widely (Gaston et al. 2011). Mean ice concentrations in winter and spring vary widely across the winter range of the murres, with generally heavy ice in the west, from Davis Strait down the Labrador Coast, and lighter ice conditions in the east, from Greenland south to offshore waters of the Atlantic (Fig. 1). To detect whether year-to-year variation in different regions affects murre demography differently, we divided the area into 4 equal quadrants and evaluated the influence of ice conditions in these quadrants separately (Table 1, Fig. 1).

Weather data for the wintering range were obtained from a coastal station at Nain, Labrador (56.55° N, 61.68° W). Monthly values for mean mini-

Table 1. Variables considered in the models. Winter ice conditions were considered for the winter range as a whole, and divided into 4 quadrants. Some variables were considered with time lags of 0 to 3 yr to acknowledge effects that may operate through food webs. AO: Arctic Oscillation index; NAO: North Atlantic Oscillation index; SST: sea surface temperature

Region of focus	Variable	Lag effects	Prediction / justification
All	AO non-breeding	Yes	Indicates severity of storms, possible food web effects
	NAO annual	Yes	Possible links to marine productivity, food web effects
	NAO winter	Yes	Possible links to marine productivity, food web effects
Winter range divided into 4 quadrants	Ice, Jan–Mar	No	Affects access to prey
	Ice, Apr	No	Affects access to prey
Winter range	SST, Jan–Mar	Yes	Affects productivity and abundance of prey
	SST, Apr	Yes	Affects productivity and abundance of prey
	Minimum temperature, Jan–Mar	No	Extreme winter weather may compromise survival
	Precipitation, Jan–Mar	No	Extreme winter weather may compromise survival
Breeding range	Summer ice concentration, Hudson Bay region	Yes	Affects abundance and availability of prey
	SST around breeding colony, annual	Yes	Affects abundance and availability of prey
	SST around breeding colony, May–Aug	Yes	Affects abundance and availability of prey
	Maximum temperature, May–Aug	No	Potential for heat stress
	Maximum wind speed, May–Aug	No	Potential effects on egg loss

mum temperatures and mean monthly precipitation were obtained from the National Climate Data and Information Archive of the Weather Office of Environment Canada (www.climate.weatheroffice.gc.ca) for January to March of 1988 to 2007.

We also considered environmental conditions within the breeding range. Annual estimates of ice concentration in the Hudson Bay region on July 16th were obtained from the Canadian Ice Service (ice-glaces.ec.gc.ca). We also obtained estimates of the mean annual SST and breeding season (May to August) SST for a 2 × 2° block (approximately 220 × 100 km) centred on the colony (NOAA ERSST.v3 from www.esrl.noaa.gov/psd/; Smith et al. 2008).

We obtained monthly maximum temperatures and windspeeds from the weather office of Environment Canada for the Coral Harbour weather station (130 km from the breeding colony; www.climate.weatheroffice.gc.ca), and used these to generate means for the breeding season, May to August. As these weather parameters were predicted to affect murres directly, no lag effects were considered.

Analytic methods

To evaluate support for our predictions, we contrasted the effect of environmental variables from throughout the breeding and non-breeding range. Although care was taken to limit the number of variables considered, the candidate set of models was large in some cases. We employed a detrending technique (see below) to limit spurious correlations, but suggest that the model selection approach be considered exploratory in nature; an attempt to identify patterns for evaluation in future, targeted studies.

We used capture-mark-recapture models, implemented in Program MARK (White & Burnham 1999), to estimate apparent survival (φ) and recapture probability (p). Support was gauged with corrected Akaike's Information Criterion (AIC_C), adjusted for small sample sizes and overdispersion ($qAIC_C$; Burnham & Anderson 1998). Logit link functions were used for all models. We report parameter estimates (β) and 95% confidence intervals in the logit scale, but also present back-transformed predictions from top models.

The total variance in estimates of survival or resighting probability includes both biological process variance and sampling variance, and accounting for sampling variance can provide more meaningful estimates of among-year patterns (Burnham & White 2002). We used random effects models to decompose the total variance into process and sampling variance, and shrink year-specific estimates towards the global mean on the basis of sample size (Franklin et al. 2002). We used these 'shrunk' estimates of annual survival and resighting probability to describe the among-year patterns and assess the predictions of our models.

Models to describe interannual variation in colony attendance, breeding success, chick mass at departure and chick diet were constructed using multiple regression in place of mark-recapture methods. Models were ranked with AIC_C (i.e. no correction for overdispersion), and constant and linear trends were investigated as the reference models.

For each demographic, nestling condition and nestling diet parameter, we contrasted the relative support for models including environmental variables from the breeding and non-breeding range. Variables were grouped into those that influence abundance or availability of prey (e.g. ice, SST), those that summarise extreme weather events (e.g. minimum and maximum temperatures), and large scale teleconnection indices (NAO or AO; see Table 1). We first assessed support for the large scale climate indices (NAO or AO), and then determined whether specific climate variables from either group (i.e. prey, extreme weather), in either the breeding grounds or non-breeding grounds, received support individually or in combination with NAO or AO. With the region and mechanism identified, we built models hierarchically to identify the variables (including lag effects) that most parsimoniously explained demographic parameters. Models including environmental covariates were tested against both a null model and a model with a linear temporal trend. Models containing additional covariates were retained only if they improved model fit by >2 $qAIC_C/AIC_C$ units.

Preliminary analyses demonstrated significant trends in some of the predicted variables over time. Several environmental variables also showed significant linear changes over time, and the potential for spurious correlations was therefore high (Graham 2003). As the long-term changes in our demographic (i.e. predicted) variables could result from decadal trends in environmental conditions, we considered models with raw predicted variables and environmental covariates. However, because our primary interest was a more mechanistic understanding of year-to-year fluctuations, we also considered relationships between 'detrended' variables (Grosbois et al. 2008) when temporal trends were apparent in our predicted variables.

We used the Residual Regression method described by Graham (2003), which evaluates the ability of environmental variables to explain the residual variation about the underlying temporal trend. Decadal trends in environmental variables were removed by regressing them on year and calculating residuals which were then used in place of the raw environmental covariates in our models. A year effect was included in all models to account for time trends in the predicted variables, and our measures of model support therefore assessed the degree to which environmental variables explained variation about the underlying long-term trends. Model selection following the procedure outlined above was then carried out using detrended environmental variables.

RESULTS

Variation and covariation in environmental variables

Winter and spring SSTs in all 4 quadrants of the non-breeding range increased over the period of our study (all R > 0.55). For January to March 1990 to 2007, the increase was estimated to be 0.93°C over the entire area (Fig. 2C). Similarly, annual and summer SSTs in the vicinity of the breeding colony increased (all R > 0.60; Fig. 2D). Most measures of winter and summer ice cover in the breeding and non-breeding areas decreased during the study period (average R = −0.50; Fig. 2A,B), with summer ice near the breeding colony decreasing by an estimated 21% (Fig. 2B). The winter NAO index also decreased over the study period (R = −0.53). These observations are consistent with the numerous other accounts of warming and reduced ice concentration in the North Atlantic and eastern Canadian Arctic (e.g. Arctic Climate Impact Assessment 2005). In contrast, our measures of air temperature and wind speed during the breeding season and air temperature and precipitation during the non-breeding season showed no significant patterns.

Adult survival rates

We included 186 individuals in the study of adult survival. As both survival rates and site tenacity were typically high, the number of newly-marked individuals within the plot was small in some years. This led

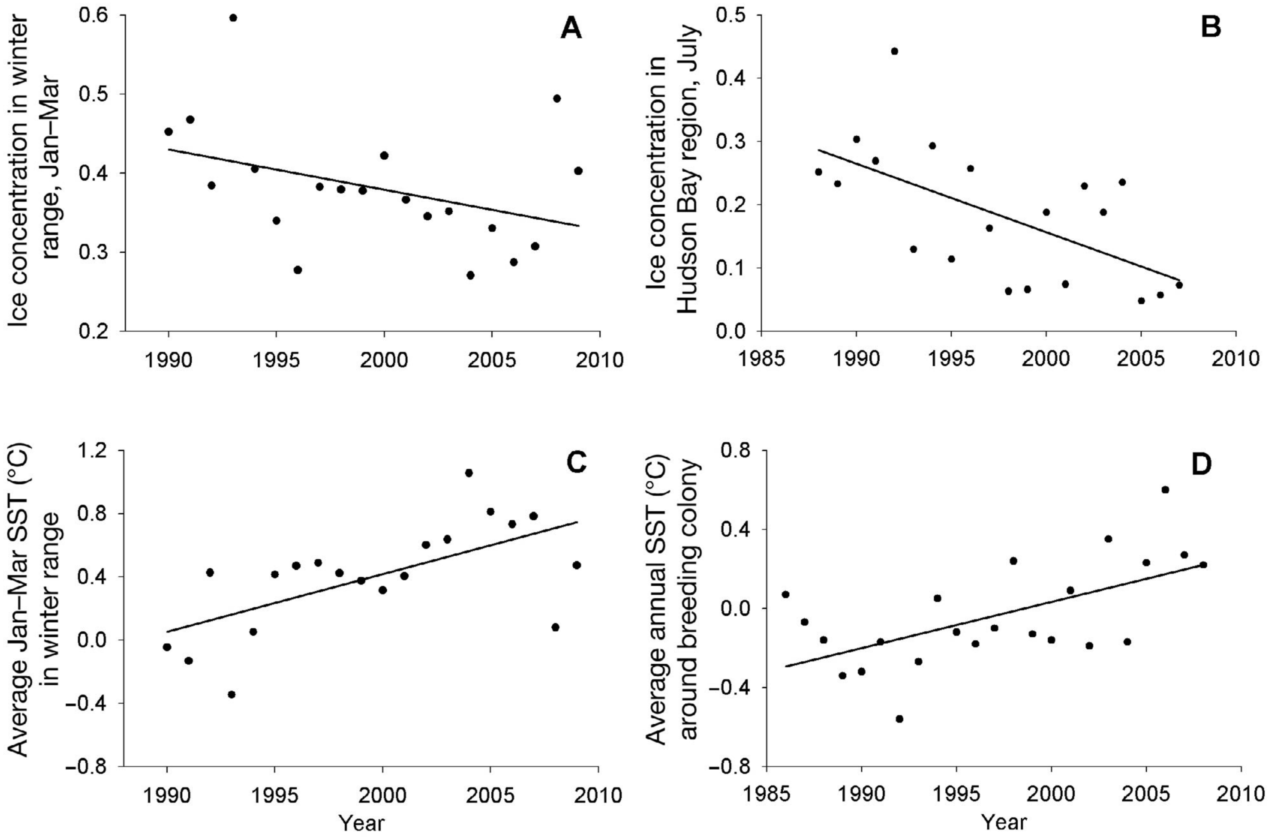

Fig. 2. (A,B) Ice concentration (1 = complete coverage) and (C,D) sea surface temperatures (SST) in (A,C) the winter range and (B,D) the breeding range of the thick-billed murre *Uria lomvia*. Solid lines: best fit

to small expected values in tests of goodness of fit in later years of the study, and some significant differences in the tests of homogeneity of survival ('Test 3' of Program RELEASE; Burnham et al. 1987). Also, some significant lack of fit was identified in Test 2, suggesting the possibility of temporary emigration. Despite this slight lack of fit for the fully time-dependent Cormack-Jolly-Seber model, the estimated dispersion parameter, $\hat{c}$, was 1.20, indicating limited extra-binomial variation overall.

Estimates of apparent adult survival did not vary dramatically among years, yielding a mean (±SD) of 0.90 ± 0.033 for year-specific estimates. We found little support for year effects in our model selection procedure. Among our structural reference models, those with constant estimates of survival across years received better support than those with year-specific estimates (Table S1 in the supplement at www.int-res.com/articles/suppl/m454p237_supp.pdf). We found no support for linear or quadratic trends in apparent survival. In contrast, we found strong support for quadratic temporal trends in resighting probability (year-specific estimates varied from 0.86 to 1.00; presumably owing in part to our reduced resighting effort in several years in the middle of the study period), and used this quadratic resighting effect when evaluating all subsequent models relating apparent survival to environmental covariates.

Our model selection procedure indicated modest support for an effect of the AO during the non-breeding season on apparent adult survival. Addition of this climate index reduced the qAIC_C by 3.0 units compared to the model with constant survival. Inclusion of additional climate variables improved model fit slightly; a model combining additive effects of AO and winter SST received marginally better support (qAIC_C 2.4 units lower), as did a model with AO and ice conditions in April in the south-west quadrant of the wintering range (qAIC_C 2.5 units lower than the AO-only model; Table 2, Table S2).

Parameter estimates for the 3 top models all indicated a negative effect of AO (top model: $\beta = -0.69$, 95% CI = −1.20 to −0.18, on a logit scale). The variable describing April ice extent in the south-western quadrant of the wintering range had a positive relationship with apparent survival ($\beta = 3.65$, 95% CI = 0.24 to 7.06, on a logit scale), while SST bore a negative relationship with survival ($\beta = -0.91$, 95% CI = −1.78 to −0.04, on a logit scale). Thus, survival was slightly higher following winters with lower AO indices, more ice in the southern extent of the winter range, and relatively cooler SSTs.

Support for these parameters was modest, and even the best model was only 5.5 qAIC_C units better supported than a model with a constant estimate of survival. Survival as predicted by this top model did not display a tight correspondence with the shrunk year-specific estimates from a random effects model.

Table 2. *Uria lomvia*. Environmental variables included in the top model explaining variation in each demographic or diet variable, and the model's Akaike weight (w_i). Additional model selection results appear in Tables S1 to S8 of the supplement. AO: Arctic Oscillation index; NAO: North Atlantic Oscillation index; SST: sea surface temperature. SW: south-west quadrant of wintering range

Predicted variable	Environmental variables in top model	w_i
Survival, φ	AO + Ice April SW	0.43
Proportion of laid eggs fledging	SST around colony 1 yr lag + NAO 2 yr lag + Summer SST around colony 2 yr lag	0.57
Chick departure mass (g)	SST around colony 1 yr lag	0.68
Diet PC 1	Detrended SST around colony 2 yr lag	0.86
Diet PC 2	Detrended summer ice Hudson Bay 2 yr lag + Detrended summer ice Hudson Bay 3 yr lag + Detrended Coats summer SST 1 yr lag + NAO 2 yr lag	0.64
Energy delivered $\text{chick}^{-1}\ \text{h}^{-1}$	Detrended SST around colony 2 yr lag + NAO 3 yr lag	0.69
Colony attendance	Detrended ice April SW	0.50

Breeding success

As murres have high breeding-site fidelity, the proportion of chicks departing successfully from a given set of breeding sites might be influenced by whether the adults that bred there previously survived and returned to breed. Accordingly, survival was a significant predictor of departure success ($R^2 = 0.30$, $p = 0.029$). As the factors influencing survival were explored separately, we used the proportion of eggs that resulted in chicks surviving to departure as our metric of breeding success.

This metric ranged from 54% to 89% (mean ± SD = 0.69 ± 0.088). No significant increases or decreases over time were identified. The most influential single predictor of breeding success was the SST in the vicinity of the colony, lagged by 1 yr. This model was a marginal improvement over a null model (AIC_C 2.1 units lower; Table S3), but received more substantial support when an effect of NAO (2 yr lag) was included. The top model ($R^2 = 0.61$; an improvement of 6.9 AIC_C units over the null model) also included an effect of summer SST near the colony, lagged by 2 yr (Table 2). Parameter estimates were all positive ($\beta_{\text{SST colony 1 yr lag}} = 17.9 \pm 5.4$, $\beta_{\text{NAO 2 yr lag}} = 3.0 \pm 0.8$, $\beta_{\text{Summer SST colony 2 yr lag}} = 10.6 \pm 4.6$), suggesting that breeding success was higher when SSTs and the NAO index in previous years were higher.

Departure mass

The mean mass of departing chicks varied among years from 212 ± 27 g to 245 ± 23 g. SST in the vicinity of the colony lagged by 1 yr was found to be the most influential single predictor of chick mass at departure. Years with higher past SSTs were associated with lower departure masses ($\beta = -33.3 \pm 12.17$, $R^2 = 0.33$; Table S4). No additional covariates improved model fit. This top model was only an improvement of 3.4 AIC_C units over the null model, however, and only 2.5 units better supported than a linear trend in departure mass. This latter effect, a linear decline in departure mass, was not significant at $\alpha = 0.05$, and no detrended analyses were therefore explored (mass vs. year $R^2 = 0.22$, $p = 0.06$).

Chick diet

When chick diet was condensed into orthogonal PCs, PC1 and PC2 captured 76% of the variability in diet. PC1 loadings were large and negative for cod and large and positive for crustaceans, sculpins and other benthic fishes (Table 3). A low PC1 score therefore reflected a diet rich in cod. PC1 for chick diet was correlated with both the total energy delivered per chick per hour (linear regression PC1 vs. kJ chick^{-1} h^{-1}, $R^2 = 0.35$, $p = 0.02$) and the average energy content per feed ($R^2 = 0.45$, $p = 0.006$). Low PC1 scores (i.e. a diet high in cod) were associated with high levels of total energy delivered to chicks and also the delivery of individual prey items with high energy contents. PC1 was a highly significant predictor of departure mass, with a low PC1 score related to a high departure mass ($R^2 = 0.57$, $p = 0.005$). PC1 was unrelated to breeding success.

Table 3. *Uria lomvia.* Component loadings for the first 2 principal components (PC1 and PC2) of chick diet, explaining 45 and 31% of variability in annual diet, respectively. Diet was described as the proportion of energy contributed from each of the diet item categories listed below

Diet item	PC1	PC2
Arctic cod	−0.84	−0.51
Capelin	0.52	0.82
Crustaceans	0.85	−0.09
Other benthic fishes	0.88	−0.22
Sandlance	−0.17	0.90
Sculpins	0.68	−0.33
Unidentified/rare prey	0.44	−0.47

The second diet component, PC2, loaded negatively on cod and positively on capelin and sandlance. In contrast to PC1, PC2 was most closely related to the number of feeds per chick per hour, with a low PC2 score (i.e. a diet high in sandlance and capelin) associated with a high rate of feeding ($R^2 = 0.33$, $p = 0.03$). Although not significant individually, this diet variable did add significantly to the prediction of departure mass among years; after accounting for the effect of PC1, a high PC2 score was associated with higher departure mass (departure mass vs. PC1 + PC2: $\beta_{PC1} = -9.13 \pm 2.19$, $\beta_{PC2} = 5.68 \pm 2.47$, $R^2 = 0.73$, $p = 0.003$). PC2 was therefore a weaker predictor of departure mass, but in contrast to PC1, a high PC2 was associated with higher breeding success ($\beta_{PC2} = 5.13 \pm 2.16$, $R^2 = 0.30$, $p = 0.03$).

Temporal trends in PC1 were significant (PC1 vs. year, $R^2 = 0.31$, $p = 0.03$), as a result of a pronounced decline in the proportion of cod in the diet. The top model to explain PC1 including raw environmental covariates suggests an influence of SST in the vicinity of the colony and NAO lagged by 1 yr ($R^2 = 0.59$). Higher SSTs ($\beta = 2.19 \pm 0.75$; Table S5) and lower NAO values ($\beta = -0.20 \pm 0.09$) are associated with higher PC1 scores (less cod, more benthic fishes and crustaceans). However, these results may reflect the strong general increase in SST and strong general decrease in proportion of cod in the diet. With these temporal trends accounted for, the SST around the colony (2 yr lag) was found to be the strongest predictor of PC1 score ($R^2 = 0.57$), but here, lower past SSTs are associated with a higher PC1 score ($\beta = -2.65 \pm 0.98$). As a high PC1 score reflects an energy-poor diet, this result is consistent with the above-described finding that energy content delivered to chicks was lower when past SSTs were lower.

Temporal trends in PC2 were also significant ($R^2 = 0.32$, $p = 0.03$); PC2 scores declined during the study period, reflecting an increase in the proportion of capelin and sandlance at the expense of cod. Among raw environmental variables, the strongest predictors of PC2 were lagged summer ice concentrations in the Hudson Bay region (2 and 3 yr lags, $R^2 = 0.68$; Table S6). Support for the ice variables was strong;

the model with both ice variables was an improvement of more than 10 AIC_C units over the null model. The model building procedure with detrended variables showed similar results, with greatest support for summer ice concentrations in the Hudson Bay region (2 and 3 yr lags), and additional support for NAO (2 yr lag) and past summer SST (1 yr lag) in the vicinity of the colony (R^2 for top model = 0.90). For both model building procedures, the ice parameters were negative, suggesting that low past ice concentrations were associated with high PC2 scores (high proportion of capelin and sandlance in the diet). Parameter estimates for SST and NAO suggested that lower past SST and higher past values for the NAO index were associated with higher PC2 scores for nestling diet.

The rate of energy delivered to chicks varied more than 2-fold among years, and although variable, this quantity declined significantly over the period of our study, from a predicted 15.3 kJ chick^{-1} h^{-1} in 1990 to 9.5 kJ chick^{-1} h^{-1} in 2007 (energy vs. year, $R^2 = 0.28$, $p = 0.04$). This decline reflected a decrease in the average energy content of feeds, rather than a decrease in the number of feeds (linear regression of energy per feed vs. year, $R^2 = 0.56$, $p = 0.001$, $\beta_{\text{Year}} = -1.85 \pm 0.43$; number of feeds vs. year, $R^2 = 0.11$, $p = 0.22$).

The strongest single predictor of the quantity of energy delivered to chicks (for raw variables) was NAO with a lag of 3 yr (Table S7), with higher NAO values corresponding with greater quantities of energy delivered to chicks ($\beta = 0.83 \pm 0.288$, $R^2 = 0.39$). With time trends removed, NAO 3 yr lag remained in the top model, but SST (2 yr lag) had greater support as an individual predictor (Table S7). In the top detrended model ($R^2 = 0.80$), higher past SSTs and higher NAO values were associated with greater quantities of energy delivered ($\beta_{\text{Detrended NAO 3 yr lag}} = 0.50 \pm 0.21$, $\beta_{\text{Detrended SST colony 2 yr lag}} = 8.94 \pm 2.09$; Table 2).

Colony counts

The total number of birds counted in fixed plots varied among years, but increased over time (35 birds yr^{-1}, $R^2 = 0.75$, $p < 0.001$). Inclusion of a linear year effect improved model fit by more than 20 AIC_C units over the null model, and this model received greater support than any model with raw environmental covariates ($R^2 = 0.78$; Table S8). Models including summer SST at the breeding grounds (1 and 0 yr lags) and ice conditions in the south-west of the wintering grounds received greater support than the null model, and achieved lower deviance than a linear time trend, but this improved fit did not justify the additional parameters (Table S8). Parameter estimates for the model including summer SSTs and winter ice conditions suggested higher colony attendance when current and past SSTs near the colony were warmer and when ice conditions in the southern extent of the previous winter were heavier. However, the strong temporal trends evident in both SST and colony counts could lead to spurious correlations.

With the longer-term temporal trends removed, current and past SSTs near the colony were poor predictors of counts, with AIC_C values at least 2 units greater than the model including only a year effect. The top model for detrended environmental variables included only the effect of April ice in the south-western quadrant of the non-breeding range (Table 2, Table S8). Parameter estimates for this effect were positive, suggesting that colony attendance was higher after a spring with heavy ice conditions ($\beta_{\text{Ice April SW}} = 701.9 \pm 326.3$, $R^2 = 0.83$). Although this model was only a small improvement, 1.4 AIC_C units, over the year-effect-only model, predictions from this top model fit the observed colony counts well.

DISCUSSION

We found that variation in environmental conditions could explain a substantial proportion of the variation in the demographic and diet parameters. Although a large number of variables were considered, a small number of key variables were recurrent in top models. Teleconnection indices, such as the AO and NAO indices, were present in some top models, but local measurements of environmental conditions generally received stronger support. Moreover, survival and counts of birds attending the colony were influenced most by conditions on the wintering grounds, whereas, not surprisingly, breeding success and chick diet were influenced most by conditions encountered near the breeding colony. Importantly, many relationships involved time lags of 1 to 3 yr, suggesting that climatic effects were indirect, mediated through changes in food availability and predator–prey interactions.

Survival

Despite a long time series, no catastrophic mortality events were identified: the lowest estimate of annual survival was 84%. However, we found that the variation in survival was best predicted by winter conditions, specifically ice concentrations and SSTs in the winter range and the AO during the non-breeding season. In all cases, the variables were included in models without lag effects, potentially suggesting that they were affecting murres directly, for example by impairing access to prey.

A positive phase of the AO, associated with lower apparent survival in our study, is associated with a more intense polar vortex, with ocean storms driven farther north by relatively higher pressure at mid-latitudes (Serreze et al. 1995). The polar vortex also traps cold air at northern latitudes, and areas in the wintering grounds of murres (i.e. between Labrador, Newfoundland and Greenland) are colder than during the negative phase. Colder SSTs in the wintering range were actually associated with higher rates of survival. However, the stormy conditions in the North Atlantic during years with a positive AO index could significantly impair foraging. High winds and waves reduce the success rate of foraging common murres *Uria aalge* during the breeding season, increasing the amount of time they spend foraging and reducing the mean energetic value of the prey captured (Finney et al. 1999). Reduced foraging efficiency, coupled with the increased costs of thermoregulation during colder, stormier winters, could account for the effects of the AO on apparent survival that we observed.

We also documented a positive link between spring ice concentration in the south-west of the wintering range and adult survival. The spring ice cover in this area is substantial, with a mean (±SD) among years of 69 ± 8%. The preference of Atlantic thick-billed murres for foraging in and around ice during the breeding season is well documented (e.g. Gaston & Hipfner 1998), and wintering birds also feed heavily on ice-associated prey such as Arctic cod and hyperiid amphipods (Rowe et al. 2000). Analyses of stomach contents and stable isotopes suggest that ice-associated crustaceans may in fact become a more significant component of the diet in late winter and early spring (Elliot et al. 1990, Moody & Hobson 2007). The presence of broken ice and ice edges concentrates prey in the upper water column where they are readily accessible to foraging murres (Bradstreet 1980). Birds' access to higher ice concentrations in the winter range in April may facilitate feeding prior to the migration through Hudson Strait in May.

Breeding success, chick mass and diet

Local SSTs and ice variables with lags of 1 and/or 2 yr were present in the top models for breeding success, departure mass, rate of energy delivery to chicks and both PC1 and PC2 of chick diet. The presence of time lags in these effects, and, in particular, the evidence of lagged effects in the energy delivery and diet variables, suggests that this environmental variation affects murres through changes at lower trophic levels.

During the breeding season, adult thick-billed murres forage heavily on both fish and invertebrates (Gaston & Bradstreet 1993, Moody & Hobson 2007, Provencher et al. 2012, this Theme Section). However, murres are single prey loaders, and in comparison to large and energy-rich fish, invertebrates constitute a poor diet item for nestlings. The fish fed to nestlings are typically >1 yr old (Elliott & Gaston 2008), suggesting that conditions in past years could influence the strength of the year classes of fish targeted by foraging murres. After accounting for strong temporal trends, our results show that higher SSTs in the vicinity of the colony 2 yr previously were associated with greater quantities of energy delivered to chicks. Similarly, a detrended analysis demonstrated that higher SSTs 2 yr previously were associated with a lower PC1 score; a diet high in energy-rich Arctic cod and low in energy-poor crustaceans and benthic fish. Finally, higher SSTs in the vicinity of the colony in the previous 2 yr also contributed to greater breeding success.

It is important to note that our results suggesting positive effects of SST are from analyses with significant time trends removed. Annual and summer SST in the vicinity of the colony increased significantly over the period of study by an estimated 0.52°C and 0.88°C, respectively. Summer ice cover also declined (Gaston et al. 2005, Tivy et al. 2011, present study). During this time, the rate of energy delivered to chicks declined significantly, and although not significant, a trend towards lower departure masses was also observed. Trends in the diet PCs (and direct observations of nestling diets) suggest a decline in the contribution of cod and an increase in the contribution of capelin, sandlance, crustaceans and benthic fish to nestling diet. Although slightly higher SSTs in year $t-2$ might have been associated with an increase in the proportion of cod in the diet, the large changes over the period of study may have fostered a regime shift towards a more sub-arctic assemblage of forage fishes, dominated by capelin and sandlance (e.g. Gaston 2003).

We also found that phase of the NAO, with time lags of 2 or 3 yr, was positively related to breeding success, rates of energy delivery to nestlings, and the proportion of capelin and sandlance in the diet (i.e.

high PC2). The NAO is associated with several phenomena that could influence the availability of prey near the Coats Island colony: for instance, interannual variation in precipitation, and consequently freshwater discharge into arctic marine environments including Hudson Bay (Déry & Wood 2004, 2005). Inflow of freshwater into Hudson Bay, in turn, plays a critical role in patterns of circulation, upwelling and the transport of macronutrients that support primary production (Kuzyk et al. 2010). Although the link between higher NAO index in year *t* – 2 and breeding success and chick diet at Coats Island requires further investigation, it is clear that the pressure differential described by this teleconnection index could influence the abundance and distribution of the murres' prey.

Colony attendance

A striking feature of the Coats Island colony in recent decades has been a pronounced increase in counts of attending birds over time. Gaston (2003) reported that year-to-year changes in counts of murres at Coats Island were positively related to body condition, and reached the conclusion that foraging conditions in winter may be driving this index of population size. After detrending, we found that more ice in spring in the south-western extent of the breeding range increased colony counts in the following summer; the same variable that was found to influence adult survival. Our mean rate of adult survival was similar to that observed for thick-billed murres breeding at Hornøya, in the Western Barents Sea (91.6%, 1989 to 2002; Sandvik et al. 2005), where a trend towards increasing colony attendance is ongoing. However, although year-to-year changes in ice cover are positively related to colony attendance, overall trends in ice cover in the winter range are weakly negative and cannot therefore explain the general trend of increasing counts.

Despite high elasticity, adult survival is often relatively invariant in seabirds and may therefore contribute little to variation in the population growth rate, λ. For example, despite contrasting population trends ranging from –3 to +11% per annum, the annual survival rates of Atlantic puffins *Fratercula arctica* in 5 colonies spanning the species' range in the east Atlantic were virtually identical over a 10 to 15 yr period (Harris et al. 2005). Although breeding success is often highly variable, λ is usually relatively insensitive to variation in reproduction (Sæther & Bakke 2000). Pre-breeding survival, in contrast, can vary markedly and also have a substantial influence on λ (Reid et al. 2004, Robinson et al. 2004). Pre-breeding survival was not studied here, but future studies relating pre-breeding survival to environmental conditions could aid in interpretation of trends in this population.

Consequences of future climate change

In general, our results suggest that breeding for thick-billed murres in northern Hudson Bay improved with a slight year-to-year warming, a result consistent with the findings of Irons et al. (2008). However, in Irons et al.'s analysis of population growth rates from colonies across the circumpolar breeding range of the species, the authors demonstrated that populations responded positively to slight warming but negatively to larger changes. We found that rates of energy delivery to chicks declined over the period of our observations, that chick diet shifted dramatically, and that departure masses of chicks also may have declined. Despite the fact that adults fed their nestlings diet items of lower energetic value, the rate of feeding did not increase, suggesting that adults may have limited capacity to increase delivery rates. Although breeding success has not yet changed, it seems plausible that if energy delivery rates continue to decline, a threshold may be reached beyond which reproductive success will suffer.

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Contribution to the Theme Section 'Seabirds and climate change'

Climate change, heightened hurricane activity, and extinction risk for an endangered tropical seabird, the black-capped petrel *Pterodroma hasitata*

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ABSTRACT: The destructiveness of major (Category 3 to 5) hurricanes along the United States Atlantic Ocean seaboard has been recognized for centuries. While the effects of hurricanes on coastal ecosystems are well known, the influence of hurricanes on pelagic seabirds is difficult to assess. During the annual Atlantic hurricane season (~1 June to 30 November), the endangered black-capped petrel *Pterodroma hasitata* aggregates in Gulf Stream habitats from Florida to North Carolina. On at least 8 occasions over the past century, hurricanes have driven petrels far inland (sometimes as far as the Great Lakes), suggesting the demise of 10s to 100s of individuals. This paper models >100 yr of data to characterize and compare key aspects of hurricanes that did and did not drive petrels inland. Our model suggests that the predicted increase in the frequency of Category 3 to 5 hurricanes in the region due to climate change could nearly double the expected number of wrecked petrels over the next century and place an endangered species at greater risk of extinction.

KEY WORDS: Petrel · Hurricane · Gulf Stream · Climate change · Mortality · Wreck · North Atlantic

INTRODUCTION

On a decadal basis, the 20th century included quiet periods for major hurricanes (1970s, 1980s, and early 1990s) as well as periods of heightened activity (1940s, 1950s, early 1960s, mid-1990s through mid-2000s) (Landsea et al. 1999). Recently, global climate models suggest that rising ocean sea-surface temperatures may increase the frequency and intensity of hurricanes in the northwest Atlantic Ocean (Knutson & Tuleya 2004, Michaels et al. 2006). Models predict that over the next century, major hurricanes are expected to make landfall from Florida to North Carolina at nearly double their historical rates (Bender et al. 2010, Turner 2011), with some observations suggesting that such a change has already occurred (Trenberth 2005, Mann et al. 2009).

For more than a century, ornithologists have noted seabirds displaced inland following major hurricanes (Saffir-Simpson Wind Scale Categories 3 to 5) that struck the eastern seaboard of the United States (e.g. Lindahl 1899, Allen 1904, Murphy 1936). Over the past 30 yr, with a notable increase in the number and strength of tropical cyclones in the North Atlantic (Emanuel 2005, Webster et al. 2005), 1000s of coastal and pelagic seabirds, comprising >40 species, have been killed or observed far inland by such storms (e.g. Fussell & Allen-Grimes 1980, Brinkley et al. 1997). Over the past 110 yr, dozens of displaced and dead black-capped petrels *Pterodroma hasitata* (BCPE), an endangered species (IUCN 2010), including 27 specimens found in the United States and 21 in southern Canada (Kaufman 1990, Curry 1996, Brinkley et al. 1997) have been documented (Table 1).

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Table 1. *Pterodroma hasitata*. Major hurricanes making landfall north of Florida (1893 to 2003) with total count of black-capped petrel carcasses. (Dead or moribund petrels corroborated by photograph, specimen, or description. Does not include live petrels seen inland that may have died later.) Cape Verde refers to origination east of 36° W. Strength of hurricanes uses the Saffir-Simpson wind scale. Recurved refers to the hurricane's distance from the coast upon turning north in units of hurricane-force winds (62.5 nautical miles) — higher positive numbers indicate farther offshore

Year	Hurricane name	Cape Verde	Origin (long., °W)	Landfall month	Landfall lat. (°N)	Max. strength	Landfall strength	Landfall angle (°)	Recurved (radii)	Carcasses
1893	Sea Islands (No. 6)	Yes	20	Aug	32	3	3	45	−1	5
1898	No. 7	No	58	Oct	30	4	3	90	−7	3
1933	Chesapeake Potomac	No	48	Aug	36	3	2	135	−2	1
1938	New England	Yes	22	Sep	41	5	3	90	9	1
1955	Connie	Yes	36	Aug	35	4	2	180	0	1
1989	Hugo	Yes	20	Sep	33	5	4	90	−6	9
1996	Fran	Yes	21	Sep	34	3	3	90	−7	26
2003	Isabel	Yes	31	Sep	35	5	2	90	−9	2
										Total = 48

With an estimated breeding population of 1000 to 2000 pairs (Lee 1999, Brooke 2004), the susceptibility of BCPE to major hurricanes is of concern.

Here, we tested the hypothesis that the effects of climate change — operating through the frequency and intensity of Atlantic tropical cyclones — could further threaten this species. To test this hypothesis, we examined 110 yr of hurricane data and modeled the attributes of hurricanes that caused — and did not cause — observed mortality of BCPE. Through this modeling, we: (1) described the critical characteristics of hurricanes that threaten BCPE and (2) quantified the potential consequences of climate change and heightened hurricane activity on the population of this species over the coming century.

MATERIALS AND METHODS

We conducted an exhaustive search of museum collections and literature for storm-wrecked specimens of black-capped petrel *Pterodroma hasitata*. Because the species is strictly pelagic, it was relatively easy to link specimens to particular tropical cyclones. Where feasible, we attempted to determine the age of wrecked birds, in order to consider effects of mortality on population dynamics.

Specimen and tropical cyclone data

The disposition of BCPE carcasses salvaged between 1893 and 2003 was largely derived from: the ORNIS data portal (http://ornisnet.org; accessed on August 31, 2011) and the Canadian Biodiversity Information Facility, which are national catalogs of ornithological holdings in museums. We also reviewed seasonal sightings summarized in the regional reports of 'North American Birds' and predecessor journals. We then made direct communication with collection managers and/or curators from the following museums where specimens of the species were known (or suspected) to reside: American Museum of Natural History, New York, NY; Birdcraft Museum, Fairfield, CT; Buffalo Museum of Science, Buffalo, NY; Canadian Museum of Nature, Gatineau, QC; Carnegie Museum of Natural History, Pittsburgh, PA; Cornell University–Museum of Vertebrates, Ithaca, NY; Museum of Comparative Zoology, Harvard University, Cambridge, MA; North Carolina Museum of Natural Sciences, Raleigh, NC; Peabody Museum of Natural History, Yale University, New Haven, CT; Royal Ontario Museum, Toronto, ON; Smithsonian National Museum of Natural History, Washington, DC; and University of Connecticut Biological Research Collections, Storrs, CT. For each specimen, we requested information on location, date of collection, sex, and age (via molt, skull ossification, and bursa development). We linked each specimen to a specific tropical cyclone based on collection date. All carcasses were found within 3 wk of the associated hurricane's passage (most within 1 to 10 d), with the last-salvaged tending to be the most decomposed. Displaced *live* petrels were seen in Lake Erie, Ontario, for 2 wk following Hurricane Fran (Brinkley et al. 1997), so relatively fresh carcasses could be found for weeks. To assess the ages of wrecked petrels, we evaluated patterns of molt and feather wear (per Imber 1984, Brown et al. 1986). In such cases, the primary criterion to distinguish hatch-year birds from adults (all ages after hatch year) is the uniformly fresh, unworn plumage of juveniles versus the patchwork of crisp and worn feathers characteristic of older birds.

Table 2. *Pterodroma hasitata*. Major hurricanes making landfall north of Florida (1893 to 2003) with no associated black-capped petrel carcasses. Cape Verde refers to origination east of 36° W. Strength of hurricanes uses the Saffir-Simpson wind scale. Recurved refers to the hurricane's distance from the coast upon turning north in units of hurricane-force winds (62.5 nautical miles) — higher positive numbers indicate farther offshore

Year	Hurricane name	Cape Verde	Origin (long., °W)	Landfall month	Landfall lat. (°N)	Max. strength	Landfall strength	Landfall angle (°)	Recurved (radii)
1893	No. 4	Yes	36°	Aug	41	3	1	135	4
1893	No. 9	Yes	25°	Oct	33	3	3	0	1
1896	No. 2	No	59°	Sep	42	3	1	90	10
1899	San Ciriaco	Yes	31°	Aug	35	4	4	60	4
1916	No. 2	No	52°	Jul	33	3	1	180	7
1916	No. 4	No	71	Jul	33	3	2	90	–3
1933	No. 13	No	58°	Sep	35	3	2	180	0
1944	Great Atlantic	No	58°	Sep	41	4	2	135	2
1954	Hazel	No	59°	Oct	34	4	4	135	0
1955	Diane	No	43°	Aug	34	3	1	90	–3
1955	Ione	No	43°	Sep	35	3	1	135	–3
1959	Gracie	No	68°	Oct	32	4	3	90	8
1961	Esther	Yes	32°	Sep	44	4	0	135	9
1969	Gerda	No	77°	Sep	45	3	2	135	18
1976	Belle	No	73°	Aug	41	3	1	90	11
1979	David	Yes	36°	Sep	31	5	1	135	–1
1984	Diana	No	77°	Sep	34	4	1	45	3
1985	Gloria	Yes	24°	Sep	41	4	1	180	4
1991	Bob	No	75°	Aug	41	3	2	180	5
1996	Bertha	Yes	34°	Jul	34	3	2	135	3
1998	Bonnie	No	48°	Aug	34	3	2	180	2
1999	Floyd	No	46°	Sep	34	4	2	135	3

Predicting wrecks based on storm characteristics

Because not all storms produced specimens of BCPEs (i.e. 'wrecks'), we compared characteristics of storms that resulted in wrecks with those that did not. Information on the path, strength, and timing of tropical cyclones was obtained through internet archives (www.nhc.noaa.gov/pastall.shtml). All attributes of hurricanes summarized in Tables 1 & 2 (hurricane name, maximum strength, etc.) were derived from NOAA data. Using model selection, we fitted data on the occurrence/non-occurrence of wrecks resulting from major storms (Category 3 or greater) off the eastern seaboard between 1893 and 2003. During this time, there were a total of 30 major landfalling hurricanes, of which 8 produced wrecks (Fig. 1, Table 1). Of these, 6 were 'Cape Verde' hurricanes that originated east of 36° W. Seven of the 8 storms struck the coast directly (only 1 collided with the coastline at an angle of <45° or >135°), and all made landfall as Category 2 storms or greater. Hurricanes that had nearly parallel paths to the coastline (i.e. landfall angles that were very acute or obtuse) seldom produced mortality or inland petrels (Table 2). From these observations, we generated a candidate set of models with storm-specific occurrence/non-occurrence of wrecks as a binomial response (logit link) and, fixed effects of Cape Verde classification (categorical), month (continuous), landfall strength (categorical), recurvature (categorical), latitude at landfall (continuous), landfall angle (continuous), maximum storm strength (categorical), and radii at recurve (continuous). Maximum hurricane-force winds generally extend 62.5 nautical miles (n miles; ~115.75 km) from the center of a storm (also termed the 'strike circle'); therefore, to quantify how far from the coast a hurricane turned north (recurved), we used the number of hurricane-force wind radii as the unit of measure — with higher positive numbers indicating farther offshore and lower negative numbers signifying turns occurring farther inland. Using StepAIC (a library for the R statistical package) we identified a set of 4 model formulations that resulted in the greatest parsimony, and then calculated the model weights of these models based on their Akaike's information criterion (AIC) scores (Table 3).

Simulating future wrecks

In order to simulate the expected number of petrel mortalities due to storms over the next 100 yr, we: (1) generated 100 000 random draws of integers from a Poisson distribution fitted to data on the number of yearly storm occurrences between 1893 and 2003,

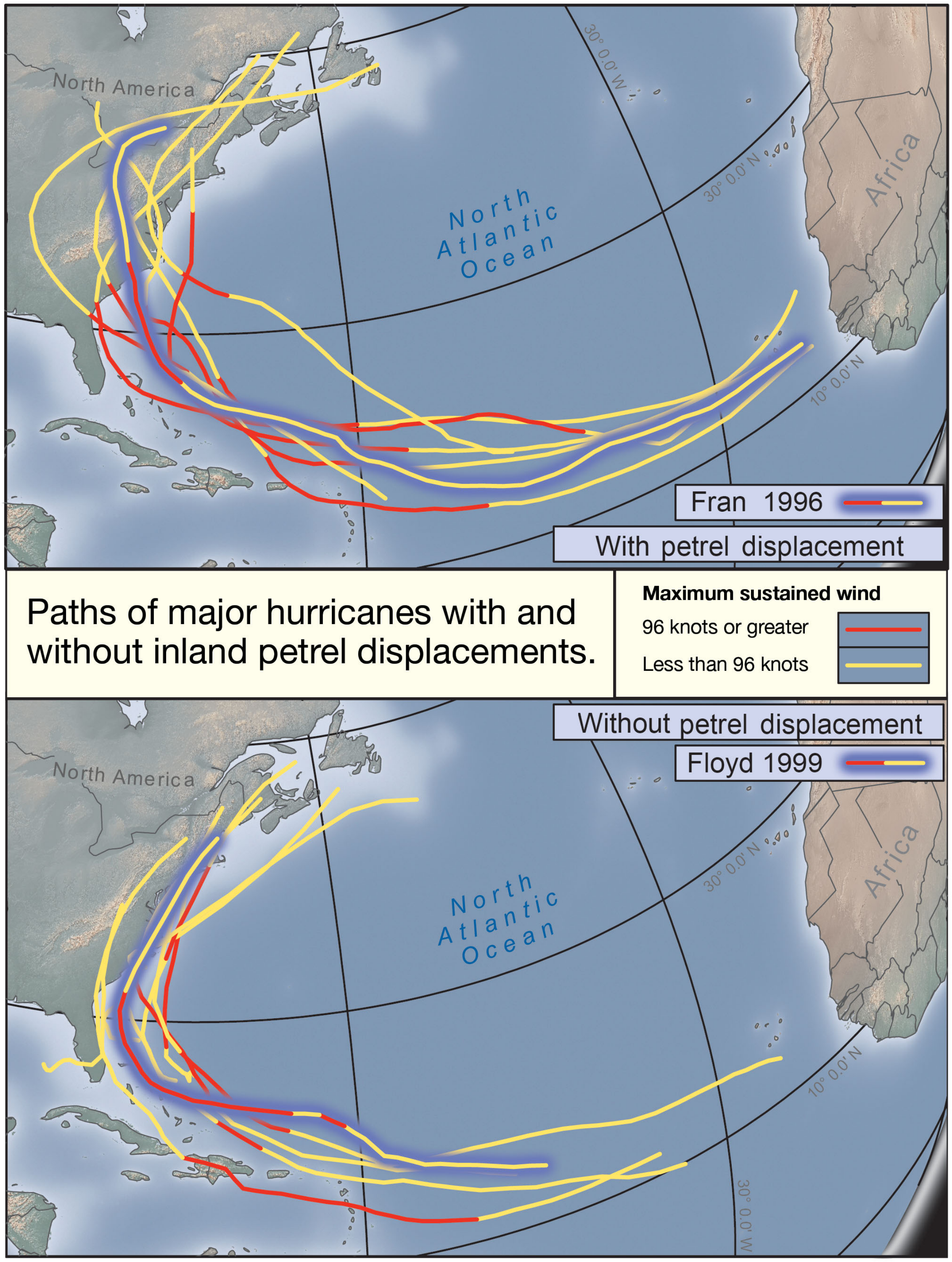

Fig. 1. *Pterodroma hasitata*. Top: paths of all major landfalling hurricanes (1893 to 2003) that displaced black-capped petrels inland exhibit origins near Cape Verde and strike the coast before recurving. Highlighted path is that of Hurricane Fran (1996), a typical storm-track for this category. Bottom: paths of all major landfalling hurricanes (1960 to 2003 only) that did not displace black-capped petrels show more westward origins and recurving trajectories than those producing petrel specimens. Highlighted path is that of Hurricane Floyd (1999), a typical storm-track for this category. Key characteristics (e.g. maximum strength, landfall date, etc.) for each hurricane are summarized in Tables 1 & 2. Map generated using NOAA Coastal Services Center data (http://csc-s-maps-q.csc.noaa.gov/hurricanes/viewer.html)

Table 3. *Pterodroma hasitata*. Goodness-of-fit models and scores of Akaike's information criterion (AIC). Variables include: whether a Cape Verde-type hurricane (VERDE), latitude at landfall (LANDFALL_LAT), strength at landfall (LAND_STRENGTH), distance from coast when hurricane turned north (RECURVE_RAD), maximum hurricane strength (MAX_STRENGTH), angle of hurricane landfall along coast (ANGLE), and month of landfall (MONTH)

Model formulation	AICc	ΔAICc	Weight
VERDE + LANDFALL_LAT + LAND_STRENGTH + RECURVE_RAD	25.03	0	0.49
VERDE + LANDFALL_LAT + MAX_STRENGTH + LAND_STRENGTH + RECURVE_RAD	25.93	0.9	0.31
VERDE + MONTH + LANDFALL_LAT + MAX_STRENGTH + LAND_STRENGTH + RECURVE_RAD	27.46	2.43	0.14
VERDE + MONTH + LANDFALL_LAT + MAX_STRENGTH + LAND_STRENGTH + ANGLE + RECURVE_RAD	29.825	4.22	0.06

(2) re-sampled the coefficient values for the models in Table 3 with replacement using storm data between 1893 and 2003, and (3) generated random draws from a log-normal distribution fitted to data on the number of BCPEs present off the eastern seaboard based on monthly boat-based transects between July and September (month included as a continuous effect). For 100 000 simulations, annual mortality in each of the next 100 yr based on simulated storm occurrences for each year (based on random draws in 1 above), their likelihood of causing wrecks (based on the coefficient draws in 2 above), and the number of birds wrecked (based on random draws in 3 above) was derived. The likelihood that storms caused wrecks was calculated based on model averaging (Table 3). In other words, we used predictions from each model in proportion to their model weights. To evaluate the overall model fit within the candidate model set used, we conducted a receiver-operating characteristic (ROC) analysis to assess the sensitivity and specificity of the model with the lowest AIC score (Fig. 2). The area-under-the-curve score (true positive rate) of 0.943 resulting from this analysis suggests that our candidate model set was well specified.

Predicting hurricanes from climate change

Recent stochastic and dynamic climate models predict a slight increase in the intensity of future North Atlantic hurricanes (7 and 10.3%, Turner 2011 and Emanuel et al. 2008, respectively), largely due to the increased genesis of long-lived and powerful Cape Verde hurricanes (Knutson et al. 2010). Bender et al. (2010) anticipate that landfall rates for Category 4 to 5 hurricanes will increase 10% per decade over the next century—doubling their incidence by 2100. Similarly, Turner (2011) forecasts that Category 3 to 5 hurricanes will nearly double in landfall frequency between 2011 and 2015 and that continued 'warm scenario' conditions will promote increased genesis of Cape Verde hurricanes. Consequently, we integrated a 1%-per-year increase in the incidence of major hurricanes over the next 100 yr to our model.

RESULTS

Wrecked petrels

In the literature and museum records, we located at least 82 inland records of black-capped petrels *Pterodroma hasitata* (1893 to 2003) associated with the passage of tropical cyclones that were classified as 'major' (Saffir-Simpson Categories 3 to 5) during some point in their development. No petrel carcasses were recovered after a major (or minor) hurricane made landfall in Florida, so we restricted our analysis to hurricanes that came ashore north of Florida (Tables 1 & 2). Petrels have occasionally been seen

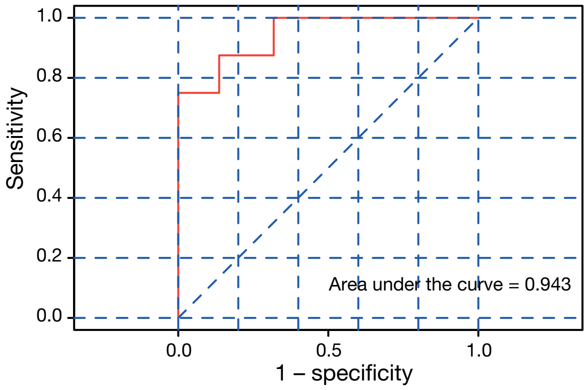

Fig. 2. Plot of the relationship between true positive (sensitivity; *y*-axis) and false positive rate (1 – specificity; *x*-axis) based on the parameters derived from the model with the lowest score of Akaike's information criterion (AIC) identified in Table 3. The area under the curve term indicates the true positive rate resulting from the model prediction

from shore during smaller (Categories 1 to 2 maximum) hurricanes. So far, however, none of the smaller magnitude storms have displaced petrels inland or resulted in mortality (based on museum holdings). For instance, although 3 petrels were seen from shore in North Carolina following the landfall of Category 1 Hurricane Ophelia in 2005, no dead petrels were reported (Dinsmore & Farnsworth 2006). Since minor hurricanes and tropical storms do not appear to be significant mortality agents, we have excluded such records from our analysis. Of the 82 sight records of inland BCPEs, 48 were substantiated by a bird-in-the-hand. The present study concentrated only on the most recent carcass material, from 1989–2003, or 37 total specimens, because birds salvaged in recent decades tended to have more consistent data recorded for molt, sex, and body condition.

The Carnegie Museum of Natural History prepared 2 skins of BCPEs associated with Hurricane Hugo (1989) and another after Hurricane Fran (1996); all 3 showed evidence of molt in rectrices or contour feathers, strongly suggesting they were adult birds. Birds only a few months past fledging would almost certainly not be in active molt of rectrices (Imber 1976, Warham 1996). Also associated with Hurricane Fran, 8 petrels stored at the Royal Ontario Museum (ROM) showed evidence of molt and were categorized as adults. Only 4 of those 8 individuals were salvaged in good enough condition to allow evaluation of the bursa of Fabricius. None had a bursa, confirming their status as likely breeding-age adults (Broughton 1994). Furthermore, of the 8 intact skulls among the ROM specimens, all showed full ossification (i.e. fusion) of the frontal/prefrontal bones, confirming their ages as after hatch-year (Harper 1978). Two Smithsonian specimens wrecked by Hugo were molting females, but 1 of them had a bursa, indicating that it was greater than 1 yr old but likely of prebreeding age. At the Cornell University Museum of Vertebrates, the 2 petrels salvaged after Fran have uniformly fresh plumage, and were categorized as hatch-year birds. Thus, in our sample of 15 specimens, adult birds outnumbered young (probable yearlings) birds by a ratio of 13:2. This adult bias is not surprising given that the ratio of adult to hatch-year birds collected at sea off North Carolina is 56:3 (T. R. Simons et al. unpubl. data). While males outnumber females by a ratio of 2:1 in those specimens (not 9:1 as reported by Lee 1999), we found that among the 13 wrecked petrels for which sex could be determined, an opposite sex ratio was apparent (5 males:8 females). Although our model is based on deaths of individuals, it assumes a 50:50 sex ratio.

Mechanism of displacement

A direct path toward the coast is key to whether a hurricane wrecks petrels or not (Tables 1 & 2). We hypothesize that when west-approaching hurricanes recurve (turn north to northeast) north of Florida, the flight space and prevailing winds that exist between the storm's perimeter and the coastline serve as a corridor through which birds are funneled to shallower, nearshore waters along the eastern seaboard (Fig. 3). Indeed, on average, hurricanes that did not produce specimens tended to recurve when almost 240 n miles east of the coast, while those producing carcasses pushed inland nearly 180 n miles before turning north (Tables 1 & 2).

Simulated consequences for breeding population

The mode value in our simulation (Fig. 4) suggests that over the next century, in the absence of climate change, landfalling hurricanes would most likely kill approximately 437 petrels. Because of the preponderance of adults among the wrecked specimens (>80%) and in the population at sea off the southeastern United States (95%), this represents an anticipated loss of at least 415 breeders — or 10.4% of the 4000 individuals estimated in the current breeding population. About 7% of the simulations result in

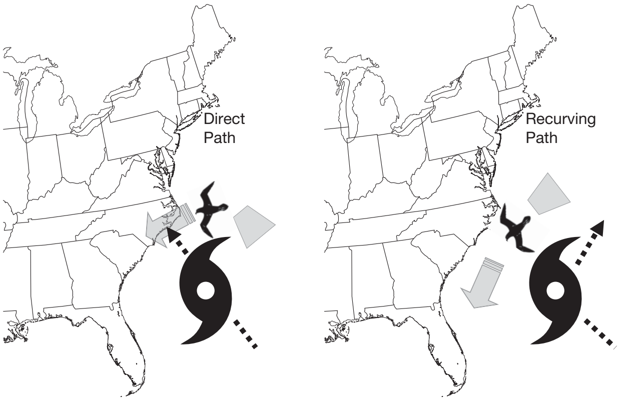

Fig. 3. *Pterodroma hasitata*. Mechanism of black-capped petrel inland displacement or non-displacement by hurricanes. On average, landfalling major hurricanes that did not produce specimens turned north (recurved) when >240 nautical miles offshore, while petrel-producing hurricanes turned north after pushing 180 nautical miles inland. When North Atlantic hurricanes recurve, the extra over-water flight space that is created between the storm's perimeter and the coastline serves as a corridor through which petrels are funneled to shallower, nearshore waters. When hurricanes make landfall on a direct course, no such corridor is created and petrels are swept inland

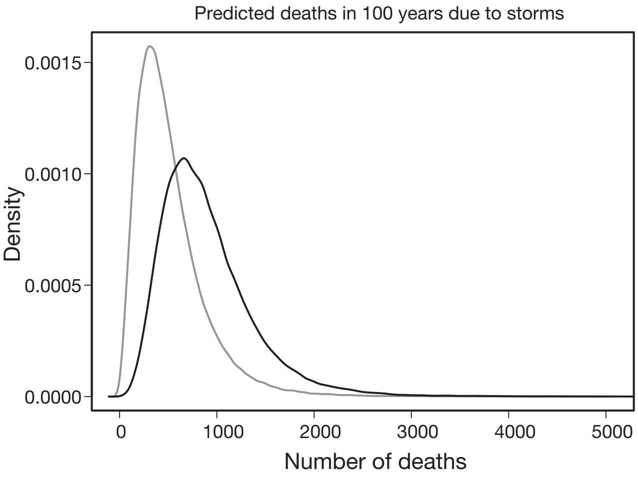

Fig. 4. *Pterodroma hasitata*. Predicted deaths of black-capped petrels in 100 yr due to storms. If the hurricane activity over the next century is similar to that over the last century, across 100 000 simulations, the median cumulative number of deaths of black-capped petrels is 437 (grey line). The chance that >1050 (or one-quarter of the estimated breeding population) will die is 7%. If the rate of major landfalling hurricanes rises 1% annually due to climate change (doubling over the next century as predicted), the median cumulative mortality is 807 petrels (black line), with a 3% chance that 2100 individuals (half the breeding population) would die due to hurricanes

mortality of >1050 individuals (or 1000 breeders)—which would reduce the extant breeding population by 25%. If the rate of major landfalling hurricanes increases by an annual rate of 1% due to climate change (Bender et al. 2010, Turner 2011), doubling by the end of this century, the median cumulative mortality is 807 petrels, with a 3% chance that 2100 individuals would die due to hurricanes. However, though some estimate the breeding population to be ~4000 individuals (Brooke 2004, Keith 2009), Lee argued more than a decade ago (Lee 1999, 2000) that the number of breeders was only 1200 to 2600 individuals—which would put the entire breeding population at risk of extinction if the cumulative mortality exceeds 1200 over the next century.

DISCUSSION

Considerable direct mortality from hurricanes has occurred over the past century

Over the last 2 decades, the documented hurricane mortality of black-capped petrels *Pterodroma hasitata* has totaled >30 individuals, although many of the additional 50 individuals observed far inland were probably weakened birds that also perished. Considering the vast areas of ocean and land that these storms affect, along with the relative dearth of people who actively seek hurricane-displaced seabirds (and even smaller number engaged in specimen salvage), the total number of BCPEs killed by hurricanes is certainly far greater than that documented by museum specimens. By systematically surveying a subset of shorelines around Lake Erie and Lake Ontario, Curry (1996) conservatively estimated that for every specimen salvaged or seen dead/floating but unretrieved (n = 23), an additional 2 petrels were killed but not found, bringing the total regional mortality to about 70 birds. At least 7 BCPEs were recovered after Hurricane Hugo, and Kaufman (1990) asserted that many times that number must have been killed by the storm. After both hurricanes Hugo and Fran, petrels not only wrecked on large bodies of water, but also in high, remote terrestrial sites—like mountaintops—that could not be systematically surveyed (Brinkley et al. 1997).

The loss of 10s to 100s of individuals during a *single* hurricane might not represent a demographic threat to a species with a world population estimated at 2000 breeding pairs (Brooke 2004). However, many climate change models suggest that rising sea-surface temperatures in the tropical North Atlantic will lead to future hurricanes that are more intense and/or greater in number (Knutson & Tuleya 2004, Michaels et al. 2006). Petrels, having evolved in a system of cyclonic activity that is subject to such multi-decadal variability, should perhaps be resilient to normal extremes. However, we propose that their populations, facing numerous other conservation challenges (nest site destruction, introduced predators, direct harvest by humans, etc.) will become increasingly vulnerable to additional decline if the coming decades/centuries continue to show cyclonic activity in the North Atlantic Ocean that is markedly higher than the long-term average (Trenberth 2005).

Petrels frequently aggregate in the likely paths of hurricanes

During 67 offshore surveys in July to September near Cape Hatteras, between 1992 and 1998, the lead author and Brian Patteson encountered extremely dense concentrations (>500 individuals seen per day) of BCPEs at sea twice (3% of daily counts) and moderately dense concentrations (>150 individuals) 10 times (15% of daily counts). The species' propensity for aggregation near Cape Hatteras, North Carolina (the area of most frequent hurricane landfall in the eastern United States) during the height of the Atlantic tropical storm season is particularly alarming, because moderately and extremely dense aggregations of petrels would be expected to be in the *direct path* of about 1 in 6 and 1 in 33 major hurricanes approaching Cape Hatteras, respectively. Haney (1987) documented similarly elevated abundances off South Carolina and Georgia, so the chance intersection between a moving hurricane and an aggregation of petrels is not confined to Gulf Stream waters off North Carolina.

Petrel flight tendencies promote vulnerability to displacement

In the Northern Hemisphere, seabirds to the north of a cyclone would tend to take a westward course when the prevailing winds shift from an easterly to a more northern component (Blomqvist & Peterz 1984), a behavior that would promote escape from recurving hurricanes. Note that the median size of petrel-producing hurricanes at landfall was Category 3 compared to Category 2 for those without carcasses; the smaller hurricanes would be surrounded by smaller wind fields (narrower radii of hurricane-force winds), broadening the crosswind/tailwind corridor for birds described above. Indeed, Adams & Flora (2010) recently demonstrated that *Pterodroma* petrels tend to travel with quartering tailwinds, allowing them to circumnavigate mega-scale high-pressure systems. Such a tendency would tend to disperse birds flying to the south of a hurricane away from the system; while petrels located north and west of the system would be vulnerable to being pushed onshore by large hurricanes making direct landfall. Whereas more than one-quarter of major hurricanes that made landfall north of Florida produced inland petrels, none of the 11 major hurricanes that struck Florida between 1893 and 2003 produced a single petrel specimen. We believe that Florida's narrow, peninsular shape and proximity to the Gulf of Mexico probably provides an opportunity for petrels to escape to the southwest.

Numerous hurricanes have blown BCPEs outside their 'normal' marine range — to colder, continental shelf waters as the storms have progressed northward in latitude (Mörzer Bruyns 1967, Finch 1972, Dinsmore & Farnsworth 2006). Such observations of multiple petrels along the advancing margins of hurricanes are contrary to the proposition that petrels are likely entrained in the calm eyewall of hurricanes and disperse after landfall (Murphy 1936). Sooty terns *Onychoprion fuscatus* are also strictly pelagic and appear particularly vulnerable to hurricane-driven displacements (Murphy 1936, Brinkley 1999). Murphy's (1936) description of flocks of sooty terns *preceding* the arrival of hurricanes in the Lesser Antilles is consistent with the mechanism of displacement for that species and BCPEs witnessed along the east coast of the United States. As the Gulf Stream between Florida and North Carolina appears to represent the principle foraging range for adult BCPEs (Haney 1987), any factor that displaces petrels far from the center of their known range is likely detrimental.

During the Atlantic hurricane season, satellite-tracking studies have revealed that the Bermuda petrel *Pterodroma cahow*, another critically endangered petrel, tends to forage in 2 principal areas — near the Azores, and north and west of Bermuda (Madeiros 2010). Both areas lie within the influence of Cape Verde hurricanes, and, furthermore, these foraging hotspots (used by the species in the non-breeding season) are located north and west of such advancing hurricanes. Because Bermuda petrels are known to use tailwinds to 'slingshot' around the perimeter of storm systems (Madeiros 2010), the positioning of these key foraging areas is likely to raise the species' vulnerability to being pushed inland as individuals transit downwind.

Persistence of Gulf Stream path during climate change should sustain petrels

At sea, the BCPE appears to be an obligate of Gulf Stream waters off the southeastern United States and aggregates where deepwater upwelling occurs (Haney 1987, Hass 1997). Hence, any changes in the circulation of the Gulf Stream due to climate change might affect the species. Lynch-Stieglitz et al. (1999) demonstrated that during the last glacial maximum, the strength of Gulf Stream transport was only two-thirds of that seen today. While it is difficult to predict how reduced transport in the Gulf Stream might affect the frequency and magnitude of many dynamic sources of upwelling (e.g. meanders and eddies), static upwelling sites, where upwelling is topographically induced (like the Charleston Bump and Cape Hatteras slope) seem likely to persist over time. Several authors have shown that a shutdown of the 'global conveyor belt' is possible during either cold or warm conditions (Alley et al. 1997, Broecker 1997). Although the Gulf Stream is likely to weaken during such a thermohaline collapse, its position is merely expected to switch from its present meridional course (heading northeast from Cape Hatteras), to a zonal heading (east from Cape Hatteras) (Matsumoto & Lynch-Stieglitz 2003, Rossby & Nilsson 2003). This should preserve the Gulf Stream's path (and processes) in the South Atlantic Bight, in the center of the petrels' pelagic range.

Climate change, human settlement and historic declines of tropical Atlantic petrels

Olson (1975) previously implicated Pleistocene 'environmental change' and associated shifts in marine productivity as leading to the decline and extinction of *Pterodroma rupinarum* and 2 other tropical tubenoses on St. Helena Island in the tropical South Atlantic. *P. rupinarum* bred on St. Helena at a comparable latitude (17° S) to BCPEs, and the already extinct Jamaica petrel *P. caribbaea* bred in the Caribbean (18° to 20° N), but declined markedly during non-glacial times. The final demise of both *P. rupinarum* and *P. caribbaea* coincided with human habitation. Recent conservation efforts for the critically endangered Bermuda petrel *P. cahow* have attempted to shift burrows/colonies to higher ground to minimize vulnerability to sea-level rise, hurricanes, and associated storm surges (Wingate & Talbot 2003). As their breeding population has grown and offshore surveys have become more frequent, Bermuda petrels have been found regularly in the Gulf Stream off North Carolina (Wingate et al. 1998, Patteson & Brinkley 2004) during the hurricane season, so it seems likely that someday this species too may appear inland among the wrecked. Because BCPEs breed on remote cliff faces in Hispaniola outside the hurricane season, they are not likely to suffer direct mortality at the nesting grounds—though hurricane-induced mudslides and destruction of vegetation could destroy burrows (Goetz et al. 2011).

Simulated hurricane-related mortality has population-level effects on petrels

When population viability analyses are used to estimate extinction risk for the long term, they usually account for episodic, but extreme catastrophes (e.g. 100 and 500 yr droughts, floods, etc.) that may lead to population bottlenecks or other adverse demographic effects. If the past century of hurricane data and seabird die-offs is representative of the long term, BCPEs will face a demographic threat from major Atlantic hurricanes for millennia. Much like migratory shorebirds that briefly aggregate at stopover sites, petrels frequently exhibit extreme aggregations in space and time. Thus, on the rare occasion that a petrel aggregation (or a known migratory or foraging hotspot) is in the path of a hurricane (or oil spill, etc.), elevated mortality will likely result.

Data from pelagic surveys suggest that moderate to extreme aggregations of BCPEs occur every 5 d at sea. Such propensity for aggregation (or flocking) means that a significant fraction of the world's population may be in jeopardy if they have happened to amass in the path of a hurricane that is: Category 3 or greater, on a direct course to make landfall, and arose in the eastern North Atlantic (Table 3). Using the past 110 yr as a baseline, our model suggests that, in the absence of climate change, the most probable scenario is the loss of about 10% of the estimated breeding population over the next century due to hurricane wrecks. When factoring in climate change—a gradual doubling in the frequency of major landfalling hurricanes—the likeliest mortality is about one-fifth of 4000 breeders. However, 1 in 33 simulations demonstrated a loss of 2000 breeders. Considering that 40% declines were already witnessed during a 2-decade lull in hurricane activity (Woods & Ottenwalder 1986), any projections of additional double-digit reductions are distressing. While the above percentages reflect the relative impacts if the breeding population is 2000 pairs (Brooke 2004, Keith 2009), Lee (1999, 2000) asserts that the number of breeders may be as low as 600 to 1300 pairs—which would magnify the proportional effects and produce a small chance that hurricanes might wipe out the entire the breeding population by 2111. Given that the species is already in rapid decline due to other sources of mortality and shows no signs of above-replacement population growth, the deaths of 2100 individuals (mostly breeders)—solely due to hurricanes—over the next century could either cause or significantly contribute to the species' demise. Since our mortality projections only examine the demographic threat posed by hurricanes, we strongly advocate for a greater understanding and mitigation of other mortality sources if the species is to avoid the risk of a population bottleneck, or worse, extinction.

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Contribution to the Theme Section 'Seabirds and climate change'

Seasonal ocean temperature and the survival of first-year little penguins *Eudyptula minor* in south-eastern Australia

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ABSTRACT: Ocean temperature has been shown to be related to various demographic parameters in several seabird species, but ultimately its influence on breeding success and survival are paramount. The timing and success of breeding of little penguins *Eudyptula minor* in south-eastern Australia have been shown to correlate with local sea-surface temperatures (SST) and the east–west sea-temperature gradient across Bass Strait several months earlier. However, the causal links between ocean temperature and these demographic variables are not readily apparent due to their lagged nature. Using 41 yr of data on little penguins in south-eastern Australia, we carried out a mark-recapture analysis to examine if the changing SST and sea-temperature gradient (east–west difference between 2 locations in Bass Strait) are associated with survival probability in the first year of life. First-year survival is correlated with (1) an east–west sea-temperature gradient in Bass Strait in the winter after fledging, with an increased temperature gradient associated with decreased survival and (2) the mean SST in the autumn after fledging, with warmer seas associated with increased survival. SST alone does not provide the best model for explaining first-year survival. Projections suggest that SST in south-eastern Australia and sea-temperature gradient in Bass Strait will both increase due to global warming. The net effect of an increased sea-temperature gradient in winter (which has a negative influence) and increased SST in autumn (which has a positive influence) on first-year survival is uncertain, given the current lack of knowledge concerning the relationship between the sea-temperature gradient and SST in Bass Strait.

KEY WORDS: *Eudyptula minor* · Little penguin · Mark-recapture · First-year survival · Sea-surface temperature · Temperature gradient · Climate change · Phillip Island · South-eastern Australia

INTRODUCTION

Climatological variables play a role in the functioning of marine ecosystems and the productivity of species at both large and local scales (Mills et al. 2008, Sydeman & Bograd 2009, Ainley & Hyrenbach 2010, Ainley et al. 2010). Changes in regional sea temperature have been shown to influence the distribution, phenology, productivity and survival of seabirds (Inchausti et al. 2003, Frederiksen et al. 2007, Irons et al. 2008, Cullen et al. 2009, Moe et al. 2009, Ainley et al. 2010, Barbraud et al. 2011, Chambers et al. 2011). These influences can be positive or negative and usually precede life-history events by months or even years (Mickelson et al. 1992, Guinet et al. 1998, Barbraud et al. 2011). These lags suggest that the mechanisms are operating on productivity at trophic levels below the apex or mesopredator levels of most sea-

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birds (Cullen et al. 2009), rather than having immediate effects on the physiology or behaviour of the birds. More immediate effects of temperature on seabirds may involve relationships between temperature and the distribution and availability of prey. For example, Ropert-Coudert et al. (2009) have proposed that the presence of thermoclines may assist foraging success in little penguins *Eudyptula minor*.

Local-scale climate signals from the marine environment (i.e. temperature, wind and precipitation) also affect demographic processes in some species (Aebischer et al. 1990, Kitaysky et al. 2000, Gjerdrum et al. 2003). In other cases, reproduction and recruitment can be influenced by both large- and local-scale climatic processes (Weimerskirch et al. 2003, Sandvik et al. 2005, Votier et al. 2005).

Several studies have shown relationships between sea temperature in Bass Strait and the breeding of little penguins from Phillip Island in south-eastern Australia (Mickelson et al. 1992, Cullen et al. 2009). Mickelson et al. (1992), who defined the east–west sea-surface temperature (SST) gradient across Bass Strait used here as the difference in SST between 2 sites in Bass Strait (Site 1: 39 to 40°S, 145 to 146°E and Site 2: 38 to 39°S, 149 to 150°E) (Fig. 1), found that a decreased east–west sea-temperature gradient (i.e. warmer west and/or cooler east SST) was associated with increased weights of adults 4 mo later and a July to August decrease in sea-temperature gradient was associated with an early start to egg-laying in September to October. They proposed that these were due to the cooler waters from the west, with their higher levels of nutrients and associated higher levels of primary and secondary production, penetrating further east into central Bass Strait and closer to Phillip Island (Mickelson et al. 1992). Cullen et al. (2009) found that the timing and success of breeding was correlated with local SST in autumn a few months prior to the onset of breeding. Their model predicted an early egg-laying date, higher average chick mass at fledging and more chicks produced per breeding pair when SST in Bass Strait is warmer than average in March. They proposed 2 potential mechanisms for the lagged positive relationship between SST and breeding which were that warmer SST allowed for a longer and hence more productive breeding period or that the warmer SST provided conditions that translated into greater availability or quality of food.

SST around south-eastern Australia is influenced by waters from 4 regions (Gibbs 1992), and, in Bass Strait, there are 2 primary influences on SST: the East Australian Current (EAC) and the easterly flowing mixture of warm, nutrient-poor subtropical water and the nutrient-rich cool subantarctic water (Gibbs 1992). Bass Strait water around Phillip Island originates mostly from the west, flowing east across South Australia along the Australian south coast as low-nutrient subtropical water from the Great Australian Bight (Fig. 1). The EAC flows southwards, bringing eddies of warm nutrient-poor tropical water from the

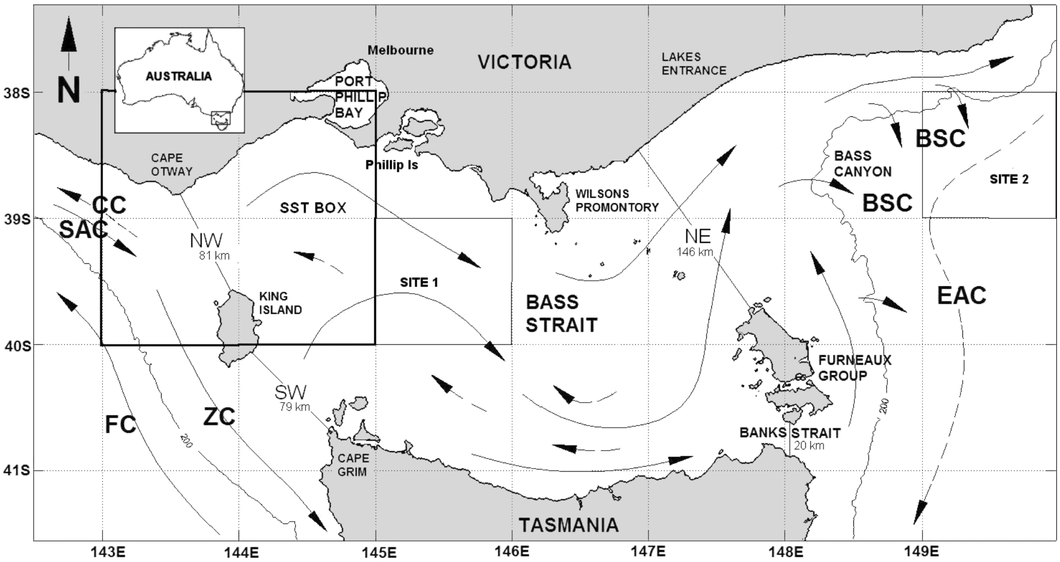

Fig. 1. Study area showing the locations of Phillip Island (38° 31′ S, 145° 08′ E), the sea-surface temperature (SST) box, and the 2 sites used to measure the sea-temperature gradient in Bass Strait. The SST box covers 143 to 145°E, 38 to 40°S; Site 1 covers 145 to 146°E, 39 to 40°S; Site 2 covers 149 to 150°E, 38 to 39°S. Also shown is a schematic representation of the currents in the Bass Strait region (from Sandery 2007). Summer currents are denoted by dashed lines. EAC: East Australian Current; SAC: South Australian Current; ZC: Zeehan Current; FC: Flinders Current; CC: summer Coastal Current; BSC: Bass Strait Cascade

Pacific Ocean into eastern Bass Strait (Ridgway & Hill 2009). Ridgway & Hill (2009) predicted that the EAC will become stronger in the future and extend further south. In the south and in deep water beyond the continental shelf on the western side of Bass Strait, the cold nutrient-rich subantarctic water originates from below the Subtropical Convergence Zone and the eastward flowing Antarctic Circumpolar Current. The interaction of these 4 water masses, which are influenced by the seasonal wind patterns, has a significant impact on the sea temperature of Bass Strait (Gibbs 1992). Within Bass Strait, the extent and influence of currents and water masses vary seasonally and inter-annually (Sandery 2007) (Figs. 1 & 2). Intrusions of cooler, nutrient-rich water through the western entrances of Bass Strait occur mainly during winter and spring and are driven primarily by local and remote winds (Newell 1966, Tomczak 1985, 1987, Gibbs et al. 1986, Middleton & Black 1994). Two areas of high productivity occur in northern Bass Strait, a localised coastal upwelling in the west (Bonney Upwelling) and a nutrient enrichment zone in the east (Bulman et al. 2011).

There is no post-fledging parental care in little penguins (P. Dann pers. obs.), and the apparent survival in the first year of life is low at 0.165 (SE = 0.007; Sidhu 2007). The peak mortality period for first-year birds is in the late summer and autumn (February to April) following fledging (Dann et al. 1992). Recoveries of flipper-banded first-year birds indicate that they travel several hundred kilometres west of Phillip Island in the months post-fledging, possibly to take advantage of the more nutrient-rich waters associated with the edge of the continental shelf and the Bonney Upwelling (Dann et al. 1992). This area is beyond the usual foraging areas of adults from Phillip Island (Dann et al. 1992, Dann & Norman 2006, McCutcheon et al. 2011) and may be indicative of more productive feeding areas. The restricted foraging range of penguins suggests that they are likely to have more precise responses to local ocean conditions in comparison to volant seabirds.

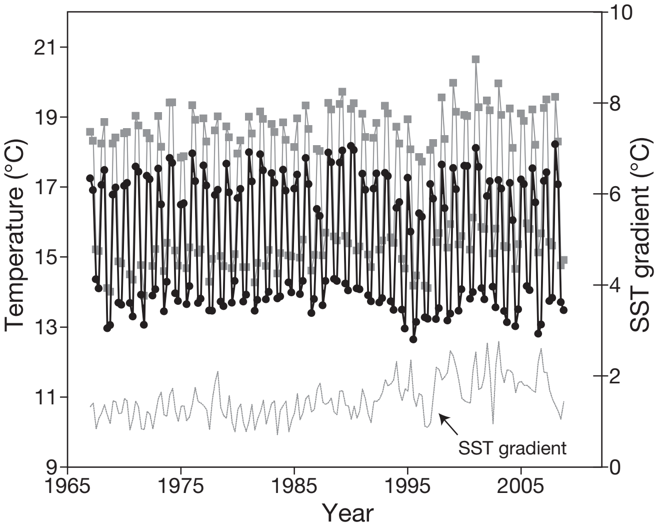

Fig. 2. Seasonal and inter-annual variability in sea-surface temperature (SST) in the Bass Strait region over the period of the study. SST at Site 1 (Fig. 1) in western Bass Strait is represented by the solid black line and circles; SST at Site 2 in eastern Bass Strait by the solid grey line and squares. The difference between SST at Site 2 and Site 1, the sea-temperature gradient, is also indicated

Given the potential effect of SST on the survival of little penguins, projected changes to ocean temperature may well have a significant effect on the viability of this species in Bass Strait, one of the strongholds for little penguins (Dann et al. 1996). Predictions are for the eastern side of Bass Strait to warm more than the western side (Hobday et al. 2008). By 2070, ocean warming around Australia is projected to be in the range of 2 to 3°C, with the greatest warming off south-eastern Australia (3°C) (Fig. 5 in Poloczanska et al. 2007). In fact, Poloczanska et al. (2007) make the following prediction: 'Waters around Australia are projected to warm by 1 to 2°C by the 2030s and 2 to 3°C by the 2070s (Fig. 5 [in Poloczanska et al. 2007]). The CSIRO climate model projects the greatest warming off southeast Australia, and this is the area of greatest warming during this century in the entire Southern Hemisphere. This Tasman Sea warming is associated with systematic changes in the surface currents on the east coast of Australia, including a strengthening of the EAC and increased southward flow as far south as Tasmania (Fig. 5 in Poloczanska et al. 2007). This feature is present in all IPCC climate model simulations, with only the magnitude of the change differing among models. Changes in currents leading to the Tasman Sea warming observed to date are driven by a southward migration of the high-latitude westerly wind belt south of Australia, and this is expected to continue in the future' (Poloczanska et al. 2007, p. 414).

Relationships have previously been reported between sea temperature and survival of adult seabirds (e.g. Harris et al. 2005, Rolland et al. 2008, Barbraud et al. 2011), but much less commonly with immature birds (Votier et al. 2008). Votier et al. (2008) found a weak negative relationship between winter SST and recruitment in immature common guillemots *Uria aalge*. An additional motivation for the present study was that since Mickelson et al. (1992) and Cullen et al. (2009) observed relationships between local SST or sea-temperature gradient and breeding variables for little penguins, an examination of the potential relationship between sea temperature and survival is the next logical step in building models to determine how sea temperature change may influence little penguins. Although our work is focussed on 1 species in 1 region, the significance of this demographic study of a marine mesopredator and the relationship with ocean temperatures over an unusually long time series has implications for marine ecosystems worldwide.

We use a 41 yr mark-recapture dataset from a breeding colony of little penguins on Phillip Island to examine the relationships between the annual first-year survival probability and local SST and sea-temperature gradient in Bass Strait. We hypothesise that increased SST is associated with increased first-year survival, in light of the significant positive relationship found between SST and the timing and success of breeding by Cullen et al. (2009). Given that Mickelson et al. (1992) found that decreased temperature gradient was associated with increases in adult weight and earlier egg-laying, we form a second hypothesis that a decreased sea-temperature gradient is also associated with increases in first-year survival.

METHODS

Mark-recapture analysis

A total of 54 484 little penguins *Eudyptula minor* were marked with devices that allowed them to be later identified: 41 660 with flipper bands between 1968 and 2003, and 12 824 with injected electronic transponders between 1987 and 2007. Initial marking and subsequent recaptures took place at Phillip Island (38° 31′ S, 145° 08′ E) in Victoria, south-eastern Australia, with the recapture data extending until 2008. These data comprise 34 483 birds marked as chicks and 20 001 marked as adults of unknown age. We have summarised these data into 12 mo cohorts (1 July to 30 June). Here 'mark' refers to the initial application of a tag (band or transponder), and 'recapture' denotes a subsequent live encounter (Catchpole et al. 1998, Sidhu et al. 2007). We use biologically realistic age structures for the model parameters that fit the lifestyles of little penguins (Sidhu et al. 2007). Recoveries of dead birds have not been included in the analysis since dead recovery data are not available for transpondered birds. A joint analysis of recovery-recapture data for banded birds and recapture-only data for transpondered birds could have been undertaken. However, Sidhu (2007) showed that the survival estimates of little penguins obtained under recovery-recapture and recapture-only analyses were almost identical and there was no improvement in the standard error when the recovery information was added.

The model parameters used are the annual survival probabilities and the recapture probabilities, defined as follows. Let $\phi_{i,j}$ be the probability that a bird survives the jth calendar year, given it was alive at the start of the year, where $i = 1$ in the first year of life and $i = 2$ for each subsequent year of life. P. Dann et al. (unpubl. data) showed that the mortality rate of banded birds is about one-third greater than that of transpondered birds. Therefore, the annual survival probabilities for both the first year of life and subsequent years are allowed to depend on whether a bird was flipper-banded or transpondered. At the sth stage of modelling, we fit $\text{logit}(\phi_{1,j}) = a_0 + a_1 V_{1,j} + \ldots + a_S V_{S,j} + bB$, where $\text{logit}(x) = \log[x/(1 - x)]$ is the log-odds ratio or logistic transform, the $V_{S,j}$ are the SST or sea-temperature gradient covariates, a_0, a_1, …, a_S and b are unknown parameters, and $B = 1$ for banded birds and $B = 0$ otherwise. At the second stage of modelling, we also incorporate a quadratic effect for the best-fitting covariate. When modelling first-year survival $\phi_{1,j}$, we allow adult survival $\phi_{2,j}$ to be fully time-varying, but with the time variation being the same for banded and transpondered birds, denoted as $\text{logit}(\phi_{2,j}) = d_j + e\,B$, where d_j and e are unknown parameters. We write this symbolically as $\phi_2(t + B)$, where t denotes time.

Let $p_{i,j}$ be the probability that a bird is recaptured in the $(j + 1)$th breeding season, given it was alive then, where $i = 1$ in the first year of life, $i = 2$ in the second year, and $i = 3$ in each subsequent year. In all of the models examined here, we use an 'age + time' model for recapture, with

$$\text{logit}(p_{i,j}) = f_i + g_j \qquad (1)$$

Here f_1, f_2 and f_3 are constants specific to the age groups, whereas g_j represents time-dependent parameters. This implies that time variation of the recapture probability is the same for each age group.

This model is a realistic reflection of the little penguin lifestyle. Separate annual survival probabilities are used for the first and subsequent years of life, as first-year birds are particularly at risk due to inexperience and internal parasitic loads (Dann 1992, Dann et al. 1992, Harrigan 1992). Furthermore, since young birds go to sea and return to Phillip Island to breed at 2 or 3 yr of age, separate recapture probabilities are needed for the first, second, and subsequent years of life (Reilly & Cullen 1981, Dann & Cullen 1990, Sidhu 2007).

The likelihood is formed as in Burnham (1993) and Catchpole et al. (1998). We redefine the parameters for this paragraph only, so that the subscript i in $\phi_{i,j}$ and $p_{i,j}$ refers to the ith bird. The observed mark-recapture history of this bird is shown as an indicator vector h_i of length equal to the length of the study (here 42), with an entry 1 indicating that the bird was seen (initial capture or subsequent recapture) and a 0 that it was not seen. Let c_i and k_i denote the years of first and last capture, respectively, and let χ_r denote the probability of never being seen again after year r. We write the probability of the history h_i, conditional on the initial capture at c_i, as:

$$L_i = \left\{ \prod_{j=c_i}^{k_i-1} \phi_{i,j} p_{i,j}{}^{h_{i,j+1}} (1-p_{i,j})^{1-h_{i,j+1}} \right\} \chi_{k_i} \tag{2}$$

and this is the likelihood for bird i. The likelihood for the whole data set is the product $L = \prod_i L_i$ over all birds. This is known as the Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965). For further details of our methods see Ganendran et al. (2011) and Sidhu et al. (2011). The analysis is conditional on the observed covariate values, and so does not assume anything about their autocorrelation structure. The main assumptions in forming the likelihood are that the population is homogeneous, and that birds behave independently of each other and of their actions in previous years (for example, that breeding in one year does not influence the likelihood of breeding and hence being captured in following years). The likelihood is then maximised (or, equivalently, the negative of the log-likelihood is minimised) using the Matlab fmincon function. Matlab code is available from http://pems.unsw.adfa.edu.au/staff/profiles/catchpole_t.

Model selection is via the Akaike information criterion (AIC; Burnham & Anderson 2002). The fit of a model with log-likelihood l is measured by the proportion of the total (time) deviance explained, $(l - l_0)/(l_{\text{full}} - l_0)$, where l_0 is the log-likelihood of the null model, with first-year survival depending only on whether or not the bird was banded, and l_{full} is that of the full model, with fully time-varying first-year survival, of the same form as that for adult survival (McCullagh & Nelder 1989, p. 33).

Seasonal SST and sea-temperature gradient

We use seasonal SST and sea-temperature gradient as covariates for first-year survival. Seasonal SST is the average over each 3 mo season (e.g. for autumn by averaging over March, April and May) for the region situated between 38 and 40°S, 143 and 145°E, as in Cullen et al. (2009). The east–west sea-temperature gradient is calculated as in Mickelson et al. (1992) and described above. See Fig. 1 for locations of sites used in this calculation. Fig. 2 illustrates the time variation of SST at each site and of the gradient. We calculate the seasonal sea-temperature gradient by averaging over each 3 mo season.

We use seasonal rather than monthly values to decrease the number of covariates, and so reduce the chances of producing spurious correlations (Federer 1955). In addition, seasonal rather than monthly values are more appropriate, since the phenomena which cause mortality of little penguins tend to span months, but are less likely to span seasons (Dann 1992).

Mickelson et al. (1992) and Cullen et al. (2009) identified lags of several months in the effects of sea temperature on breeding in little penguins. To account for lagged effects, we allow first-year survival over calendar year j to depend on mean seasonal SST and mean seasonal sea-temperature gradient over 6 seasons (18 mo), from the winter preceding the breeding event (1 June to 31 August in calendar year $j - 1$) denoted by 'WiP', to spring in the current year (1 September to 30 November in calendar year j) denoted by 'SpC'.

RESULTS

First-year and adult survival of little penguins *Eudyptula minor* both vary appreciably with time (see Fig. 3). Both vary to a similar extent on a logistic scale, and the correlation between them is quite low (0.23 on a logistic scale). It thus appears that the causes of variation in adult survival are different from those affecting first-year birds. In the present paper we concentrate on first-year birds.

The best-fitting first-stage model is that of the mean east–west sea-temperature gradient in the current winter (grdWiC; Table 1), with the negative regression coefficient $b_1 = -0.350$ (± 0.054 SE) indicating that a higher average sea-temperature gradient in the winter following fledging is associated with reduced first-year survival (see Fig. 4). Indeed, apart from the model including the sea-temperature gradient in the current summer (which is no improvement on the null model in terms of AIC), all of the regression coefficients corresponding to the temperature gradient are negative, indicating that an increasing east–west sea-temperature gradient — that is, with warming eastern SST and/or cooling western SST — is associated with lower first-year survival probabilities.

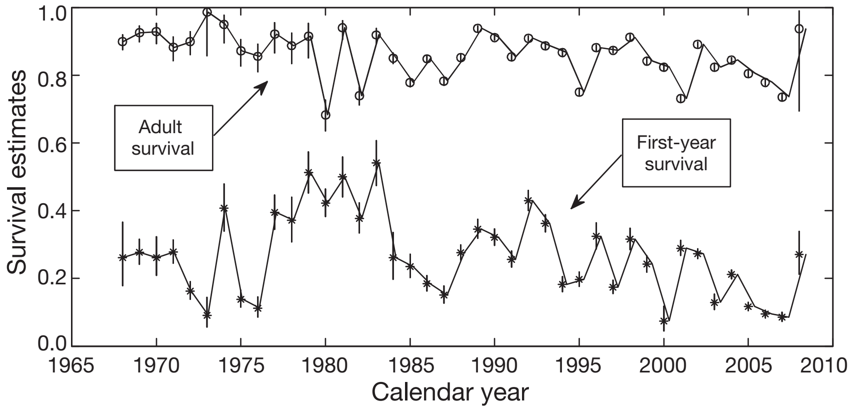

Fig. 3. *Eudyptula minor.* The variation over time for first-year and adult survival probabilities for unbanded (transpondered) birds under the full model, with an age + time structure for the recapture probability as in Eq. (1) and a survival age structure of $\phi_1(t+B)$, $\phi_2(t+B)$. Vertical bars represent 1 SE on each side of the estimate (back-transformed from the logistic scale)

Table 1. *Eudyptula minor*. Akaike's information criterion (AIC) values for various models for first-year survival probabilities. All models have a recapture probability model of age + time as in Eq. (1) and a survival age structure of $\phi_1(x+B)$, $\phi_2(t+B)$, where B denotes whether the bird was banded and x is one or more of the sea-surface temperature (denoted by 'sst') or sea-temperature gradient ('grd') covariates, ranging from WiP ('previous winter', i.e. the winter preceding the breeding event) to SpC ('current spring', i.e. the spring in the chick's first year of life). At the first stage only a single covariate is used. The second stage uses the best model (shown in bold) from the first stage, plus each of the other covariates, and so on. The AIC of the null model is 816.1. The signs of the regression coefficients corresponding to each added covariate are also given. Su: summer; Au: autumn

Covariate (x)	Stage 1st AIC	Stage 1st Sign	Stage 2nd AIC	Stage 2nd Sign	Stage 3rd AIC	Stage 3rd Sign
sstWiP	811.99	+	777.07	+	758.63	–
sstSpP	804.39	+	774.16	+	758.47	–
sstSuC	816.47	+	774.94	+	756.83	–
sstAuC	779.66	+	**756.86**	+		
sstWiC	799.41	+	776.42	+	750.90	–
sstSpC	816.68	+	777.66	–	748.61	–
grdWiP	816.45	–	777.69	+	758.45	+
grdSpP	811.53	–	777.24	–	758.59	–
grdSuC	816.52	+	775.26	+	752.29	+
grdAuC	809.20	–	776.72	–	756.92	+
grdWiC	**775.88**	–				
grdSpC	818.10	–	759.53	+	**740.73**	+

At the second stage, allowing for the sea-temperature gradient in the current winter, the best fitting covariate is SST in the current autumn (sstAuC in Table 1). The regression coefficient of sstAuC, b_2 = 0.161 (±0.035SE), means that a higher average SST in the autumn following fledging is associated with increased first-year survival. The 2 covariates grdWiC and sstAuC influence first-year survival independently: their correlation is low, with an absolute value of <0.20, and the regression coefficient of grdWiC is only slightly changed, at b_1 = −0.280 (±0.056), from its value at the first stage. Although the inclusion of both covariates is well justified in terms of AIC (Table 1), grdWiC accounts for only 7.5% of the deviance (time variation) at the first stage, and, at the second stage, sstAuC accounts for a further 3.7%. This lack of explanatory power can be seen in Fig. 4 which shows that, over the whole range of grdWiC, survival is only predicted to range from 0.15 to 0.24 (for transpondered birds), whereas 'observed' time-dependent estimates range from 0.07 to 0.54. There is no evidence for a quadratic rather than a linear effect of temperature gradient on survival — the AIC value changes from 775.9 to 777.5 when a quadratic term is added.

At the third stage, the next best covariate is the sea-temperature gradient in the current spring (grdSpC; Table 1). The regression coefficients of grdWiC and sstAuC are b_1 = −0.429 (±0.066 SE) and b_2 = 0.161 (±0.036), respectively. The regression coefficient of grdSpC is b_3 = 0.260 (±0.061), indicating that a higher east–west sea temperature gradient in the spring of the first-year of life is associated with increased survival. This result is in contrast with our findings in the earlier stages of the modelling. However, there is a substantial correlation (coefficient = 0.76) between grdWiC and grdSpC, which has caused the observed changes in the regression coefficients, and so it is unwise to include both of these covariates in the regression. The next best covariate, sstSpC, has low correlations with grdWiC and sstAuC. However, it is hardly worth including, as it increases the proportion of deviance explained by the model from 11.2% to only 11.3%.

SST and the sea-temperature gradient are both forecast to increase as a result of global warming, since eastern Bass Strait is predicted to warm more than western Bass Strait (Hobday et al. 2008). Therefore, the 2 effects we have found will act in opposite directions. For example, if sstAuC and grdWiC are both at their average values over the 41 yr of the data, the forecast value of first-year survival for a transpondered bird is 0.202 (±0.007 SE). If sstAuC increases by 2°C, while grdWiC remains fixed, this value increases to 0.259 (±0.016). If, on the other hand, sstAuC remains fixed, while grdWiC increases by

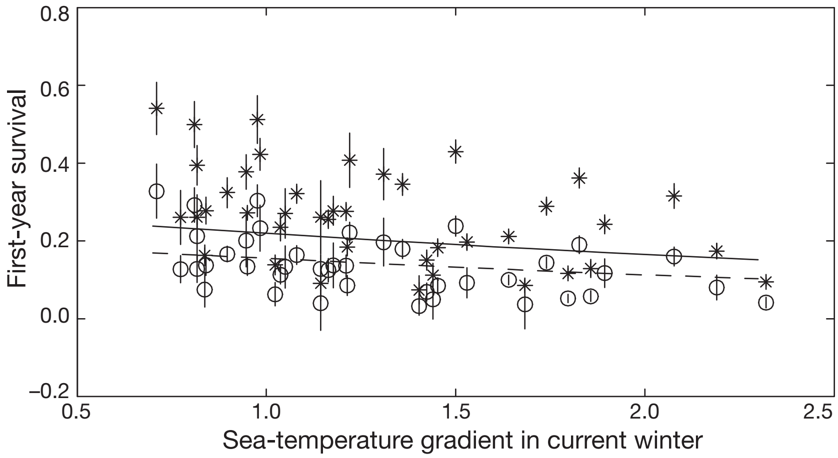

Fig. 4. *Eudyptula minor.* The relationship between time-dependent first-year survival under model $\phi_1(t+B)$ and the sea-temperature gradient in the current winter, for banded (open circles) and unbanded (stars) birds. The lines show the predicted values for first-year survival for banded (dashed line) and unbanded (solid line) birds from the fitted model ϕ_1(grdWiC+B)

1°C, the survival forecast decreases to 0.160 (±0.008). If both changes occur, then the survival would increase to 0.209 (±0.017). We have used a smaller example change for the gradient as, being a difference between sea temperatures, it is likely to change by less than SST. The example increases in sstAuC and grdWiC are both within the range of the observed data. The standard errors stated here do not account for the uncertainty in the climate forecasts.

DISCUSSION

First-year survival of little penguins *Eudyptula minor* bred on Phillip Island is most strongly related to the east–west sea-temperature gradient within Bass Strait in the winter after their main fledging period. Reduced survival is associated with an increase in the east–west temperature gradient associated with more rapid warming in the east of Bass Strait than in the west (Fig. 2). Mickelson et al. (1992) found that a winter increase in the sea-temperature gradient had negative effects on the breeding of the same population of little penguins. They hypothesised that a decrease in gradient was associated with stronger westerly winds in winter, bringing nutrient-rich water into Bass Strait which enhanced local productivity and led to earlier and more successful breeding. Ganendran et al. (2011) considered wind direction and survival of little penguins, finding a positive relationship between southerly winds in the winter before the chicks were born and a negative one with easterly winds in the preceding summer.

It appears that SST alone is not the best means of capturing the processes operating on first-year survival. The incorporation of a temperature gradient as a covariate for first-year survival provides both a better fit to the data and a fuller understanding of the marine environment in Bass Strait than SST alone, as it incorporates the effects of the EAC, water movement from the west and of prevailing winds on SST. A temperature gradient in Bass Strait in winter is likely to be indicative of both the extent of the EAC in the east and the amount of wind-driven cool water movement from the west.

Most mortality of first-year little penguins occurs in the period from late autumn to winter (Dann 1992), which is when the temperature gradient has its most apparent influence on their survival. If strong prevailing westerly winds contribute to an increased gradient in winter, by bringing cooler water into western Bass Strait, then the increased mortality of first-year penguins may be related to the prevalence of strong winds driving these incursions of cooler water and affecting their foraging efficiencies by reducing thermoclines (Ropert-Coudert et al. 2009). Conversely, if the increased gradient is due to a greater incursion of warmer water into Bass Strait from the east, then substantial local reductions may result in the availability of cool-water prey species. Both hypotheses are supported by the strong tendency for fledged birds from Phillip Island to head west to the cooler side of Bass Strait (Dann 1992), either as avoidance of warmer water in the east or tracking nutrient-rich cooler waters coming in from the west. The latter is supported by the positive association between the survival of fledged birds and autumn SST.

Over the period of this study, the sea-temperature gradient increased at around 0.02°C yr^{-1} ($p < 0.001$), consistent across all seasons. SST in Site 1, western Bass Strait, showed no significant warming trend, whereas Site 2, eastern Bass Strait, had a warming trend in summer, winter and spring, at a rate similar to that for the gradient (0.02°C yr^{-1}), suggesting the increased sea-temperature gradient was due mainly to a greater warming in the east, perhaps due to the influence of a stronger EAC.

Replacing the best first-stage covariate (grdWiC) with the corresponding SST from Site 1 only (west side of Bass Strait, see Fig. 1) and then Site 2 only (east) indicates that the contribution is almost entirely from the west side. Indeed Site 2 is a very poor predictor for first-year survival. This result is in agreement with our earlier explanation regarding inflowing nutrients from the west. In general, the sea-temperature gradient and the SST at Site 1 are not well correlated, and the sea-temperature gradient predicts first-year survival much better than the SST at Site 1.

Although the effect of the gradient on survival is mostly due to the influence of SST in Site 1 (the western side), the effect of the gradient is not entirely the same as that for Site 1. So there is some complexity in the system that is not picked up when just considering SST in Site 1. Given that the gradient has an effect different from SST, it is important to consider the possible effects of an increase in this variable.

Once the sea-temperature gradient in the winter after fledging has been included as a covariate for first-year survival, there is still a relationship between first-year survival and SST in the autumn following fledging. These 2 covariates influence first-year survival independently — 1 negatively and 1 positively. It is not surprising that there is a relationship between juvenile survival and environmental conditions in autumn. Most chicks are banded prior to fledging in December to February (Reilly & Cullen 1982), and, by the beginning of autumn, almost all of the newly fledged birds will have gone to sea. Autumn is the peak mortality period for these young birds that are inexperienced in finding food (Dann et al. 1992) and have no post-fledging parental care, and SST may well have an influence on the availability of food at this critical time. Cullen et al. (2009) argued that the importance of warmer SST in the autumn before breeding began may be due to increased productivity or juvenile fish survival increasing the availability of food for breeding. These mechanisms seem less applicable to the survival of first-year penguins as the significant periods for SST were during their critical survival period rather than some months earlier. However, increased autumn temperature may be associated with enhanced larval fish survival (Zeldis et al. 2005, Hinrichsen et al. 2007) and provide a possible mechanism for influencing first-year penguin survival.

Relationships have previously been reported between sea temperature and survival of adult seabirds (e.g. Harris et al. 2005, Rolland et al. 2008, Barbraud et al. 2011) and much less commonly with immature birds (Votier et al. 2008). The links between seabird survival and SST may either occur in the same season or be lagged so that the important periods of SST precede the mortality periods by months or even years (Votier et al. 2008, Barbraud et al. 2011). Here we have found consecutive independent seasonal responses, whereby the autumn SST as the birds fledge has a lesser and positive effect on survival and the temperature gradient in winter has a negative and greater influence.

Poloczanska et al. (2007) provide a prediction for the SST in the region of Site 2 (Fig. 1), with an increase of up to 3°C by 2070. However, since there are no existing forecasts specifically for Bass Strait, we are unable to reliably predict the SST at Site 1, and so any prediction of the change in the sea-temperature gradient would be highly speculative.

There are relatively few climatic variables available for this time series, and we chose ocean temperature as it could play a pivotal role in the trophodynamics of Bass Strait and hence show strong links with penguin survival. We need to continue to explore the utility of other variables in the first instance and then combinations of variables with a view to developing a model with more predictive power. Food availability seems the most likely proximate factor determining first-year survival, and a suite of biotic and abiotic factors are likely to ultimately determine food availability. Data on prey availability would be desirable. The abiotic factors presumably include oceanographic and climatic variables, although, based on the present study, sea temperature alone is unlikely to be sufficient. Future statistical approaches will consider looking at measures associated with marine productivity such as chlorophyll *a*, alone or in tandem with temperature. Although the time series available for chlorophyll *a* is of a shorter duration than the penguin demographic variables, this covariate may be more closely linked to penguin survival than temperature alone.

At present there is considerable uncertainty as to the expected magnitude of change in the east–west Bass Strait temperature gradient under global warming scenarios and its rate of increase relative to changes in SST. This reduces our capacity further to predict the likely overall impact of future changes in oceanographic conditions on first-year survival, given that our predictive capacity is already low due to the low explanatory power of our best model (accounting for only 11% of time variation). There is therefore great uncertainty in the magnitude of the future change in mean penguin survival with changing ocean temperature. While 'noise' may well have engulfed the true 'signal', changes in the stochastic fluctuations average out over the long term, allowing the underlying change in signal to emerge. Hence, changing ocean temperatures and the possible resulting changes in mean survival could have substantial long-term demographic effects.

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Contribution to the Theme Section 'Seabirds and climate change'

Climate affects seabird population dynamics both via reproduction and adult survival

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ABSTRACT: Climate variability can affect population dynamics via adult survival or via offspring production and recruitment. The relative importance of both processes is still an unresolved matter, especially in long-lived species, where the time lags between the climate signal and the population response differ greatly depending on the process involved. We address the issue using 378 time series from 29 seabird species from 187 breeding colonies throughout the North Atlantic. The effect of climate on population growth rate is estimated as the slope of the North Atlantic Oscillation (NAO) index at different time lags when used as a covariate in population models. Using nonlinear mixed effects models, we can demonstrate that climate affects the population dynamics of seabirds, both through adult survival and through the recruitment of offspring produced. The latter effect is stronger, and the long time lags involved make it likely that its magnitude is still underestimated. Because different processes are involved, the sign of the relationship with the NAO differs between time lags. The relationship between the NAO and the population growth rate is also highly variable, both within and across species. In a second analytical step, we address the factors that may cause this interspecific and inter-colony variation, considering the ecological, demographic and geographical characteristics of the populations. Among comparatively 'fast-lived' seabirds, i.e. species with large clutches, the relationship with the NAO reverses its sign depending on latitude, while no such trend is apparent among 'slow' species.

KEY WORDS: Climatic responsiveness · Population growth rate · Recruitment · Age at maturity · North Atlantic Oscillation · Time lag

INTRODUCTION

Climate can have profound effects on the demography and population dynamics of marine top predators. Effects of climate on seabirds have been documented in the timing of breeding, breeding proportion, breeding success and adult survival (e.g. Thompson & Ollason 2001, Durant et al. 2004a, Lee et al. 2007, Monticelli et al. 2007, Gaston et al. 2009, Jenouvrier et al. 2009, Sydeman 2009, Wolf et al. 2009). Furthermore, reviews and comparative analyses of Atlantic seabirds have shown that such results are not merely isolated findings, but can be documented across species and populations, although the degree of climatic responsiveness may vary widely between different seabird taxa (Reid et al. 1999, Durant et al. 2004b, Sandvik & Erikstad 2008, Sandvik et al. 2008a). Whereas many of the processes involved in modulating these demographic traits are increasingly well understood, it is still a long way to understanding the pathways of climatic influences on population dynamics as such. Population growth is a function of all life-history traits and, thus, integrates the environmental effects on all these parameters (Engen et al. 2009, Tuljapurkar et al. 2009), which, in addition, may operate at different time lags (Post 2004).

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An important question in both life-history theory and global change research regards the relative importance of environmental influences on population dynamics via offspring production and recruitment on the one hand and via adult survival on the other (Stearns 1992, Weimerskirch et al. 2003, Sæther & Engen 2010b). The effect of variability in a life-history trait *a* on the variance of population growth rate (λ), and thus fitness, is a function both of the variability of *a* and of this trait's elasticity *e* (relative importance for the population growth rate). In matrix notation, this dependence can be approximated as (Caswell 2001, p. 225):

$$\mathrm{Var}(\lambda) \approx \sum_{i,j} [(\mathrm{e}_{ij} \cdot \lambda / a_{ij}) \cdot \mathrm{Var}(a_{ij})] \qquad (1)$$

At the same time, the most elastic life-history trait is predicted to be under the strongest selection pressure against temporal variability (Jonsson & Ebenman 2001), so that one usually finds a negative correlation between a life-history trait's elasticity and its variability (Pfister 1998, Sæther & Bakke 2000). It is therefore not straightforward to predict the balance of demographic elasticity versus climatic responsiveness in shaping population dynamics: while a trait must be temporally variable in order to be responsive to environmental conditions such as climate, it must have a high elasticity if it is to affect the population growth rate.

The current study aims at examining whether seabird population dynamics are more strongly influenced by climate via adult survival or offspring production and recruitment. This is addressed using a modelling approach based on a large sample of time series on seabird population counts across the North Atlantic. The problem is approached by comparing the relationship between the North Atlantic Oscillation (NAO) index and population growth rates across different time lags. If climatic effects on adult survival are most important, the relevant time lag of climatic effects on population dynamics will most often be zero (assuming a direct effect of weather) or 1 yr (assuming indirect effects via the food chain). If climatic effects on offspring production are more important, however, the population dynamics are expected to be affected most strongly by the climatic conditions several years ago, where the number of intervening years is equal to the age at recruitment. This follows from the fact that the effect of climate on offspring production will not become apparent in population counts before the offspring affected has actually recruited to the population being censused—provided that the signal is not lost during the prolonged pre-breeding life-span of seabirds. With *offspring production* we here refer to the size of the cohort fledged in a certain year, which is the product of half the adult population size, the breeding proportion, clutch size, hatching success and fledging success, all of which can be affected by climate. With *recruitment* we refer to the number of birds that have not previously bred entering the breeding population in a given year, which, in turn, is determined by the initial size of the cohort recruited, pre-breeding survival and philopatry, and establishment success.

The second step of the analyses examines whether it is possible to detect general patterns in the climatic responsiveness of seabird population dynamics. Climatic responsiveness varies considerably between different species (Kitaysky & Golubova 2000, Jenouvrier et al. 2005a, Sandvik et al. 2005, Sandvik & Erikstad 2008, Sæther & Engen 2010b), but also between different populations of the same species (Mysterud et al. 2000, Sæther et al. 2003, Harris et al. 2005, Sandvik et al. 2008a, Grøtan et al. 2009). It is important to acquire better knowledge of the differential climatic responsiveness of species and populations. Taxonomy, geography, foraging ecology and life history are among the factors that may help to predict climatic responsiveness and to derive lawful (nomothetic) generalisations in climate ecology. The causal and mechanistic understanding of the links between climate and population dynamics will remain incomplete unless commonalities and differences between species and populations are addressed.

We approach these problems by analysing an interspecific dataset. Addressing the issue comparatively makes the study nomothetic rather than merely descriptive, i.e. it generalises across species. The results demonstrate that the climatic response in seabird population dynamics is indeed geographically patterned and that life-history characteristics lead to differential responses across species.

METHODS

The present comparative study is based on published time series of population estimates of North Atlantic seabirds. In order to obtain reliable estimates of population parameters, only time series of at least 12 yr length were included. The resulting data base contained 378 time series from 187 locations and 29 species. The median length of the time series was 19 yr (mean: 25 yr; maximum: 75 yr; in total 9320 observation-years). The colonies ranged from Florida (27.9° N, 80.7° W) in the southwest to Spitsbergen (78.9° N) in the north and the Kola Peninsula (37.3° E) in the east (see Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m454p273_supp.pdf). The species included Alcinae (auks: *Alca torda*, *Cepphus grylle*, *Fratercula arctica*, *Uria aalge*, *U. lomvia*), Hydrobatinae (northern storm-petrels: *Hydrobates pelagicus*), Larinae (gulls: *Larus argentatus*, *L. canus*, *L. fuscus*, *L. marinus*, *L. minutus*, *L. ridibundus*, *Rissa tridactyla*), *Pelecanus* (pelicans: *Pelecanus occidentalis*), Phalacrocoracinae (cormorants: *Phalacrocorax carbo*, *Stictocarbo aristotelis*), Procellariidae (petrels: *Calonectris diomedea*, *Fulmarus glacialis*, *Pterodroma madeira*), Stercorariinae (skuas: *Stercorarius parasiticus*), Sterninae (terns: *Chlidonias niger*, *Sterna albifrons*, *S. caspia*, *S. dougallii*, *S. hirundo*, *S. nilotica*, *S. paradisaea*, *S. sandvicensis*) and Sulidae (gannets: *Morus bassanus*). See Supplement 1 for population time series included in the analyses and their sources.

Population modelling

For each of the 378 population time series, 25 separate logistic population models were fitted. The 25 models per population included 1 climatic covariate each, viz. NAO at time lags from 0 to 24 yr. Most of the 25 time lags were assumed to be biologically irrelevant for the populations modelled. They were included in order to be able to correct for the occurrence of correlational artefacts (see below). The logistic population models had the form $N_{t+1} = \lambda_t N_t$, where N_t is the population size in year t, and λ_t is the population growth rate in year t:

$$\lambda_t = \mathrm{e}^{r(1-N_t/K)+\beta Z_{t-\tau}+\varepsilon} \tag{2}$$

with β, slope of the covariate Z; e, base of the natural logarithm; ε, independent variable with zero mean and variance σ^2_{res} (which is the part of environmental variance σ^2_{e} that is not accounted for by Z); K, carrying capacity; r, intrinsic population growth rate; τ, number of years the NAO is lagged against the population time series; and Z_t, NAO index in year t. The parameters β, K, r and σ_{res} were estimated from each population times series using maximum likelihood such that the log-likelihood:

$$\ln L \propto -\sum_{k=2}^{n}\left\{\ln\sigma^2_{\mathrm{res}} + [\ln N_k - \mathrm{E}(\ln N_k)]^2 \big/ \sigma^2_{\mathrm{res}}\right\} \tag{3}$$

was maximised over the n elements of the time series (Sæther et al. 2009), where $\mathrm{E}(\ln N_k) = \ln(\lambda_{k-1}\ N_{k-1})$ is the predicted log-population size based on the observed population size N_{k-1} and Eq. (2).

The logistic population model was chosen because it has previously been shown to describe the pattern of density regulation in avian population dynamics quite well (Sæther & Engen 2002). The model of Eq. (2) is based on the implicit assumption that population sizes N_t are measured without error. While this assumption is met in very few populations, mainly because of intermittent breeding, we have not attempted to correct for this source of noise. We contend that, while observation error makes the data more noisy, this will to a certain degree be outweighed by the large sample size and does not introduce any systematic error.

Definition of variables

The extended winter (December to March) NAO index was used as the environmental covariate of the population models (Hurrell 2005). This index was chosen because many studies have identified the winter NAO to have huge biological significance (e.g. Ottersen et al. 2001, Sandvik & Erikstad 2008), and because the signal:noise ratio of the NAO is strongest in winter (Barnston & Livezey 1987, Hurrell et al. 2003). The estimated slope β (Eq. 2) of the standardised climatic covariate was used as a measure of climatic effects on population dynamics. We refer to this slope as *relationship to the NAO*. It is close to +1 if the population growth rate increases proportionally with the NAO index and −1 if the relation is inverse.

A second measure, referred to as *climatic responsiveness*, was defined in a way that preserves the magnitude, but ignores the sign of the climate effects. Because $|\beta|$ or β^2 yield distributions that are truncated at zero, climate responsiveness was defined as $1 + \ln|\beta|$. This measure thus approaches $-\infty$ if population growth rate is entirely unrelated to the NAO index. It is positive if the population growth rate is strongly affected by the NAO index, irrespective of the direction of this relationship.

The relationship with the NAO and climatic responsiveness were entered as dependent variables into the following analyses, which aimed at explaining the variation in these measures among populations and species. Explanatory variables considered were body mass, life history, foraging distance, diving depth, latitude and longitude. Body mass, foraging distance and diving depth were log-transformed. Life history was defined as the first axis in a principal component analysis (PCA) incorporating the species' ages at maturity and clutch size. Large positive values of 'life history' indicate species at the fast end of the slow–fast life-history continuum (e.g. large clutch size and low age at maturity; Sæther & Bakke 2000, Bennett & Owens 2002; for details on the PCA see Supplement 2 at www.int-res.com/articles/suppl/m454p273.pdf). Ages at maturity were the best estimates of each species' median age at first breeding (not physiological maturity). Longitude was, because of this measure's bimodal distribution, replaced by a binary variable (American vs. European coast). Because local estimates of the explanatory variables were unavailable for most colonies, life-history traits and foraging ecology of the species were inferred from the literature (Poole & Gill 1992–2003, Schreiber & Burger 2002). Some of the variables were unavailable in a few species, and these were extrapolated based on a phylogeny of the related species (cf. Supplement 2).

Time lags and covariates of climatic effects

The effect of climate was investigated using non-linear mixed-effects models (Pinheiro et al. 2006), analysing the climate effects estimated at all 25 time lags of all 378 populations simultaneously, with population as random factor and taking account of the correlation structure between the different time lags within each population by assuming an autoregressive process of order 1. Species, higher taxon and region (North Sea, Baltic Sea, Barents Sea, etc.) were also tested as nested random factors in addition to population. The non-linear function used was a bell curve centred on the time lag $t = t_0 + t_1\alpha$ and with a variance of 0.5 (Fig. 1, Supplement 2):

$$f(i,\tau) = \kappa + \left(b_0 + \sum_k b_k X_k\right) \cdot \mathrm{e}^{-(\tau - t_0 - t_1\alpha(i))^2} + U_i + \varepsilon_{i\tau} \qquad (4)$$

with $\alpha(i)$, age at maturity of population i; $b = b_0 + \sum b_k X_k$, magnitude of the population response to climate (b_0 being the intercept and b_k the slope of the response on covariate X_k); $\varepsilon_{i\tau}$, residual error; $f(i,\tau)$, response, i.e. climatic responsiveness or relationship with the NAO, of population i to the NAO conditions prevailing τ years ago; i, population (dummy variable used as identifier); κ, background correlation across all time lags; $t = t_0 + t_1\alpha$, time lag of the population response (t_0 being the intercept and t_1 the slope of time lag on age at maturity α); τ, number of years the NAO was lagged against the population time series; U_i, population-specific random effect; and X_k, explanatory variable k. The choice of a variance of 0.5 was arbitrary.

Using this model, the magnitude of climate effects can be estimated simultaneously with the relevant time lag. The occurrence of correlational artefacts is buffered by the nuisance variable κ, which allows the unbiased estimation of the magnitude of climate effects (b) by subtraction of κ (Fig. 1). In other words, b is a measure of the magnitude of the effects of climate at time t on population growth *over and above* the effects (real or artifactual) that climate at the other 24 time lags was estimated to have. The model equation can also be used to specify a null model (letting b_0, b_i, t_0, $t_1 = 0$) or test fixed time lags (letting $t_1 = 0$ and t_0 = time lag).

Because of the complex model structure and high sample sizes, modelling was divided into 3 steps. (1) A non-linear mixed-effects model was used to test the relevance of different time lags without considering covariates ($b_1 = 0$). (2) At time lags equalling 0 yr, 1 yr and each species' age at maturity, relevant covariates were searched for using linear fixed-effects models. (3) The results of the second analysis step were re-inserted in non-linear mixed-effects models to corroborate the previous findings. The results of the intermediate (second) step are not shown.

Time series length and data quality may influence the results obtained, because short time series may give rise to spurious correlations and because data

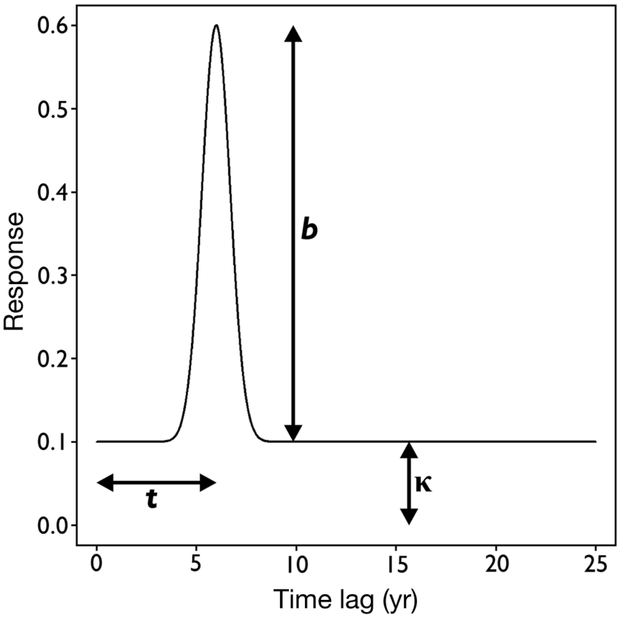

Fig. 1. Schematic presentation of the non-linear model structure used in explaining climate effects on population dynamics. The 3 parameters b, κ and t are estimated from the data. In order to account for correlational artefacts, the nuisance parameter κ estimates the 'baseline correlation' across all time lags, including the biologically uninformative ones. The magnitude b of climate effects is then estimated as the height of the peak over and above this baseline. Time lags t can be specified, or estimated simultaneously with b and κ (cf. Eq. 1)

obtained using poor sampling design may contain huge observation errors. We checked this by including time series length (number of years) and data quality (a score from 1 to 9; see column 'Type' in Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m454p273.pdf) as covariates. Both variables affected the nuisance parameter κ in climatic responsiveness (length, $p < 10^{-12}$; quality, $p = 0.038$). This was not the case for the relationship with the NAO, nor did length or quality influence the magnitude of climatic responsiveness or of the relationship with the NAO at any time lag (all $p \gg 0.1$). Because no parameters other than κ were affected by the inclusion of length or quality, the latter variables were therefore omitted from the analyses.

Model selection

Model selection was based on Akaike's Information Criterion (AIC). We report ΔAIC values relative to the null model (i.e. subtracting the AIC of a model excluding covariates from all other models' AICs), such that large negative ΔAIC values indicate well-supported models. If 2 or more nested models deviated by <2 AIC units, the most parsimonious model was preferred, i.e. the one requiring fewest parameters.

The phylogenetic inertia of the relationship with the NAO and of climatic responsiveness was estimated as the variance explained by sister taxa. See Supplement 2 for more details and for the references used to infer the seabird phylogeny.

All computations were carried out in the R environment (R Development Core Team 2006). Estimates are presented as means ± SE throughout.

RESULTS

Climate effects were tested with 25 time lags, most of which must be assumed to be biologically irrelevant. The following analyses correct for potential biases by estimating and subtracting a general 'baseline correlation' across all time lags (nuisance parameter κ; Fig. 1).

In the first step of the analyses, the time lags at which climatic responsiveness was largest (i.e. at which most variability in population growth rate was explained by the climatic covariate) were identified (see Table 1). If no time lag was specified, the non-linear model estimated the most important time lag to be only marginally different from zero (0.75 ± 0.42 yr, ΔAIC = −1.13, $p = 0.071$). Specifying a fixed time lag of 1 yr resulted in a better model (ΔAIC = −2.52) than fixing the time lag at 0 yr, however (ΔAIC = −0.04).

When the most important time lag was defined to be a function of each species' age at maturity, a well-supported model was obtained (ΔAIC = −2.66). Most importantly, the coefficient of age at maturity was highly significant (1.45 ± 0.25, $p < 10^{-8}$), and also the magnitude of climatic responsiveness was larger than at the remaining time lags (0.16 ± 0.06, $p = 0.0033$). The intercept of the function was not different from zero (−1.34 ± 0.96, $p = 0.16$). The model could be simplified further by recognising that the coefficient of age at maturity was only marginally different from unity (0.45 ± 0.25, $p = 0.068$). This simplified model was the best one overall (ΔAIC = −2.72), but received very similar support as the model with a constant 1 yr time lag.

Climatic responsiveness was larger than at the remaining time lags for a time lag equalling 1 yr or age at maturity (>0.11 ± 0.05, $p < 0.04$). This was not the case for the unlagged effect of climate (0.08 ± 0.06, $p = 0.15$).

In the next step, the importance of covariates in explaining the magnitude of the populations' climatic responsiveness was modelled. At fixed time lags of 0 and 1 yr, none of the covariates was able to explain

Table 1. Identification of the most relevant time lags of climatic responsiveness of population dynamics across 378 seabird populations. Each row represents estimates from 1 non-linear mixed-effects model. Numbers that were specified rather than estimated are given in square brackets. Time lags are either the same across all species (0, 1 and t_0 years) or a function of the age at maturity (α_j) of each species j. The magnitude of climatic effects is abbreviated as b_0 (no covariates were considered, i.e. $b_1 = 0$). See Eq. (4) and Fig. 1 for abbreviations used and their meaning. The nuisance parameter κ was estimated as −2.36 ± 0.16 in all models. ΔAIC (Akaike's information criterion) values are provided relative to the null model (i.e. containing only random effects and κ as the sole main effect), which had 5 parameters and AIC = 29714.47. The best models are in **bold**. Significance levels = $p^{***} < 0.001 \le p^{**} < 0.01 \le p^{*} < 0.05 \le p^{+} < 0.1$)

Time lag	Parameter estimates b_0	 t_0	 t_1	No. of parameters	ΔAIC
None	–	–	–	5	0.00
0	0.080 ± 0.056	[0]	–	6	−0.04
1	**$0.115 \pm 0.054^{*}$**	**[1]**	**–**	**6**	**−2.52**
t_0	$0.124 \pm 0.055^{*}$	$0.750 \pm 0.415^{+}$	–	7	−1.13
$t_0 + t_1\alpha_j$	$0.161 \pm 0.055^{**}$	−1.343 ± 0.958	$1.448 \pm 0.246^{***}$	8	−2.66
$t_1\alpha_j$	$0.140 \pm 0.055^{*}$	[0]	$1.135 \pm 0.094^{***}$	7	−2.53
α_j	**$0.119 \pm 0.055^{*}$**	**[0]**	**[1]**	**6**	**−2.72**

Table 2. Covariates explaining the magnitude of climatic responsiveness of population dynamics across 378 seabird populations. The climatic covariate (North Atlantic Oscillation) is lagged by each species' age at maturity (which means that all models are nested within the last model of Table 1). Each column represents estimates from 1 non-linear mixed-effects model. Only the set of best models is shown. See Table 1 for further explanations

Parameter	Parameter estimates			
[Intercept]	+1.21 ± 0.60*	+0.66 ± 0.51	+0.53 ± 0.47	0.83 ± 0.43^{+}
Body mass	–0.023 ± 0.075	+0.061 ± 0.058	+0.078 ± 0.051	–
Feeding depth	–1.57 ± 0.93^{+}	+0.06 ± 0.11	–	–
Body mass × Feeding depth	+0.24 ± 0.14^{+}	–	–	–
Latitude	–0.018 ± 0.008*	–0.017 ± 0.008*	–0.016 ± 0.008*	–0.013 ± 0.008^{+}
No. of parameters	10	9	8	7
ΔAIC	–3.35	–2.25	–3.92	–3.55

the variation in the magnitude of climate responsiveness, the best supported covariates being diving depth (–0.099 ± 0.091, p = 0.28) for unlagged climate and American versus European coast (–0.23 ± 0.24, p = 0.33) for Time Lag 1. Compared to the models with intercepts only (see Table 1), the models' AIC increased by at least 0.8 units. At time lags equal to each species' age at maturity, several models performed slightly better than the intercept-only model (Table 2), including effects of body mass, diving depth, their interaction and latitude. However, none of those models represented improvements by >2 AIC units. This means that the intercept-only model for climatic responsiveness lagged by age at maturity was preferred over the models in Table 2.

In models of climatic responsiveness, a considerable amount of variation was observed at the levels of species (standard deviation, 0.27) and higher taxon (0.37), in addition to the population level (0.69; residual SD, 1.11). These models therefore include 3 nested random effects.

Climatic responsiveness, as defined here (see 'Materials and methods'), ignores the sign of the climatic effect. When considering the relationship between population growth rate and the NAO, all 3 time lags turned out to be important (Table 3), and differences between the American and the European coasts of the North Atlantic appeared at all time lags. The unlagged relationship with the NAO was more positive at the European than at the American coasts of the North Atlantic, whereas the reverse was true for the relationship with the NAO lagged by 1 yr and by each species' age at maturity. At the latter time lag the relationship with the NAO was more positive in species with fast life histories (Table 3). However, closer inspection revealed that this positive relationship between life history and climate effect was most pronounced at low latitudes, while the relationship tended to be negative at high latitudes (Fig. 2). There was a weak tendency that larger species had a stronger relationship with the unlagged NAO (Table 3).

Table 3. Covariates explaining the relationship between the North Atlantic Oscillation and population growth rate across 378 seabird populations and at different time lags. Each column represents estimates from 1 non-linear mixed-effects model. ΔAIC values are provided relative to the null model (i.e. intercept and random effects only), which had 3 parameters and AIC = –5990.71. The best model is in **bold**. See Table 1 for further explanations

Time lag	Parameter	Parameter estimates					
0	[Intercept]	–0.23 ± 0.06***	**–0.17 ± 0.05*****	–0.18 ± 0.05***	–	–0.05 ± 0.04	–0.19 ± 0.05***
0	Body mass	+0.011 ± 0.008	**–**	–	–	–	–
0	Coast	+0.17 ± 0.05***	**+0.17 ± 0.05*****	+0.18 ± 0.05***	–	+0.05 ± 0.04	+0.19 ± 0.05***
1	[Intercept]	+0.18 ± 0.04***	**+0.18 ± 0.04*****	+0.19 ± 0.04***	+0.07 ± 0.03*	–	+0.20 ± 0.04***
1	Coast	–0.19 ± 0.05***	**–0.19 ± 0.05*****	–0.19 ± 0.05***	–0.08 ± 0.04*	–	–0.21 ± 0.04***
α	[Intercept]	+0.12 ± 0.07^{+}	**+0.12 ± 0.07^{+}**	+0.11 ± 0.07	+0.13 ± 0.07^{+}	+0.14 ± 0.07^{+}	–
α	Life history	+0.15 ± 0.06**	**+0.15 ± 0.06****	+0.18 ± 0.05***	+0.15 ± 0.06**	+0.15 ± 0.06**	–
α	Latitude	–0.000 ± 0.001	**–0.000 ± 0.001**	–0.001 ± 0.001	–0.000 ± 0.001	–0.000 ± 0.001	–
α	Life history × Latitude	–0.003 ± 0.001**	**–0.003 ± 0.001****	–0.003 ± 0.001**	–0.003 ± 0.001**	–0.003 ± 0.001**	–
α	Coast	–0.089 ± 0.044*	**–0.089 ± 0.044***	–	–0.099 ± 0.044*	–0.11 ± 0.04*	–
	No. of parameters	13	**12**	11	10	10	7
	ΔAIC	–43.20	**–42.92**	–40.75	–33.10	–29.88	–17.14

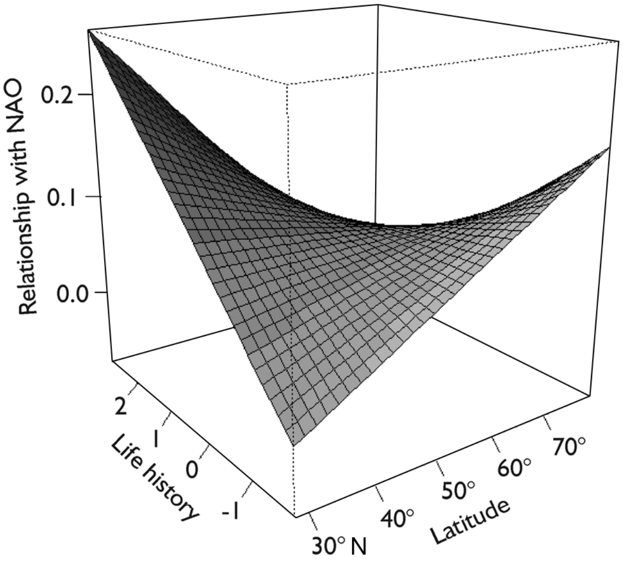

Fig. 2. Relationship between population growth rate and the North Atlantic Oscillation (NAO) across 378 North Atlantic seabird populations is affected by life history and latitude. Overall, the relationship with the NAO increases with faster life histories (Table 3), this pattern becoming weaker and even reversing towards the north. (The climatic covariate, NAO, is lagged by each species' age at maturity. Life history is represented as a species' 'demographic speediness', i.e. high values indicate comparatively large clutches and low ages at maturity.)

Overall, the time lag with the most explanatory power was age at maturity (AIC increased by >25 units when omitting these effects; Table 3). The second most important time lag was 1 yr (ΔAIC = 13). Omitting the unlagged effects still deteriorated the model by almost 10 AIC units.

The only random factor retained in models of relationship with the NAO was the population. The variation at the species or higher taxon level was negligible (SD < 0.005; residual = 0.176).

There was no evidence of phylogenetic inertia in relationship with the NAO (all $r^2_{\text{phylo}} < 0.16$, $p > 0.2$). Climatic responsiveness showed considerable phylogenetic inertia at Time Lags 0 ($r^2_{\text{phylo}} = 0.35$, $p = 0.021$) and 1 ($r^2_{\text{phylo}} = 0.30$, $p = 0.031$), but not so at the time lag equalling age at maturity ($r^2_{\text{phylo}} = 0.14$, $p = 0.17$).

DISCUSSION

Relative importance of climatic effects on recruitment and adult survival

The population dynamics in 378 populations of 29 different species of North Atlantic seabirds are shown to be clearly affected by climate, as measured by the NAO index. The most important time lag at which climate effects operated, was not a constant lag, but one that varied across species, viz. the one that corresponded to each individual species' age at maturity. In the sample considered, ages at maturity varied between 2 and 9 yr.

A time lag in population dynamics equalling age at maturity is caused by the recruitment of new breeders to the adult population. Finding that the effect of climate is most pronounced at this time lag, therefore, means that offspring production is the fitness component in North Atlantic seabirds that responds most to climatic variability. The findings thus have a direct bearing on what has been termed 'tap/tub hypothesis' (Sæther et al. 2004), i.e. the question whether population dynamics are mainly affected through offspring production and recruitment ('tap' hypothesis) or through adult survival ('tub' hypothesis). As the underlying processes are not mutually exclusive, however, one might better speak of 'tap' and 'tub' *effects* than of competing *hypotheses*. Our results show that both effects are relevant in seabirds; however, the 'tap' effect is more pronounced.

The latter finding is in accordance with the expectation that adult survival in seabirds should exhibit low temporal variability. In long-lived species such as seabirds, adult survival is the life-history parameter of greatest importance for population growth rate, i.e. the trait with the greatest elasticity (Gadgil & Bossert 1970, Lebreton & Clobert 1991, Wooller et al. 1992). At the same time, natural selection canalises the most elastic life-history traits, so that a negative correlation between elasticity and temporal variance is expected and found (Pfister 1998, Sæther & Bakke 2000, Wisdom et al. 2000, Jonsson & Ebenman 2001, Gaillard & Yoccoz 2003). Empirical data from seabirds corroborate that adult survival has high elasticity and low temporal variability (Jenouvrier et al. 2005b, Stahl & Oli 2006). It seems rather intuitive that a low temporal variability translates into a low climatic responsiveness of the trait in question.

The latter conclusion does not follow with necessity, however: the high elasticity of adult survival might also lead to the opposite expectation, viz. that even a relatively small response of adult survival to climatic variation may have a greater effect on long-term population growth than a comparatively much greater response in reproduction would have (cf. Eq. 1). After all, population viability is affected more by changes in the environment that increase the temporal variance in demographic traits with high elasticity than in traits with low elasticity (Lande 1993, Sæther & Bakke 2000). If, for instance, the climatic variability during the past decades exceeded the levels that a species has been adapted to (in either variance or mean), one might observe maladaptive responses even in highly elastic parameters. Several recent studies have documented effects of climate on seabird survival in the North Atlantic (Grosbois & Thompson 2005, Harris et al. 2005, Sandvik et al. 2005, Frederiksen et al. 2008, Lavers et al. 2008). The current study, too, demonstrates that a non-trivial fraction of the climatic impacts on population dynamics is due to adult survival (Table 3). It might be feared that these effects are evidence of maladaptive responses to atypical conditions. However, the present study clearly shows that, at least when averaged across seabird species, population dynamics have so far been more strongly affected by climate through offspring production than through adult survival.

Several factors make it difficult to obtain reliable estimates of the magnitude of environmental effects on population dynamics that are exerted through recruitment. The most important among these factors are the prolonged recruitment period in long-lived species and the variance and uncertainty of age at maturity. Because immature birds are not counted as part of the breeding population, they are 'invisible' to population models during the 2 to 9 yr (or more) prior to the birds' recruitment. The environmental influences (climatic and otherwise) that accumulate during this period and lead to pre-breeding mortality or emigration may be expected to erase or swamp the effect that climate has had on any given cohort during breeding. Furthermore, the birds of a given cohort do not all recruit in the same year. Finally, birds may return to their breeding colony several years before they in fact start to breed (Sandvik et al. 2008b). Most studies making up the raw data of our sample (n = 378) used actual breeding pairs (n = 258) or nests occupied (n = 71) as their counting unit, however, minimising this error source. In any case, all the factors mentioned render our estimates conservative; in other words, our estimate is, if anything, an underestimate of the climatic impact on population dynamics via recruitment.

Similar to the response of adult survival, the response of offspring production to climate may itself be lagged because the effect is mediated through the food chain. Across species, however there was no evidence of the lag being longer than age at maturity (Table 1).

Relationship with the NAO

We examined whether the interspecific variation in climatic responses could be explained using the life history or feeding ecology of the species, or the geography of the populations. The relationship with the NAO lagged by age at maturity exhibited a striking difference between species with comparatively fast and slow life histories (i.e. large vs. 1-egg clutches, and low vs. high age at maturity; for discussions of the slow–fast life history continuum see Sæther & Bakke 2000, Bennett & Owens 2002). Among 'fast' species, the relationship with the NAO decreased with increasing latitude (Fig. 2). This result corroborates earlier findings from the analysis of breeding success (Sandvik et al. 2008a) and shows that the patterns found for breeding success retain their relevance for population dynamics throughout the entire pre-recruitment period. The findings are further strengthened by the fact that only 17 populations entered into both analyses (corresponding to 52 % of the time series used in the earlier study and merely 4 % of the current study). However, the current study extends the earlier results by showing that the decrease of the NAO relationship with latitude is restricted to species with fast life histories (Fig. 2, Table 3). While species with slow life histories (clutches of 1) respond much less to climate, 'fast' species exhibit positive relationships with the NAO at southern latitudes and negative relationships at northern latitudes. A possible explanation for this pattern is that recruitment is more variable in species with large clutches, being a consequence of the fact that the lowest possible recruitment is the same (viz., 0) irrespective of clutch size, while the maximum possible recruitment will increase with clutch size. Climatic effects on fecundity will thus result in larger impacts on population dynamics if clutch sizes are large. That the effect actually changes its sign is, in turn, most likely due to the different oceanographic 'meaning' of the NAO at different latitudes (Wang et al. 2004, Sandvik et al. 2008a).

The relationship between population growth rate and climate differed among populations on the American and European coasts of the North Atlantic. This could be due to differences in the marine environment and the meteorological 'meaning' of the NAO on the 2 coasts, i.e. due to different relationships between regional and local climate (cf. Hurrell et al. 2003).

Owing to hugely differing sample sizes (n_{Am} = 21, n_{Eur} = 357) and the fact that the American data only came from terns and pelicans, the difference may also be an artefact, e.g. because these taxa have lower average annual adult survival rates (0.825 ± 0.025) than other seabird groups (0.879 ± 0.010; based on the species sampled for the present paper). Interestingly, the signs of the effect are not the same at the 3 time lags considered: the relationship between the unlagged winter NAO and the population growth rate is more positive in Europe than in America. However, the relationship is more positive in America than in Europe for longer time lags. This indicates that, on average, a NAO condition that exerts a negative effect on adult survival, has a positive effect on reproduction in the following breeding season, and vice versa.

Climatic responsiveness

In analysing climatic effects on population dynamics, we distinguished between the relationship with the NAO and climatic responsiveness (see 'Methods' for definitions). The latter variable ignores the sign of the climatic effects while retaining its magnitude. Previous studies have shown that large climatic effects of different signs can cancel each other out in analyses where effects are averaged across multiple populations of the same species (Sandvik & Erikstad 2008, Sandvik et al. 2008a), so that climatic responsiveness might be interpreted as a propensity or potential of a species rather than a fixed attribute. The actually realised magnitude and even sign of the climatic response may vary on comparatively small geographical scales due to local oceanographic, trophic, or other conditions (Sæther et al. 2003, 2004, Harris et al. 2005, Irons et al. 2008). This explanation is compatible with our findings: the present study has documented different average signs of relationship with the NAO at different latitudes; there was considerable phylogenetic inertia in climatic responsiveness, but not in relationship with the NAO; and species and higher taxon were rejected as random effects in models of relationship with the NAO, but could not be omitted in models of climatic responsiveness.

Climatic responsiveness lagged by age at maturity showed a marginal trend to decrease with the population's latitude. According to the model that obtained the lowest AIC value (Table 2), there was also a very weak positive effect of body mass on climatic responsiveness; however, none of these models outperformed the more parsimonious model without covariates (Table 1).

It has been suggested that foraging range or diving depth can predict the responsiveness of seabirds to environmental variation (Furness & Ainley 1984, Furness & Barrett 1991, Furness & Tasker 2000). In our dataset, however, apart from some weakly supported tendencies (cf. Table 2), feeding ecology did not explain any across-species variance in climatic responses.

Methodological considerations

The use of a high number of time lags and the estimation of a nuisance parameter κ turned out to be an effective way of providing unbiased estimates of the time lag and magnitude of demographic responses to climatic variability (cf. Fig. 1 and Eq. 4). The estimates were, therefore, not affected by the length of the time series or the quality of the data. The analysis did not correct for the presence of observation error in population counts, e.g. due to intermittent breeding or methodological limitations. Likewise, the relationships with the NAO — being estimates from population models and not measurements — were treated as point estimates in subsequent analyses, which amounts to an additional simplifying assumption. However, the fact that data quality did not affect the estimates, gives some indication that the results are robust, at least against a certain level of observation error. This would have to be verified using methods that are able to quantify observation error and to take error propagation into account, however.

A number of other factors remains uncorrected for, such as non-linear responses to climate or different strengths and forms of density regulation in different species (Sæther & Engen 2010a). While providing topics for further detailed study of single species, it may be premature to address these issues at the cross-specific level. In the analyses presented here, these factors most likely take the form of noise rather than systematic errors.

In age-structured populations, apparent environmental effects that are lagged by the age at maturity may occur purely because of autocorrelations in the population time series (Lande et al. 2002, 2003). This potential artefact cannot account for the findings reported here, because, in this case, the same environmental covariates would also show an unlagged effect of the same sign and an even greater magnitude. To the contrary, the climatic effect lagged by age at maturity was actually stronger than the unlagged one and had the opposite sign.

Conclusions and outlook

To summarise, we found evidence in an interspecific dataset that the population dynamics of North Atlantic seabirds are affected by climate, both through an effect on offspring production and on adult survival. Although the climatic signal of offspring production on population dynamics is weakened by conditions experienced by immature birds during the years prior to recruitment, this effect had nevertheless the greatest magnitude.

The current warming of global climate, which is predicted to continue and accelerate during the next century at least (IPCC 2007), will doubtlessly affect seabirds, too. Given that the patterns documented in the present study using data from the past century (1920 to 2005) hold true for the next century, too, our findings allow some predictions about seabird population responses to climatic change.

First, the signs of the climate effects differed for different time lags: climate conditions that affect population growth rate negatively by unlagged effects on adult survival tend to have positive effects on population growth rate by lagged effects via offspring recruitment, and vice versa. This finding, which has also been reported from the Southern Hemisphere (Croxall et al. 2002, Jenouvrier et al. 2005a), may entail a certain amount of buffering of population dynamics against climatic variability.

On the other hand, if positive-phase NAO conditions become more frequent in the future, as has been predicted based on coupled general circulation models (Monahan et al. 2000), the following responses of seabird population may be predicted: species of Atlantic seabirds with small clutches and high annual adult survival rates will tend to exhibit lower population growth rates (or more decreasing long-term trends) than species with the opposite life-history strategy. This difference will be most pronounced for populations breeding at lower latitudes.

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Contribution to the Theme Section 'Seabirds and climate change'

Effects of climate change and fisheries bycatch on Southern Ocean seabirds: a review

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ABSTRACT: Over the last century, major climate changes and intense human exploitation of natural living resources have occurred in the Southern Ocean, potentially affecting its ecosystems up to top marine predators. Fisheries may also directly affect seabirds through bycatch and additional food resources provided by discards. The past 20 yr of research has seen an increasing number of studies investigating the effects of climate change and fisheries activities on Southern Ocean seabirds. Here, we review these studies in order to identify patterns in changes in distribution, phenology, demography and population dynamics in response to changes in climate and fisheries bycatch. Shifts in distribution and breeding phenology were documented in parallel to increases in sea-surface temperatures and changes in sea-ice cover. Above all warm sea-surface temperatures negatively affected demographic parameters, although exceptions were found. Relationships suggest non-linear effects of sea-ice cover on demographic parameters and population dynamics, with optimum sea-ice cover conditions appearing to be the rule. Fishing efforts were mainly negatively related to survival rates, and only for a few species positively related to breeding success. A handful of studies found that chronic mortality of immature birds due to fisheries negatively affected populations. Climate factors and fisheries bycatch may simultaneously affect demographic parameters in a complex way, which can be integrated in population models to project population trajectories under future climate or fisheries scenarios. Needed are studies that integrate other environmental factors, trophic levels, foraging behaviour, climate–fisheries interactions, and the mechanisms underlying phenotypic plasticity, such as some pioneering studies conducted elsewhere.

KEY WORDS: Seabirds · Bycatch · Population dynamics · Demography · Distribution · Phenology · Sea ice · Sea-surface temperature

INTRODUCTION

Several studies have shown that recent climate change and variability have affected a wide range of species (Walther et al. 2002, Parmesan & Yohe 2003, Root et al. 2003, Parmesan 2006), including seabirds (e.g. Montevecchi & Myers 1997, Kitaysky & Golubova 2000, Kitaysky et al. 2000, Sydeman et al. 2001, Frederiksen et al. 2004). A major challenge in ecology and conservation is to predict the effect of future climate change on populations, species' distributions and ecosystems. In the Southern Ocean, there has been strong evidence for important climate changes over the last century. Among the most important changes that may have affected seabird distribution, phenology and populations are:

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1. A large-scale change in the atmospheric circulation of the high southern latitudes, the major mode of variability being the southern annular mode (SAM). Since the late 1970s, the SAM has become more positive, resulting in a 15 to 20% increase of westerly winds around the Antarctic continent, an increase in temperature and a decrease in sea ice in the coastal region of West Antarctica, as well as changes in the frequency and intensity of cyclones south of 40° S. The change in SAM coincided with the development of the ozone hole (Marshall 2003, Turner et al. 2009).

2. An increase in atmospheric temperatures for the sub-Antarctic South Georgia, Macquarie, Kerguelen, Heard and Marion Islands and on the Antarctic Peninsula (British Antarctic Survey 1987, Adamson et al. 1988, Frenot et al. 1997, Budd 2000, Smith 2002, Meredith & King 2005, Solomon et al. 2007).

3. An increase in the frequency and intensity of El Niño events, with some El Niño signals being detected in the Antarctic (Solomon et al. 2007).

4. An increase of CO_2 concentration south of 20° S in the southern Indian Ocean (Solomon et al. 2007, Turner et al. 2009).

5. An increase in Antarctic air temperatures by about 0.2°C on average since the late-nineteenth century, with a particular increase in West Antarctica since the early 1950s (Masson-Delmotte et al. 2003, Vaughan et al. 2003, Turner et al. 2009).

6. A warming of the Antarctic Circumpolar Current waters by 0.06°C decade^{-1} at depths of 300 to 1000 m from the 1960s to 2000s, and by 0.09°C decade^{-1} since the 1980s (Levitus et al. 2000, Gille 2002). The warming is more intense on the southern side of the Antarctic Circumpolar Current than north of it.

7. An average increase of 2.3°C over the last 81 yr in the upper 150 m of the waters around South Georgia (Trathan et al. 2007).

8. An increase in sea-surface temperatures of the southern Indian Ocean over the period 1960 to 1999 (Alory et al. 2007).

9. A decrease in sea-ice extent in the Bellingshausen Sea and an increase in sea-ice extent in the Ross Sea from 1979 to 2006, and a decrease in sea-ice extent in East Antarctica from the 1950s to 1970s (Curran et al. 2003, de la Mare 2009, Ainley et al. 2010a).

10. A decrease of the sea-ice season duration (later advance and earlier retreat of sea ice) in the Bellingshausen Sea and an increase (earlier advance and later retreat of the sea ice) in the Ross Sea (Parkinson 2004).

These physical changes may have had profound effects on several components of the Southern Ocean ecosystems and across a range of trophic levels (Forcada et al. 2006, Murphy et al. 2007, Nicol et al. 2007, Trathan et al. 2007). For example, in the southern Atlantic Ocean, long-term surveys suggest a 38 to 81% decline in krill stocks since the mid-1970s (Atkinson et al. 2004). Although the causes (or predators) of this decline are still being debated (Hewitt et al. 2003, Ainley et al. 2007), a significant negative correlation between krill density and mean sea-surface temperature at South Georgia has been found for the period from 1928 to 2003, suggesting a large-scale response of krill and of the entire open-ocean ecosystem to climate change (Whitehouse et al. 2008). The length of the sea-ice season duration or the timing of sea-ice advance or retreat may have profound consequences on the structure of food webs and their productivity as recently shown in the Bering Sea (Hunt et al. 2011). In the Southern Ocean it has been established that ice-edge blooms have a productivity 4- to 8-fold that of open water (Smith & Nelson 1986), and have high densities of krill (Brierley et al. 2002, Nicol 2006).

Seabirds provide some of the best time series data for Southern Ocean animals because of their accessibility in land-based colonies where they can be studied. Although most seabird time series data may be too short to provide evidence for climate change effects on populations, several studies have found significant changes in demographic and behavioural parameters in relation to climate, such as sea-surface temperature or sea-ice extent (e.g. Fraser et al. 1992, Barbraud & Weimerskirch 2001a, Jenouvrier et al. 2003, Forcada et al. 2006, Trathan et al. 2006).

However, predicting population responses to projected climate change using population dynamics theory and models remains challenging because other environmental factors may affect individuals and population dynamics (Fig. 1). Among these, the accidental mortality of seabirds caused by fisheries has been recognised as a main factor potentially affecting seabird populations. Indeed, the high numbers of seabirds that are killed annually in fishing gear ('bycatch'; Perrin 1969, Weimerskirch & Jouventin 1987, Brothers 1991) have focused attention on the ecological effects of bycatch in industrial fisheries (Brothers et al. 1999, Sullivan et al. 2006, Watkins et al. 2008), and may act as a confounding factor when trying to predict the population dynamics under different scenarios of climate change. To date it remains unclear to what extent simultaneous changes in climate and bycatch have affected and will affect seabird populations. Recently, several studies have investigated the effects of climate change

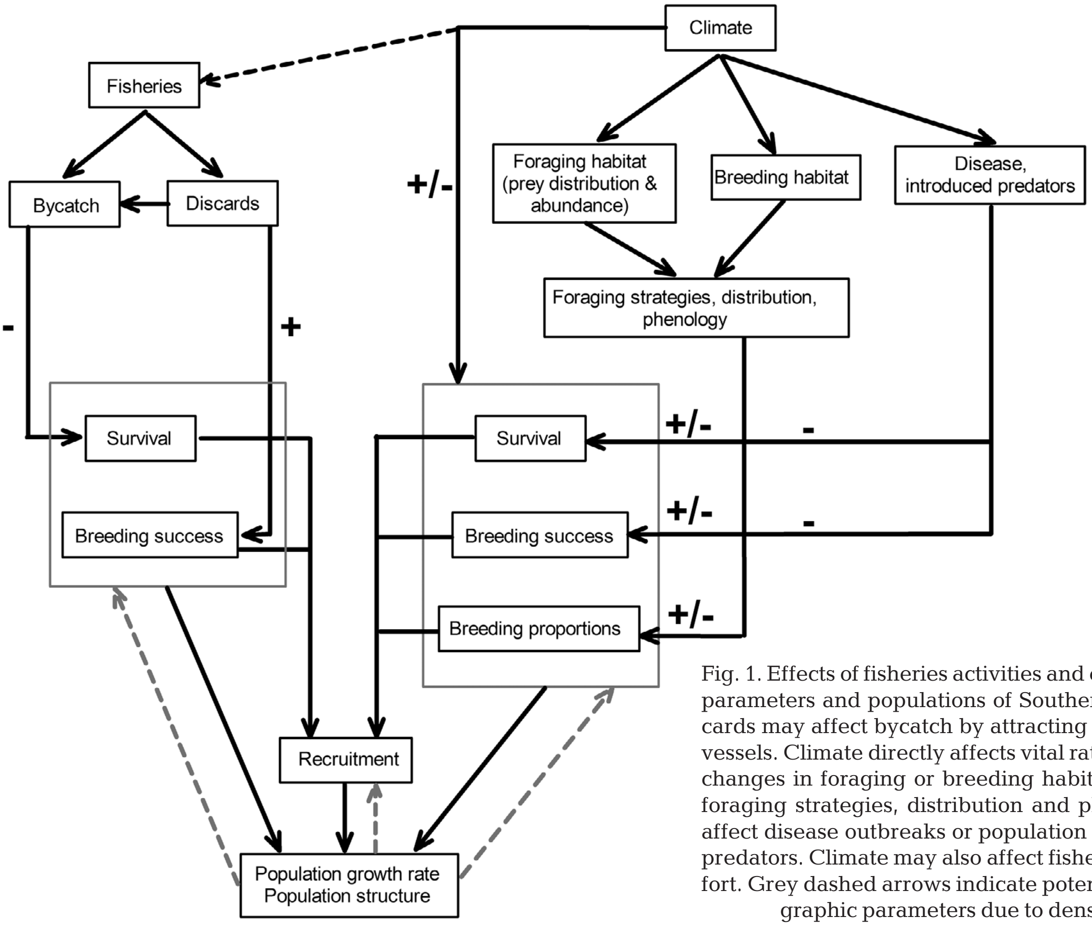

Fig. 1. Effects of fisheries activities and climate on demographic parameters and populations of Southern Ocean seabirds. Discards may affect bycatch by attracting seabirds behind fishing vessels. Climate directly affects vital rates or indirectly through changes in foraging or breeding habitat, which in turn affect foraging strategies, distribution and phenology. Climate may affect disease outbreaks or population dynamics of introduced predators. Climate may also affect fisheries distribution and effort. Grey dashed arrows indicate potential feedback on demographic parameters due to density dependence

(e.g. Peacock et al. 2000, Barbraud & Weimerskirch 2001b, Sydeman et al. 2001, Thompson & Ollason 2001, Ainley et al. 2005, Jenouvrier et al. 2005, Forcada et al. 2006, Le Bohec et al. 2008, Wolf et al. 2010) and bycatch (e.g. Oro et al. 1995, Tuck et al. 2003, Cuthbert et al. 2003, Votier et al. 2004, Lewison et al. 2004, Véran et al. 2007, Frederiksen et al. 2008) separately on seabirds worldwide, but few have addressed both issues simultaneously (Frederiksen et al. 2004, Rolland et al. 2009a). Here, we review the current research on the effects of climate and fisheries bycatch on Southern Ocean seabird demography and population dynamics.

In the Southern Ocean, the twentieth century was also characterised by intensive human exploitation of natural resources, particularly whales and fishes (Pauly et al. 1998, Myers & Worm 2003, Croxall & Nicol 2004, Ainley & Blight 2008, Ainley et al. 2010b). Although the relative importance of bottom-up or top-down processes on the effect of fish and whale harvesting on Southern Ocean top predators such as seabirds are highly debated (Ainley et al. 2007, Nicol et al. 2007, Ainley & Blight 2008, Barbraud & Cotté 2008, Ainley et al. 2010b), it is at present difficult to quantify the effects of either process given the lack of long-term data that incorporate both physical and biological drivers of ecosystem processes. Better documented are the direct interactions between seabirds and fisheries, and more particularly bycatch, which may have been implicated in population declines of several species of seabirds in the Southern Ocean (e.g. Weimerskirch et al. 1997, Tuck et al. 2001). However, the effect of bycatch on demographic parameters and population dynamics remains poorly known for several populations, and even less is known about the potential interactions between bycatch and climate on seabird population dynamics.

Recent technological developments in tracking devices (miniaturisation, memory capacity) have permitted the tracking of seabirds year round and the identification of foraging areas throughout the year (Wilson et al. 2002, Weimerskirch 2007, Burger & Schaffer 2008). This has allowed a better understanding of the spatial and temporal interactions between seabirds and fisheries, which was an important step in developing more realistic models to test the effects of bycatch and climate on population dynamics (Rolland et al. 2008). Simultaneously, the application of the theory of exploited populations to seabird bycatch (Lebreton 2005, Véran et al. 2007) has permitted the development of a robust theoretical background to test for the effects of bycatch on seabird demographics.

In the present paper, we first review the effects of climate change on the distribution and phenology of Southern Ocean seabirds. We then review Southern Ocean studies on seabirds to determine how climate variability, fisheries bycatch and effort affect their demographic parameters and population dynamics. We were more specifically interested in attempting to determine whether general patterns are emerging in the effect of climate and fisheries bycatch on vital rates. In addition, we also consider how Southern Ocean seabird populations may respond to future climate change in light of the recent modelling efforts to tackle this question.

METHODS

This work is based on the analysis of contents from research articles published before September 2011. Research articles were selected with the ISI Web of Knowledge (Thomson Reuters) search engine, using the following search criteria:

Topic = (seabird* OR penguin* OR albatross* OR petrel* OR fulmar* OR shearwater*) AND (southern ocean OR Antarctic) AND (climate OR fisher* OR bycatch).

Timespan = All Years.

These search criteria returned 409 papers to which we added papers collected based on expert knowledge. From these, only papers reporting data on Southern Ocean seabird phenological, distributional, or demographic changes and at least 1 climate or fishery (effort or bycatch) associated variable were retained. Although the Southern Ocean is often defined as the ocean from the coast of Antarctica north to 60° S (www.scar.org/articles/southernocean.html), we here extended the northern limit of the Southern Ocean to 30°S. This allowed us to include in our review many studies that investigated the effects of climate and bycatch on seabird species that breed in the southern hemisphere and frequent the Southern Ocean and its vicinities. This yielded a total of 71 publications on which our review is based (Fig. 2). We recognize that some relevant publications may have been missed, but our review should be representative of research in the field.

The following questions were used to characterize the analyses presented in the reviewed manuscripts: (1) What was the demographic, phenological, or distribution parameter analyzed? (2) What was the climate or fishery (effort, bycatch) variable used? (3) What was the sign of the relationship between climate or fishery variables and seabird variables?

Responses to these questions were then summarized in order to quantify the type of climate or fishery variables affecting seabird variables and the sign of the relationships. Most studies that investigated statistical relationships between climate variables, fishing effort or bycatch, and Southern Ocean seabird demographic parameters (Appendix 1, Tables A1 & A2) focused on a handful of demographic parameters (mainly numbers of breeding pairs, breeding success or adult survival). Few studies focused on juvenile survival, recruitment, breeding proportions, or dispersal. However, these parameters were included in our review since we believe they will be more extensively studied in the future given the increasing number of long-term studies and the development of adequate statistical tools to estimate these parameters.

EFFECTS OF CLIMATE ON SOUTHERN OCEAN SEABIRD PHENOLOGY, DISTRIBUTION, DEMOGRAPHY AND POPULATION DYNAMICS

Distribution

Although, most observations worldwide of climate change responses have involved changes in species' phenology and distribution (Crick et al. 1997, Parmesan et al. 1999, Hüppop & Hüppop 2003), particularly for terrestrial species of the Northern Hemisphere (Parmesan & Yohe 2003, Root et al. 2003, Gaston et al. 2005), evidence remains scarce for Southern Ocean seabirds.

From a historical perspective, there is paleological evidence for major shifts in the distribution of Adélie penguin *Pygoscelis adeliae* populations in the Ross Sea during the Holocene, with 2 periods of large-scale abandonment at 5000 to 4000 and 2000 to 1100 calendar yr BP corresponding to cooling episodes that caused unfavourable marine conditions for breeding penguins (Emslie et al. 2007). There is also evidence for distributional changes in response to climate change for this species at other localities in East Antarctica (Emslie & Woehler 2005) and on the Antarctic Peninsula (Baroni & Orombelli 1994, Sun et al. 2000, Emslie 2001, Emslie & McDaniel 2002,

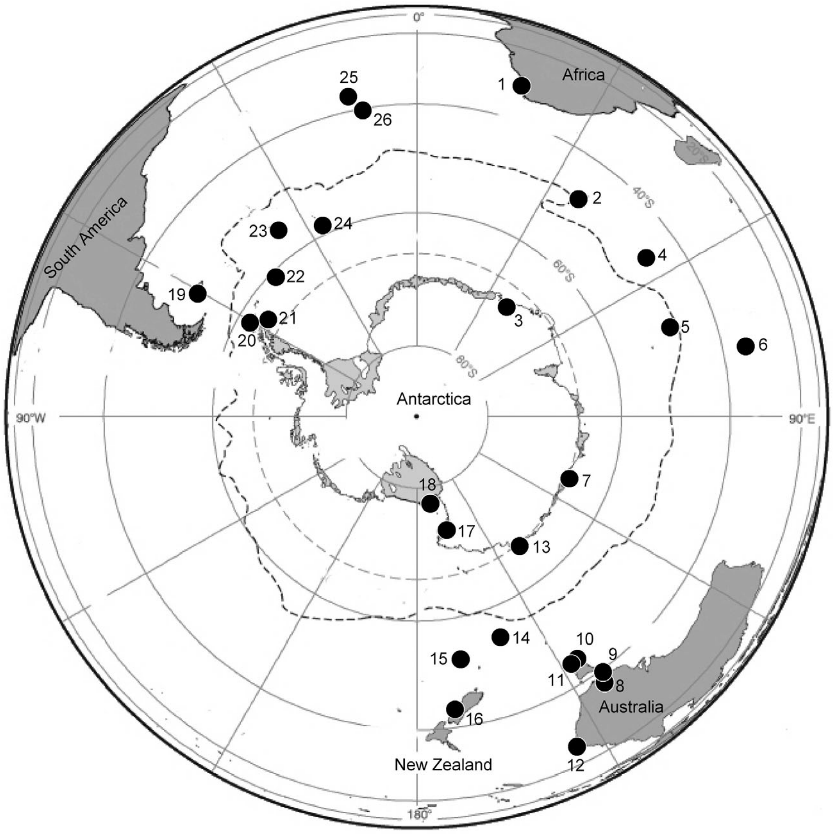

Fig. 2. Location of long-term monitoring studies where the effects of climate variability and fisheries bycatch on demography and population dynamics of Southern Ocean seabirds were investigated. Studied species in parentheses. 1: Malgas Island (cape gannet); 2: Marion & Prince Edward Islands (wandering albatross); 3: Showa (Adélie penguin); 4: Crozet Islands (king penguin, wandering albatross, sooty albatross, light-mantled sooty albatross, southern giant petrel, northern giant petrel, white-chinned petrel); 5: Kerguelen Islands (black-browed albatross, blue petrel, thin-billed prion, grey petrel); 6: Amsterdam Island (Amsterdam albatross, indian yellow-nosed albatross, sooty albatross); 7: Casey (snow petrel); 8: Philipp Island (little penguin); 9: Albatross Island (shy albatross); 10: Mewstone (shy albatross); 11: Pedra Branca (shy albatross); 12: Lord Howe (flesh footed-shearwater); 13: Dumont d'Urville (emperor penguin, Adélie penguin, Antarctic fulmar, snow petrel); 14: Macquarie Island (wandering albatross, grey-headed albatross, black-browed albatross); 15: Campbell Island (rockhopper penguin); 16: Otago Peninsula & Oamaru (yellow-eyed penguin, little penguin); 17: Coulman Island (Adélie penguin); 18: Ross Island (Adélie penguin); 19: Falkland Island/Islas Malvinas (thin-billed prion); 20: South Sandwich Islands (Adélie penguin, chinstrap penguin); 21: western Antarctic Peninsula (Adélie penguin, chinstrap penguin, gentoo penguin); 22: South Orkney Islands (Adélie penguin, chinstrap penguin, gentoo penguin); 23: South Georgia (king penguin, gentoo penguin, macaroni penguin, wandering albatross, black-browed albatross, grey-headed albatross); 24: South Shetland Islands (Adélie penguin, chinstrap penguin); 25: Tristan de Cunha (Atlantic yellow-nosed albatross); 26: Gough Island (Atlantic yellow-nosed albatross). Taxonomic names see Appendix 1

Emslie et al. 2003). Historical distributional changes in response to the advance or retreat of the Antarctic continental ice sheet are also documented for snow petrels *Pagodroma nivea* (Hiller et al. 1988, Verkulich & Hiller 1994, Steele & Hiller 1997). More recently, on centennial to decennial time scales, there is evidence that open-ocean feeding penguins, the chinstrap *P. antarctica* and the gentoo *P. papua*, spread southward between 20 and 50 yr ago along the Antarctic Peninsula, where the most rapid climate changes have been observed, with paleoevidence that gentoo had been absent from the Palmer region for 800 yr previously (Fraser et al. 1992, Emslie et al. 1998).

By contrast, colonies of the pagophilic (i.e. ice dependent) Adélie penguin situated at the northern part of the Antarctic Peninsula have declined dramatically during the past decades in response to a decrease in sea-ice extent and sea-ice season duration (Fraser et al. 1992, Ainley et al. 2005, Forcada et al. 2006, Hinke et al. 2007, but see Trivelpiece et al. 2011). On the other hand, gentoo populations are increasing, which has been interpreted in response to sea ice too because this species needs ice-free habitat around the colonies to breed (the sea-ice hypothesis; Fraser et al. 1992). However, populations of chinstrap penguins show contrasted responses, with some colonies declining while southernmost colonies increase (Fraser et al. 1992, Hinke et al. 2007), which suggests much more complex mechanisms than the sea-ice hypothesis.

Long-term changes in at-sea distribution of Southern Ocean seabirds are still poorly documented due to the scarcity of long-term at-sea observations. In the Prydz Bay area, at-sea observations conducted between 1980 and 1992 by Woehler (1997) revealed a decrease in abundance of 5 non-resident sub-Antarctic species (wandering albatross *Diomedea exulans*, black-browed albatross *Thalassarche melanophrys*, light-mantled sooty albatross *Phoebetria palpebrata*, northern giant petrel *Macronectes halli*, white-chinned petrel *Procellaria aequinoctialis*). However, these changes were not analysed in the light of climate changes in the region during the period of the study. By contrast, in the southern Indian Ocean southward shifts in the distributions of wandering albatross and prions *Pachyptila* spp. between the early 1980s and 2000s could be ascribed to species redistribution or decrease in abundance due partly to the warming of subtropical waters (Péron et al. 2010). Surprisingly, the white-chinned petrel distribution shifted northward, suggesting more complex mechanisms, such as the expansion of fisheries activities in subtropical waters since the 1980s (Tuck et al. 2003). Péron et al. (2010) studied 12 seabird species and showed that the greatest warming of sea-surface waters was observed at 30 to 35° S. Their results suggest that the abundance at sea of the northernmost distributed species (those observed north of 38° S) tended to decline contrary to the southernmost species. Similar patterns and processes were documented elsewhere in other ocean basins (California Current System: Hyrenbach & Veit 2003; Bay of Biscay, North Atlantic: Hemery et al. 2008).

On shorter time scales, there is evidence that migratory movements of seabirds are affected by oceanographic conditions. Ballard et al. (2010) studied the migratory movement and wintering areas of Adélie penguins breeding on Ross Island (Ross Sea, Antarctica) during 3 consecutive years. They showed that the wintering areas were situated at the edge of the consolidated pack ice, well south of the large-scale ice edge itself, and that the wintering area shifted north in years of more extensive ice. Ballard et al. (2010) further suggested that this would move the penguins closer to the Antarctic Circumpolar Current Southern Boundary, where there is less food available. One can conjecture that this may increase winter mortality or breeding proportions in the following breeding season, although this remains to be quantified.

Phenology

Phenological changes were only recently documented for Southern Ocean seabirds. On a regional scale, data on first arrival and laying of first eggs over a 55 yr period for 9 species of Antarctic seabirds in East Antarctica revealed a clear tendency toward later arrival and laying (Barbraud & Weimerskirch 2006). On average, species now arrive at their colonies 9 d later and lay eggs 2 d later than in the early 1950s. This tendency was unexpected and inverse to most of those observed in the northern hemisphere for terrestrial species. Interestingly, these delays were partly linked to a decrease in sea-ice extent that has occurred in East Antarctica, and possibly to an increase in sea-ice season duration. Both factors may have contributed to reduce the quantity and accessibility of the food supplies available in early spring and may partly explain the delays observed, with seabirds needing more time to build up the reserves necessary for breeding. However, more detailed studies at an individual level are needed to understand the proximate and ultimate drivers of Southern Ocean seabirds breeding phenology and the effect of phenological changes on fitness. The fitness and population consequences of these phenological changes are currently unknown but could be serious for these top predators if they become less synchonized with the phenology of their food supplies. A brood that hatches later than expected may suffer from higher environmental deterioration, such as resource depletion, competition, or predation risk for the offspring (e.g. Lack 1968, Verhulst & Nilsson 2008). This could potentially affect reproductive success or juvenile survival. Although few studies have investigated the fitness consequences of a change in the timing of breeding in Southern Ocean seabirds, some observational and experimental studies suggest a decrease in reproductive success in individuals breeding late in the season (Barbraud et al. 2000a, Goutte et al. 2011).

Demography and population dynamics

The climate variables which were used for testing relationships with demographic parameters included large-scale climate indices (Southern Oscillation Index [SOI], Southern Annular Mode [SAM], Indian Ocean Dipole [IOD]) and local climate variables (sea-surface temperature [SST], sea-ice extent [SIE], sea-ice concentration [SIC], air temperature [T], sea-surface height [SSH]). SOI is related to wind stress, sea-surface temperature and precipitation anomalies worldwide (Trenberth 1984). SAM is the leading mode of atmospheric circulation variability in the Southern Hemisphere (Gong & Wang 1998). IOD is related to wind stress, sea-surface temperature and precipitation anomalies over the Indian Ocean (Saji et al. 1999). Positive values of IOD are associated with a warm SST anomaly over the western Indian Ocean and a cold SST anomaly over the eastern tropical Indian Ocean. Although measured in the northern Indian Ocean, IOD also affects SST over the southern Indian Ocean <35° S. We found a total of 35 published studies concerning 22 species of seabirds.

The types of relationships between climate variables and demographic parameters are indicated in Table 1. Most relationships between demographic parameters and sea-surface temperature were negative (~50 %). This is consistent with positive relationships between demographic parameters and SOI (~32 % of the relationships were positive, whereas only ~16 % were negative). Indeed, signals of El Niño–Southern Oscillation (ENSO) variability in the tropical Pacific are known to propagate to high latitudes through atmospheric teleconnections and oceanic processes (Kwok & Comiso 2002, White et al. 2002, Liu et al. 2004, Turner 2004). SOI and SST are inversely correlated in most parts of the Southern Ocean, with positive SOI globally corresponding to negative SST anomalies (Murphy et al. 2007).

Negative effects of warm sea-surface temperature anomalies on demographic parameters have also been found for a number of seabird species worldwide (e.g. North Atlantic Ocean: Kitayskiy & Golubova 2000, Durant et al. 2003, Harris et al. 2005; Pacific Ocean: Veit et al. 1997, Bertram et al. 2005). In several coastal and oceanic ecosystems, and particularly in upwelling and frontal areas, warm sea-surface temperature anomalies are known to have negative effects on primary and secondary production (Wilson & Adamec 2002, Behrenfeld et al. 2006). Cooler temperatures and higher wind stress can produce deeper convective mixing and increased nutrient supply to support higher spring and summer chlorophyll concentrations, whereas warmer sea-surface temperatures and reduced wind stress can produce shallower mixed layers, leading to reduced nutrient entrainment, and reduced spring and summer chlorophyll (Daly & Smith 1993). Therefore, the negative relationships between demographic parameters and SST (positive for SOI) may reflect the effects of limited food resources on the demographic traits of seabirds. Although climatic fluctuations are often suspected to affect seabird populations through integration along the trophic web up to top predators, one may not exclude direct mechanisms. For example, snowfall or atmospheric temperatures may directly affect breeding success in some species (Murphy et al. 1991, Chastel et al. 1993). A small proportion of relationships between SST and demographic parameters were positive, as also detected in other oceanic ecosystems (Sandvik et al. 2008), suggesting the existence of local or regional oceanographic processes (e.g. see Blain et al. 2001, Park et al. 2008a,b for the Kerguelen plateau).

Although sample sizes were relatively small, the effect of sea ice (SIE and SIC) was contrasted between demographic parameters, probably because different mechanisms were involved (Table 1). About 44 % of the relationships between SIE or SIC and breeding success were negative (~25 % were positive), whereas ~37 % of the relationships between SIE or SIC and adult survival were positive (~12 % were negative), and ~54 % of the relationships between SIE or SIC and breeding population size were positive (~38 % were negative). An increase in SIE or SIC may reduce breeding success because it directly affects the foraging habitat of pagophilic species. When sea-ice extent is greater than normal or when sea-ice concentration is particularly high, Antarctic breeding species feeding within the pack ice or at the edges of the pack ice may have to cover greater distances between the nest and the foraging grounds because they are central place foragers during the breeding season. This would increase the amount of time spent travelling and therefore decrease the feeding frequency of chicks during the

Table 1. Numbers and percentages (in parentheses) of positive, negative and null relationships between climate variables and demographic parameters found in the literature review of Southern Ocean seabirds for all climate variables, and for sea-ice variables for 3 demographic parameters. See Appendix 1 for the definition of variables

	Effect		
	Positive	Negative	Null
Climate variables			
SST	9 (20)	22 (50)	13 (30)
SOI	10 (32)	5 (16)	16 (52)
SIE or SIC	18 (37)	16 (33)	15 (30)
SAM	2 (22)	5 (56)	2 (22)
T	3 (25)	6 (50)	3 (25)
IOD	1 (33)	0 (0)	2 (67)
Effect of SIE or SIC on			
Adult survival	3 (37)	1 (12)	4 (50)
Breeding success	4 (25)	7 (44)	5 (31)
Breeding pairs	7 (54)	5 (38)	1 (8)

chick rearing period, or exceed the fasting capacity of the incubating partner during incubation. Overall this would lead to a decrease in breeding success. This is typically the case for penguins such as the emperor penguin *Aptenodytes forsteri* or the Adélie penguin *Pygoscelis adeliae* (Ainley & LeResche 1973, Ancel et al. 1992, Barbraud & Weimerskirch 2001a, Massom et al. 2009).

Conversely, an increase in SIE or SIC may increase (indirectly) adult survival because it positively affects the Antarctic food web, more particularly its productivity. Sea-ice conditions are known to affect Antarctic food webs, which may in turn affect demographic parameters such as survival and breeding proportions. Several studies suggest a positive relationship between winter SIE or SIC and the abundance of key species of the Antarctic ocean food web such as the Antarctic krill *Euphausia superba* (Loeb et al. 1997, Nicol et al. 2000). Therefore, we hypothesise that extensive sea ice in winter may correspond to higher levels of food resources for seabirds during spring and summer, which may affect their adult survival and their decision to breed (Barbraud & Weimerskirch 2001a, Jenouvrier et al. 2005). Indeed, it is well known that in seabirds the proportion of individuals engaging in reproduction depends in part on physical body condition, which might be directly affected by the amount of food resources available (Drent & Daan 1980, van Noordwijk de Jong 1986, Chastel et al. 1995).

Eventually, these contrasted effects of sea ice on different vital rates affect population size. Indeed, breeding population size in a given year is the outcome of the variations of lower level demographic parameters such as survival, breeding success, breeding proportions and recruitment. Therefore, the effect of SIE or SIC on breeding population size may be mediated through the effects of these climate variables on lower level demographic parameters. Table 1 shows that population size was often found to be positively linked to SIE or SIC. This is not surprising for long-lived species for which the population growth rate is extremely sensitive to adult survival. However, breeding success can also play an important role in population dynamics because it is more variable than adult survival (Gaillard & Yoccoz 2003). For example, the decrease in breeding success limits the population recovery of an emperor penguin population in East Antarctica (Jenouvrier et al. 2009). In addition, since population size in seabirds is often measured by the number of breeders at a colony, the amount of food available in a given year or the following winter may affect the number of birds attempting to breed in the following year, although there may have been no actual change in the population size.

Recruitment and breeding proportions are also important parameters to take into account to understand population responses to sea ice. For example, in the Adélie penguin a negative effect of SIE on breeding population size with a 5 to 6 yr lag is suspected to result from negative effects of large SIE on juvenile survival, which has an effect on breeding population size when individuals recruit to the breeding population at ~6 yr of age (Wilson et al. 2001, Jenouvrier et al. 2006). Extensive sea ice may limit access of penguins to productive waters, with starvation or increased predation disproportionately affecting less-experienced birds.

The complex contrasted effects of sea ice (and to a lesser extent sea-surface temperature) on demographic rates strengthen the importance of considering the entire life cycle to understand the effects of climate on populations. The example of sea ice on seabirds is particularly interesting because it suggests the existence of optimal SIE or SIC conditions which may maximise demographic parameters and population growth rates of seabirds depending on a sea-ice habitat. Ballerini et al. (2009) found a quadratic relationship between Adélie penguin survival and winter SIE and hypothesised that high SIE may limit access to food resources, whereas low SIE may limit abundance of food resources. Interestingly, an increasing number of studies have found non-linear relationships between seabird demographic parameters and climate variables (Gjerdrum et al. 2003, Barbraud et al. 2011), suggesting the widespread existence of optimal environmental conditions for population growth rates. Such non-linear relationships have also been proposed to explain the contrasted population trends of Adélie penguins in Antarctica (Smith et al. 1999), with optimal population growth corresponding to intermediate frequencies of heavy sea-ice conditions (Fig. 3). This conceptual model of optimal environmental conditions may help explain the contrasted responses observed among different populations in the Southern Ocean and other ocean basins (Sandvik et al. 2008).

Mainly documented are relationships between climate variables and breeding success, adult survival and numbers of breeding pairs. The last 2 are the most easily and cost effectively obtained in the field, and statistical developments in capture-mark-recapture methods during the last 3 decades have allowed researchers to obtain robust estimates of adult survival (Williams et al. 2002). Very few studies have investigated the effects of climate on juvenile survival or recruitment (Appendix 1). However, these parameters may potentially be more sensitive to climate variability, since in such long-lived species, juvenile survival is predicted to be less environmentally canalised (canalisation here refers to a reduction in the variability of a trait) against temporal variability (and potentially environmental variability) than adult survival (Pfister 1998, Gaillard & Yoccoz 2003). In accordance with this prediction, some studies have found stronger relationships between survival of younger individuals and climate factors than with older individuals (Nevoux et al. 2007).

The effects of climate variability on breeding dispersal of Southern Ocean seabirds have only recently been investigated. Dugger et al. (2010) estimated breeding dispersal of Adélie penguins between 3 different colonies in the south-western Ross Sea and found that movement probabilities of breeding adults from one year to the next were higher in years with extensive sea ice or blockage to usual migration patterns (Fig. 4).

Part of the contrasted responses within species may be caused by the spatial variability in food webs of the Southern Ocean (Trathan et al. 2007). Different areas of the Southern Ocean are dominated by different food webs. For instance, the lower trophic levels of the Scotia Sea region are dominated by krill (Croxall et al. 1988, Murphy et al. 2007), whereas those of the southern Indian Ocean are dominated by myctophids (Pakhomov et al. 1996, Connan et al. 2008, Cherel et al. 2008). Given the variation of habitat preferences of the lower trophic levels we may thus expect different effects of climate change in different food webs and regions, and consequently contrasted upper trophic level responses (Trathan et al. 2007).

The interspecific variability in trophic niche and foraging strategies of seabirds (Weimerskirch 2007) may also partly explain the observed contrasted responses. For instance, at South Georgia, warm sea-surface temperature anomalies have positive effects on the breeding success of black-browed albatrosses *Thalassarche melanophrys* (Nevoux et al. 2010a) but negative effects on the breeding success of gentoo penguins *Pygoscelis papua* (Trathan et al. 2006).

Although several relationships between demographic parameters and climate variables were found for a number of seabird populations in the Southern Ocean, our understanding of the underlying ecological mechanisms remains extremely limited. This is mainly because long-term time series of abundance for prey species of Southern Ocean seabirds are scarce due to sampling difficulties and associated costs. This results in a poor understanding of how biological and physical processes interact across spatial and temporal scales. Perhaps best understood are the demographic and behavioural responses of seabirds breeding in the South Atlantic, where the food webs of this region have been studied since the beginning of the last century (Trathan et al. 2007). The food web of the South Atlantic and Scotia Sea is highly dominated by krill. Atmospheric teleconnections with ENSO generate anomalies in SST in the South Pacific sector of the Southern Ocean which are propagated eastward via the Antarctic Circumpolar Current and reach the South Atlantic with several months lag. Changes in the South Atlantic

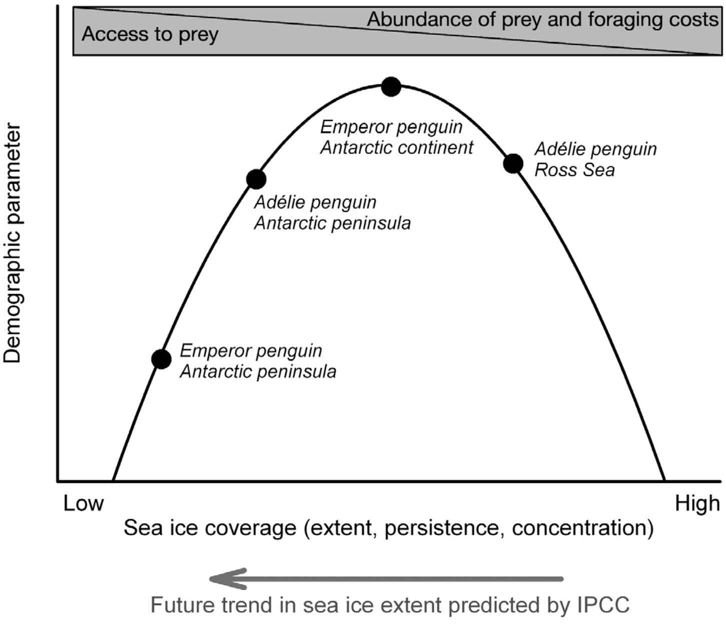

Fig. 3. Conceptual model adapted from Smith et al. (1999) illustrating the consequences of sea-ice coverage variation on abundance and access to prey of Antarctic seabirds, and its potential effect on seabird demographic parameters. Dots show the hypothetical positions of populations of penguins. In the Antarctic Peninsula, 1 emperor penguin colony was recently reported as extinct probably as a consequence of sea-ice disappearance during the last decades (Barbrand & Weimerskirch 2001a). On the Antarctic continent colonies appear to be stable during the past 2 decades (Woehler & Croxall 1997, Kooyman et al. 2007, Jenouvrier et al. 2009, Barbraud et al. unpubl. data, Robertson et al. unpubl. data), although major declines were reported during the late 1970s at some colonies (Barbraud & Weimerskirch 2001). The future trend in sea-ice coverage as predicted by IPCC scenarios and models is indicated, and is expected to negatively affect the northernmost penguin colonies (Jenouvrier et al. 2009, Ainley et al. 2010a). Taxonomic names see Appendix 1

sector of SST and related fluctuations in SIE affect the recruitment and dispersal of krill, which, in turn, affects the breeding success and populations (Fig. 5) of seabirds that depend on this prey species (Reid et al. 2005, Forcada et al. 2006, Murphy et al. 2007). Similar processes seem to occur south of Kerguelen in the southern Indian Ocean. In this region SST anomalies are also linked to ENSO through atmospheric teleconnections and possibly eastward propagation of SST anomalies generated in the South Pacific (Guinet et al. 1998, Park et al. 2004, Murphy et al. 2007). During warm SST anomalies the diet of blue petrels *Halobaena caerulea* breeding at and foraging south of the Kerguelen Islands is highly skewed towards crustaceans (euphausiids and *Themisto gaudichaudii*), whereas fishes (mainly myctophids) constitute the main part of their diet during normal years (Connan et al. 2008). Interestingly the per capita energetic content of crustacean species consumed during warm SST anomalies is less important than the energetic value of fish species consumed, and body condition, breeding probability and success, and adult survival are all negatively affected by warm SST and positive SSH anomalies south of Kerguelen (Guinet et al. 1998, Barbraud & Weimerskirch 2003, 2005).

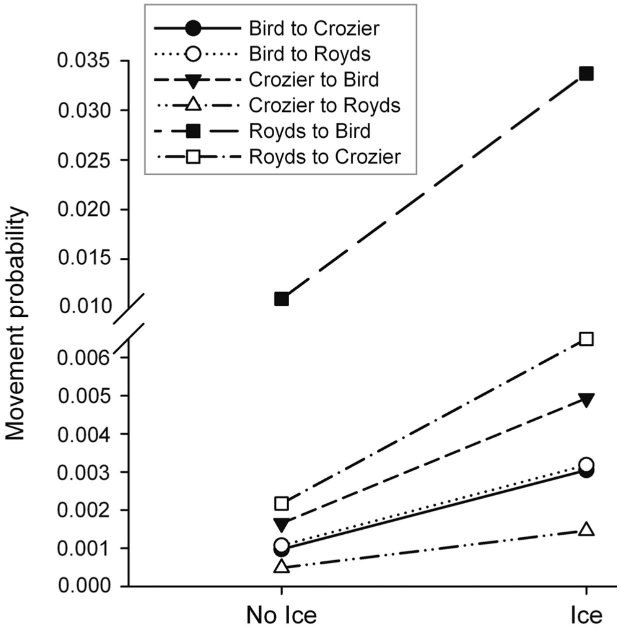

Fig. 4. *Pygoscelis adeliae.* Effect of sea-ice variability on annual breeding dispersal probability of adult Adélie penguins breeding in the south-western Ross Sea, from 1996 to 2007. Movement probabilities differed between colonies but were higher in years with extensive sea ice or when icebergs were present serving as physical barriers and altering the spring migration route of penguins. From Dugger et al. (2010)

EFFECTS OF FISHERIES BYCATCH ON DEMOGRAPHY AND POPULATION DYNAMICS OF SOUTHERN OCEAN SEABIRDS

Although accidental bycatch of seabirds in fishing gear has been an acknowledged problem for a relatively long time (e.g. Perrin 1969, Weimerskirch & Jouventin 1987, Brothers 1991), most studies examining the effects of fisheries bycatch on demographic parameters and population dynamics are relatively recent (Oro et al. 1995, Cuthbert et al. 2003, Tuck et al. 2003, Lewison et al. 2004, Votier et al. 2004, Véran et al. 2007, Barbraud et al. 2008, Frederiksen et al. 2008, Rolland et al. 2008, Véran & Lebreton 2008). The species reported most frequently caught in longlines worldwide include albatrosses, petrels and shearwaters (Brothers et al. 1999), most of which have highly unfavourable conservation status (Baker et al. 2002). In the Southern Ocean, accidental mortality in trawling fisheries may also be high (Sullivan et al. 2006, Croxall 2008, Watkins et al. 2008).

Table 2 summarizes the studies that investigated the effect of fisheries bycatch on 5 demographic parameters of Southern Ocean seabirds. Although some studies tested for explicit relationships and others inferred an effect of bycatch on population dynamics using population models including additive mortality effects, the majority of studies found negative effects of fishing effort or bycatch rates on demographic parameters (~64%). Despite positive effects of fisheries activities on breeding success of

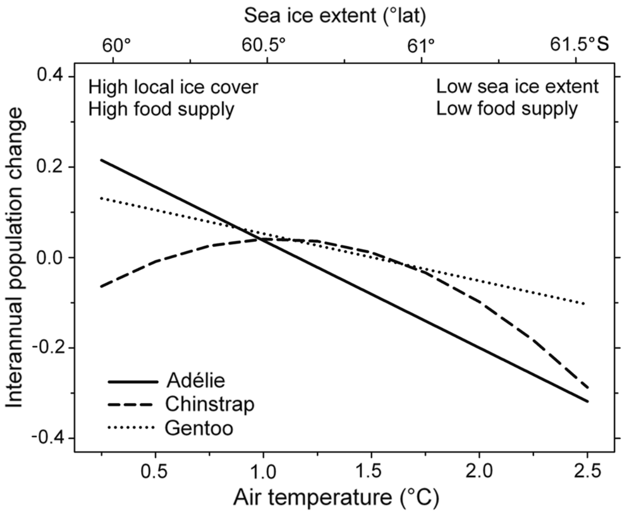

Fig. 5. *Pygoscelis* spp. Representation of the diversity of penguin population responses (interannual changes in numbers of breeding pairs) to the environment at Signy Island, South Orkney Islands. Responses may be linear or non-linear depending on the species' ecological requirements. From Forcada et al. (2006)

some species, probably due to additional food resources such as bait, offal, or discards (Northern Hemisphere: Garthe et al. 1996, Oro et al. 1996; Southern Hemisphere: Grémillet et al. 2008), most studies reported negative effects on adult survival. This may have severe consequences on populations of long-lived species, whose population growth rate is highly sensitive to small variations in adult mortality (Lebreton & Clobert 1991).

For methodological reasons, very few studies have investigated the effects of fisheries activities on juvenile survival or recruitment, and they also suggest negative effects. Even if population growth rate of seabirds is less sensitive to variations in these parameters, chronic mortality of the younger age classes may in the long term have detrimental effects on populations (Barbraud et al. 2008) as it would deplete the pool of future breeders. Higher vulnerability of younger individuals to fishing gear has been reported in several seabird species (Murray et al. 1993, Gales et al. 1998, Bregnballe & Frederiksen 2006). Younger birds may (1) spend more time in areas with high longline efforts than adult birds, (2) be less efficient foragers than adults and may therefore attempt to fish behind vessels more frequently, (3) be more hungry than adults and take more risks behind vessels, and (4) be less experienced than adults in foraging behind vessels without getting hooked. For a number of studies (~24 %), no significant effect of fishing effort on demographic parameters was found. This may be due to a lack of statistical power or methodological problems, or the implementation of mitigation measures to limit bycatch. Indeed, mitigation measures (mainly within Exclusive Economic Zones and in the Convention on the Conservation of Antarctic Marine Living Resources area) have drastically reduced bycatch rates in some fisheries of the Southern Ocean during the last decades (Croxall & Nicol 2004, Robertson et al. 2006, SC-CCAMLR 2006, Delord et al. 2010), and it was generally assumed that the level of bycatch was proportional to the fishing effort (Véran et al. 2007) because very little information was available to directly estimate harvest rates. Further modelling is needed to take into account and specifically test whether the decrease in bycatch following mitigation measures can be detected on demographic parameters such as adult survival.

It is known that there are no detailed demographic data for several species of Southern Ocean seabirds affected by bycatch. This causes many difficulties in estimating the impact of bycatch on these species. The potential biological removal approach offers an interesting alternative way for assessing the potential for populations to sustain additional mortalities (Wade 1998, Taylor et al. 2000, Niel & Lebreton 2005). This method has recently been further developed and used to assess the potential effects of bycatch on Southern Ocean seabirds (Hunter & Caswell 2005, Dillingham & Fletcher 2008).

Table 2. Numbers and percentages (in parentheses) of positive, negative and null relationships between fishing effort (trawl and longline) and demographic parameters found in the literature review of Southern Ocean seabirds

	Effect		
	Positive	Negative	Null
Adult survival	1 (5)	14 (64)	7 (31)
Juvenile survival	0 (0)	2 (67)	1 (33)
Recruitment	0 (0)	1 (100)	0 (0)
Breeding success	3 (100)	0 (0)	0 (0)
Breeding pairs	0 (0)	4 (100)	0 (0)

The effect of fisheries on Southern Ocean seabird populations through the harvest of intermediate trophic level species remains largely unexplored (Wagner & Boersma 2011). Studies using predator–prey models or ecosystem models remain largely theoretical (May et al. 1979) and often suffer from a shortage of empirical data (Hill et al. 2006). Major fisheries have operated in the Southern Ocean since the early 1970s and have led to the overexploitation of several species such as marbled rock cod *Notothenia rossi* and icefish *Champsocephalus gunnari* (Croxall & Nicol 2004), but their potential effect on seabird population remains poorly known. However, correlations between predator populations and fish biomass in predator foraging areas suggest that several predator populations including seabirds (gentoo penguin, macaroni penguin, imperial shag *Phalacrocorax* spp.) that feed extensively on exploited fish species declined simultaneously during the 2 periods (early 1970s and mid-1980s) of heavy fishing (Ainley & Blight 2008).

The effect of the depletion of whale stocks during the 1950s to 1960s on Southern Ocean seabirds remains speculative, essentially because very few monitoring and trophic studies were underway during the whaling period (Ainley et al. 2010b). Given the major role of cetaceans in the structuring of Southern Ocean food webs (Balance et al. 2006), the demise of large whale species in the Southern Ocean may explain some changes in the population dynamics of several seabird species, through a release of trophic competition and the resulting krill surplus or an effect of upper level predators though top-down forcing (Ainley et al. 2010b).

Although the krill fishery has been the largest fishery in the Southern Ocean since the late 1970s, its impact on upper trophic levels, such as seabirds, is still poorly understood and remains to be quantified. There is evidence for ecosystem responses to the regional warming of the West Antarctic Peninsula that has occurred during the past 50 yr. In particular, decreased sea-ice extent and duration altered the phytoplankton and zooplankton communities and had negative effects on krill recruitment and on top predator populations such as Adélie and chinstrap penguins (Ducklow et al. 2007, Hinke et al. 2007, and references in Appendix 1). However, Trivelpiece et al. (2011) recently suggested that, in addition to climate, fisheries may have played an important role in shaping the population dynamics of penguins in the West Antarctic Peninsula and the Scotia Sea. According to their scenario (Fig. 6), favourable climate conditions and reduced competition for krill following the massive and large-scale harvesting of seals, whales, ice fishes and notothenioids from the early 1820s to the 1980s may have favoured Adélie and chinstrap penguins whose populations increased. Since the late 1970s climate changes (sea-ice loss), increased competition for krill following the recovery of marine mammal populations, and the expansion of the krill fishery resulted in poor environmental conditions for penguins (decrease in krill density), the populations of which declined.

COMBINED EFFECTS OF CLIMATE AND FISHERIES BYCATCH ON POPULATION DYNAMICS

Comparing the relative effects of climate factors and bycatch levels on demographic parameters remains a difficult task at present due to the heterogeneity of the methods used to estimate their respective effects. To be comparable, both effects need to be tested within the same statistical and modelling framework and the variables need to be standardised (Grosbois et al. 2008). This was possible for a limited number of studies on 4 albatross species of the southern Indian Ocean (Rolland et al. 2010). The mean ± SE of the slopes of the relationships between adult survival (which was found to be the parameter affected by fishing effort) and the standardised fishing effort (assumed to be proportional to bycatch) was −0.237 ± 0.041. This mean was 0.162 ± 0.020 for the relationships between breeding success (which was found to be the parameter most frequently related to climate variables) and the standardised climate variables. Although these mean slopes are not statistically different at the 0.05 level ($\chi^2 = 0.172$, $p = 0.10$), the mean effect of fishing effort is nevertheless 46.3% higher than the mean effect of climate variables. Because it mainly affects adult survival, one might conclude that for these 4 albatross species the population-level effect of fishing effort (and bycatch) is probably more important than the influence of climate variability.

The effects of climate variability on the one hand and of fisheries activities on the other were shown to be related to several demographic parameters in seabird populations in the Southern Ocean and other ocean basins (Appendix 1, Tables A1 & A2). However, very few studies have combined both effects into fully parameterized population models to understand past population changes and to predict population growth rates under several scenarios of climate and fishing effort. In the North Sea, Frederiksen et al. (2004) built a matrix population model integrating the effect of SST on adult survival and breeding success of the kittiwake *Rissa tridactyla*, which were also negatively affected by the lesser sandeel *Ammodytes marinus* fishery. Their model suggested that the observed changes in the demographic parameters related to changes in SST and fisheries activities could explain the observed change in population growth rate of the kittiwake population. Furthermore, stochastic modelling indicated that the population was unlikely to increase if the fishery was active or SST increased and that the population was almost certain to decline if both occurred. The same approach was used by Barbraud et al. (2008) on a population of the most frequently killed Southern Ocean seabird species by longline fisheries, the white-chinned petrel *Procellaria aequinoctialis*. The present study showed contrasted effects of fishing efforts, with a positive effect of toothfish *Dissostichus eleginoides* fishing effort on breeding success, and negative effects of toothfish and hake *Merluccius* spp. fishing effort on petrel recruitment. Climate (SOI) was found to mainly affect adult survival in this species. The population trajectory of a population matrix model explicitly integrating the relationships between environmental parameters and demographic parameters was very similar to the observed population growth rate estimated from independent survey data. Population modelling suggests that when fisheries are operating (and assuming a proportional level of bycatch), the population growth rate is more sensitive to a decrease in the mean or to an increase in the variance of SOI than to a change in the fishing effort. If the fisheries continue to operate at current levels of bycatch, it is likely that the population will probably

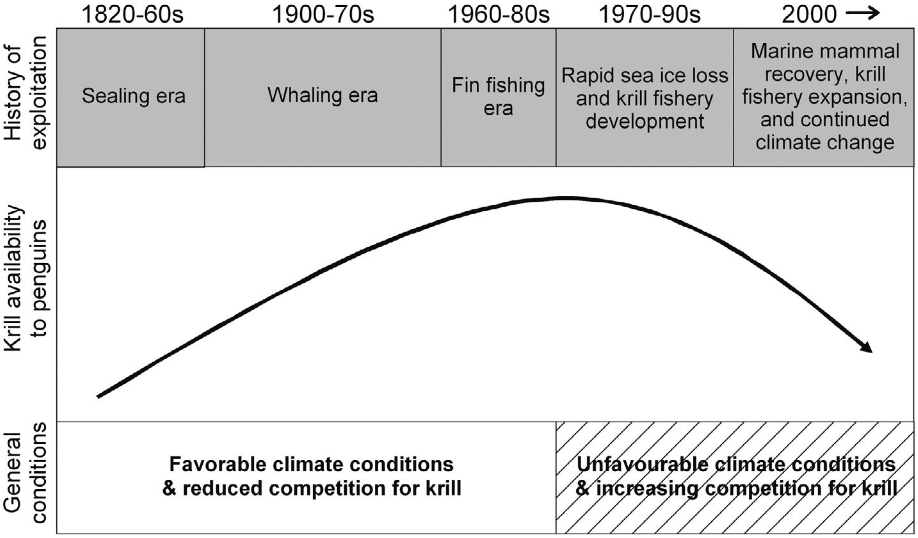

Fig. 6. *Pygoscelis adeliae*, *P. antarctica*. Diagram of ecosystem perturbations in the Scotia Sea. From the early 1820s to the 1980s climate conditions were favourable for Adélie and chinstrap penguins, and exploitation of seals, whales and fin fishes resulted in a reduced competition for krill. From the 1970s, climate conditions became progressively unfavourable, and recovery of marine mammal populations and the expansion of the krill fishery resulted in increased competition for krill. From Trivelpiece et al. (2011)

not recover from its past decline. However, due to the additive effects of SOI and fishing effort on adult survival, an increase in SOI (corresponding to a decrease in frequency and intensity of El Niño events) may compensate for the negative effects of fisheries bycatch.

For the black-browed albatross *Thalassarche melanophrys*, whose adult survival and breeding success are affected by SST and bycatch mortality, population modelling indicated that population equilibrium was precarious, resulting from multiple factors and complex relationships between demographic parameters and environmental conditions (Rolland et al. 2009a). If fishing effort (and bycatch) stops over the wintering area of the studied population, the population would increase at 3.5 % yr^{-1}, suggesting that bycatch mortality probably currently limits the growth of the black-browed albatross population at Kerguelen (Fig. 7). These studies illustrate the importance of population models for quantifying the effects of climate and fisheries activities on populations and for projecting the possible trajectories of a population according to predicted climate change and possible modifications in human activities.

SUMMARY AND CONCLUSIONS

Overall, our review suggests that climate fluctuation mainly affected low elasticity demographic traits (fecundity, productivity), contrary to bycatch which mainly affects high elasticity traits (survival). Because seabirds are long-lived organisms, bycatch represents a serious threat to several seabird populations and mitigation strategies may be effective (decrease fishing effort to preserve populations from the effect of climate change, e.g. Igual et al. 2009). Population models also suggest that climate can act synergistically with bycatch and accelerate population declines or may partially counteract additional mortality.

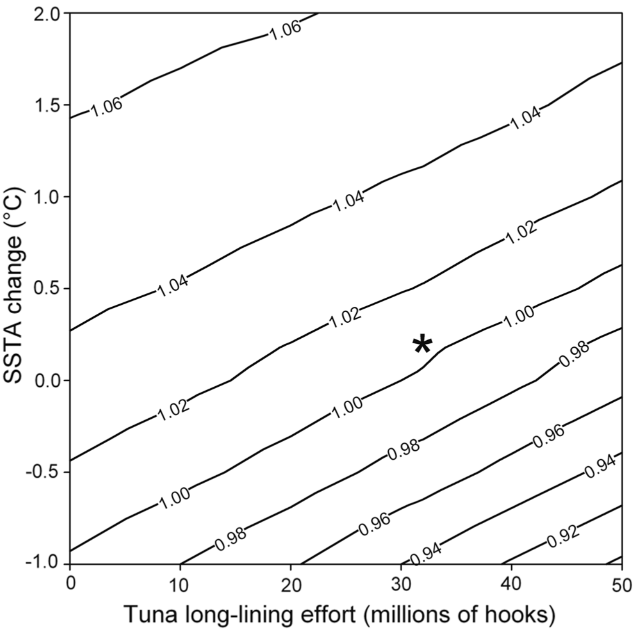

Fig. 7. *Thalassarche melanophrys*. Interaction between the effects of climate variability (sea-surface temperature anomalies [SSTA] in the foraging areas used during the breeding period) and fisheries bycatch (long-lining effort in the area used during the non-breeding period) on the population growth rate of a black-browed albatross population at Kerguelen Island. The star represents the conditions of fisheries and sea-surface temperature at the time the study was performed, and solid lines are isoclines where population growth rates are constant for different parameter values. From Rolland et al. (2009a)

Although climate factors that affect seabird demographic parameters are only to some extent within human control, any policy changes aimed at reversing the warming trend and decreasing trend in sea-ice extent in the Southern Ocean will be slow to take effects due to the inertia of the earth climate system. The microevolutionary responses of Southern Ocean seabirds to climate change are also limited due to the long generation time of these species and the fast environmental changes, although they probably can track some environmental changes through phenotypic plasticity. For example, life-history theory predicts that an increase in adult mortality should select for an earlier age at first reproduction and for an increase in reproductive effort (Gadgil & Bossert 1970, Schaffer 1974, Law 1979, Charlesworth 1994). Such responses have experimentally or empirically been reported for a number of fish species (e.g. Reznick et al. 1990, Rochet et al. 2000), and the decrease in age at first reproduction observed in a wandering albatross *Diomedea exulans* population during a period of high adult mortality caused by fisheries bycatch is consistent with this prediction (Weimerskirch & Jouventin 1987). The decrease in female age at sexual maturation in the crabeater seal *Lobodon carcinophagus* through time is also possibly linked to an increase in food availability following the decline of baleen whales due to whaling (Bengtson & Siniff 1981). However, evolutionary constraints specific to most Southern Ocean seabirds may limit their response capacity to an increase in mortality induced by fisheries bycatch. Clutch size is limited to 1 egg yr^{-1}, breeding frequency is highly constrained by the seasonality of the Southern Ocean, and size at maturity is constrained in those species with finite structural growth (Warham 1990).

Thus, it seems prudent and in accordance with the precautionary principle to evaluate and quantify the effect of fisheries bycatch and to apply mitigation measures when necessary for those fisheries known to interact with threatened populations. Population models can help identify the demographic parameters most affected by bycatch. The influence of other environmental factors on Southern Ocean seabird population dynamics also need to be assessed. For example, the population growth rate of Indian yellow nosed albatrosses *Thalassarche carteri* at Amsterdam Island is known to be limited by outbreaks of avian cholera causing high chick mortality rather than by climatic conditions or fishery-induced bycatch (Rolland et al. 2009a). Introduced predators are known to affect seabird demographic parameters and population dynamics too (Marion Island: Cooper et al. 1995; Possession Island: Jouventin et al. 2003; Réunion Island: Dumont et al. 2010; cats: Nogales et al. 2004; rats: Jones et al. 2008), and several Southern Ocean islands host one or several species of introduced predators. Southern Ocean seabirds are also increasingly exposed to marine debris, pollutants and chemicals, which may also potentially affect their physiology, behaviour and demography (Burger & Gochfeld 2002). For example, in common guillemots *Uria aalge* breeding in the North Atlantic there was a doubling of adult mortality associated with major oil spills in the wintering areas of the birds, and recruitment was higher in years following oil spills than following non-oil-spill years, probably through reduced competition and compensatory recruitment at the breeding colony (Votier et al. 2008). Finally, increased freshwater input from melting glaciers and ice shelves acts to increase stratification along coastal margins, which, in turn, may affect phytoplankton blooms (Moline et al. 2008) and release persistent organic pollutants into the ecosystem where they may accumulate in higher trophic level predators (Geisz et al. 2008).

FUTURE CHANGE AND RESEARCH NEEDED

Predictions from climatologists in the 4th IPCC assessment can be used directly in population models to help determine the future of populations (Jenouvrier et al. 2009, Hare et al. 2010, Wolf et al. 2010, Barbraud et al. 2011). Future population models may eventually need to consider potentially important effects such as non-linear relationships between demographic parameters and climate or fishery variables (Mysterud et al. 2001, Gimenez & Barbraud 2009), density dependence (Frederiksen et al. 2001, Lima et al. 2002), synergistic effects with other environmental factors (Brook et al. 2008), or microevolutionary changes (Kinnison & Hairston 2007, Coulson et al. 2010, Ozgul et al. 2010). From a methodological point of view recent developments in capture-mark-recapture models permit robust estimates of juvenile survival, recruitment and dispersal (e.g. Lebreton et al. 2003). These methods are particularly appropriate for seabirds with delayed maturity, and we believe there will be an increasing use in the near future. Future studies aimed at testing the effects of climate factors on these demographic parameters (and others) should use robust and standardised statistical methods so that future results can be integrated into meta-analyses (Grosbois et al. 2008).

One additional uncertainty in the future concerning the combined effects of fisheries and climate on seabird populations is the effect of climate on fisheries. Longline fisheries are large-scale mobile fisheries the distribution and effort of which are influenced by environmental factors and especially large-scale climatic processes (Tuck et al. 2003, Lehodey et al. 1997, 2006). Thus, future climate change will undoubtedly affect target species of large migratory fishes such as tuna (Hobday 2010). Lacking are model-based projections of the spatio-temporal distribution of fisheries activities in the Southern Ocean that would help build more realistic scenarios for Southern Ocean seabirds.

Consequently, fisheries distribution and effort, and therefore future interactions, will be complex and more difficult to predict. Intensive land- and at-sea-based long-term studies remain the only source of consistent data allowing evaluation of population trends, dynamics and how they are affected by environmental factors, and engaging in such studies should be a high priority for research and management (Clutton-Brock & Sheldon 2010). Additional measurements on other trophic levels (abundance of prey), foraging behaviour, climate–fishery interactions, bycatch rates, and on the mechanisms underlying phenotypic plasticity will increase the comprehensive and predictive power of these long-term studies (Visser 2008).

Studies combining seabird demographic, trophic, behavioural (foraging) and physiological data will be most promising in order to understand the mechanistic responses of seabirds to climate change and to improve our ability to build sound scenarios for the effects of future climate changes. For example, in the Northern Hemisphere, pioneering studies have examined the links between food abundance, nutritional stress (hormone corticosterone), reproduction and survival of individuals of the kittiwake *Rissa tridactyla* (Kitaysky et al. 2010). When possible, future studies will also have to take into account potential ecological processes of trophic cascades, competition, predation and facilitation when attempting to address climate effects on Southern Ocean seabird populations (Ainley et al. 2010b).

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Appendix 1. Table A1. Studies that investigated the effects of climate factors on demographic parameters of Southern Ocean seabirds. ✓: demographic parameters investigated (Sa: adult survival; Sj: juvenile or immature survival; Re: recruitment; Pr: breeding proportions; Bs: breeding success; N: number of breeding pairs); SST: sea-surface temperature; SIE: sea-ice extent; SIC: sea-ice concentration; T: air temperature; SSH: sea-surface height; SOI: Southern Oscillation Index; SAM: Southern Annular Mode; IOD: Indian Ocean Dipole

Species	Sa	Sj	Re	Pr	Bs	N	Climate factor	Region	Reference
Emperor penguin *Aptenodytes forsteri*		✓		✓	✓	✓	SST, SIE, SIC, SOI, T, SAM	Adélie Land	Barbraud & Weimerskirch (2001a), Ainley et al. (2005), Jenouvrier et al. (2005), Massom et al. (2009)
King penguin *Aptenodytes patagonicus*	✓				✓		SST, SOI	South Georgia, Crozet Islands	Olsson & van der Jeugd (2002), Le Bohec et al. (2008), Saraux et al. (2011)
Adélie penguin *Pygoscelis adeliae*	✓				✓	✓	SST, SIE, SIC, T, SOI, SAM	Ross Sea, Adélie Land, Enderby Land, Antarctic Peninsula, Antarctica, Signy Islands	Fraser et al. (1992), Wilson et al. (2001), Ainley et al. (2005), Jenouvrier et al. (2006), Emmerson & Southwell (2008) Lescroël et al. (2009), Ballerini et al. (2009), Forcada & Trathan (2009)
Chinstrap penguin *Pygoscelis antarctica*					✓	✓	SIE, T, SAM	Antarctic Peninsula, Signy Islands	Forcada et al. (2006), Forcada & Trathan (2009)
Gentoo penguin *Pygoscelis papua*					✓	✓	SST, SIE, T, SAM	South Georgia, Antarctic Peninsula	Forcada et al. (2006), Trathan et al. (2006), Forcada & Trathan (2009)
Yellow-eyed penguin *Megadyptes antipodes*	✓				✓	✓	SST	New Zealand	Peacock et al. (2000)
Rockhopper penguin *Eudyptes chrysocome*						✓	SST	New Zealand	Cunningham & Moors (1994)
Macaroni penguin *Eudyptes chrysolophus*						✓	SAM	South Georgia	Forcada & Trathan (2009)
Little penguin *Eudyptula minor*					✓		SST, SOI	New Zealand, Australia	Perriman et al. (2000), Chambers (2004)
Wandering albatross *Diomedea exulans*	✓				✓	✓	SST, SOI	Crozet Islands	Inchausti et al. (2003), Delord et al. (2008), Rolland et al. (2010)
Amsterdam albatross *Diomedea amsterdamensis*	✓	✓		✓	✓		SST, IOD	Amsterdam Island	Rivalan et al. (2010), Barbraud et al. (2011)
Black-browed albatross *Thalassarche melanophrys*	✓	✓	✓		✓		SST, SOI	Kerguelen Islands, South Africa, South Georgia, South Australia	Pinaud & Weimerskirch (2002), Inchausti et al. (2003), Nevoux et al. (2007, 2010a,b), Rolland et al. (2008, 2009a), Barbraud et al. (2011)
Atlantic yellow-nosed albatross *Thalassarche chlororhynchos*	✓		✓		✓	✓	SOI	Tristan da Cunha, Gough	Cuthbert et al. (2003)
Indian yellow-nosed albatross *Thalassarche carteri*	✓				✓		SST, SOI	Amsterdam Island	Rolland et al. (2009b)
Sooty albatross *Phoebetria fusca*	✓				✓	✓	SST, SOI	Crozet Islands, Amsterdam Island	Inchausti et al. (2003), Delord et al. (2008), Rolland et al. (2010)
Light-mantled sooty albatross *Phoebetria palpebrata*					✓	✓	SST, SOI	Crozet Islands	Inchausti et al. (2003), Delord et al. (2008)
Southern giant petrel *Macronectes giganteus*						✓	SOI	Crozet Islands	Delord et al. (2008)
Northern giant petrel *Macronectes halli*						✓	SOI	Crozet Islands	Delord et al. (2008)
Antarctic fulmar *Fulmarus glacialoides*	✓	✓	✓	✓	✓		SIC, SST	Adélie Land	Jenouvrier et al. (2003)
Snow petrel *Pagodroma nivea*	✓	✓		✓	✓	✓	SIE, SIC, T	Adélie Land, Wilkes Land	Barbraud et al. (2000b), Barbraud & Weimerskirch (2001b), Jenouvrier et al. (2005), Olivier et al. (2005), Barbraud et al. (2011)
Blue petrel *Halobaena caerulea*	✓						SST, SSH, SOI	Kerguelen Islands	Guinet et al. (1998), Inchausti et al. (2003), Barbraud & Weimerskirch (2003), Barbraud & Weimerskirch (2005)
Thin-billed prion *Pachyptila belcheri*	✓				✓		SST, SIC	Kerguelen Islands, Falkland Islands	Nevoux & Barbraud (2005), Quillfeldt et al. (2007)
White-chinned petrel *Procellaria aequinoctialis*	✓		✓		✓		SST, SOI	Crozet Islands	Barbraud et al. (2008)
Grey petrel *Procellaria cinerea*	✓		✓		✓		SST, SOI	Kerguelen Islands	Barbraud et al. (unpubl. data)

Table A2. Studies that investigated the effects of fisheries activities (mainly fishing effort) on demographic parameters of Southern Ocean seabirds. ✓: demographic parameters investigated (Sa: adult survival; Sj: juvenile/immature survival; Re: recruitment; Bs: breeding success; N: number of breeding pairs)

Species	Sa	Sj	Re	Bs	N	Type of fishery	Region	Reference
Wandering albatross *Diomedea exulans*	✓	✓			✓	Longline	Southern Ocean, South Atlantic, South Indian	Weimerskirch et al. (1997), Tuck et al. (2001), Nel et al. (2003), Terauds et al. (2006), Delord et al. (2008), Rolland et al. (2010)
Amsterdam albatross *Diomedea amsterdamensis*	✓					Longline	South Indian	Rivalan et al. (2010)
Black-browed albatross *Thalassarche melanophrys*	✓			✓		Longline, trawl	South Pacific, Tasman Sea, Kerguelen Islands, South Atlantic	Terauds et al. (2005), Arnold et al. (2006), Sullivan et al. (2006), Rolland et al. (2008, 2009a)
White-capped albatross *Thalassarche steadi*	✓	✓				Longline	South Pacific, South Atlantic	Baker et al. (2007)
Shy albatross *Thalassarche cauta*	✓	✓				Longline	South Pacific, South Atlantic	Baker et al. (2007)
Grey-headed albatross *Thalassarche chrysostoma*	✓					Longline	South Pacific	Terauds et al. (2005)
Atlantic yellow-nosed albatross *Thalassarche chlororhynchos*	✓					Longline	South Atlantic	Cuthbert et al. (2003)
Indian yellow-nosed albatross *Thalassarche carteri*	✓					Longline	South Indian	Rolland et al. (2009b)
Sooty albatross *Phoebetria fusca*	✓				✓	Longline	South Indian	Delord et al. (2008), Rolland et al. (2010)
Light-mantled sooty albatross *Phoebetria palpebrata*					✓	Longline	South Indian	Delord et al. (2008)
Southern giant petrel *Macronectes giganteus*					✓	Longline	South Indian	Delord et al. (2008)
Northern giant petrel *Macronectes halli*					✓	Longline	South Indian	Delord et al. (2008)
White-chinned petrel *Procellaria aequinoctialis*	✓		✓	✓		Longline, trawl	South Indian	Barbraud et al. (2008)
Grey petrel *Procellaria cinerea*	✓		✓	✓		Longline, trawl	South Indian	Barbraud et al. (unpubl. data)
Flesh-footed shearwater *Puffinus carneipes*	✓					Longline	Australia	Baker & Wise (2005)
Cap gannet *Morus capensis*				✓		Trawl	South Atlantic	Grémillet et al. (2008)

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