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Responses of piscivorous seabirds at the Pribilof Islands to ocean climate

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ABSTRACT

Climate variability and change are expected to influence the seasonal cycle in North Pacific sub-arctic marine ecosystems. The hypothesis that timing of nesting and productivity of piscivorous seabirds [kittiwakes (*Rissa tridactyla* and *Rissa brevirostris*) and murre (*Uria aalge* and *Uria lomvia*)] at the Pribilof Islands are related to variation in ocean climate as indexed by changes in sea-ice concentrations (SICs) and sea-surface temperatures (SSTs) was tested. To test this hypothesis, timing and productivity of the seabirds were correlated with the winter sea-ice extent, defined as area-averaged SICs, and with winter, spring, and summer SST near the Pribilofs over a 32-yr period, 1975–2006. Timing and productivity for the two species of kittiwake were strongly correlated with each other and between the two breeding locations, St. George and St. Paul islands. Similar results were found for the two species of murre, although kittiwakes and murre were not strongly correlated with each other. Kittiwakes bred progressively earlier, advancing their hatching dates by 0.58 to 0.88 d/yr over the study period. In contrast, there were no overall trends for murre, with the exception of thick-billed murre at St. Paul that nested progressively later, delaying breeding by 0.47 d/yr. Because of these trends, residuals from quadratic regressions were used to “detrend” the data (including cases where no significant trend was observed) for interannual comparisons with climate variables. Detrended kittiwake timing was inversely correlated with maximum SIC and positively correlated with winter SST. We found no strong relationships between the timing of murre nesting and SIC or SST with either raw or detrended data. Both raw and detrended data revealed a positive relationship between kittiwake productivity and SIC, and an inverse relationship with winter and spring SST. Murre productivity was correlated negatively with summer SST, but unrelated to SST in other seasons and to SIC. Timing and productivity were correlated inversely for murre and kittiwakes at both sites, but were significant only for raw (i.e. non-detrended) murre data and for detrended kittiwake data. Detrending emphasizes high-frequency (interannual) variability by suppressing low-frequency (interdecadal) variability, indicating that low-frequency change in murre timing has an effect on productivity, whereas interannual variation is responsible for the timing–productivity relationship for kittiwakes. These contrasting responses of surface-foraging kittiwakes and deep-diving murre provide insight into how the eastern Bering Sea ecosystem is responding to climate variability and change, and suggest that the food web has changed more substantially in the upper water column than at depth.

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1. Introduction

Climate changes alter seasonal cycles and food webs in terrestrial and marine systems (IPCC, 2001; Ottersen et al., 2004). In turn, changes in the seasonal cycle may influence phenology for animals. Both terrestrial (Crick et al., 1997) and marine (Abraham and Sydeman, 2004; Fredericksen et al., 2004) birds can be influenced by temperature changes, though correla-

tions may be negative in some cases and positive in others (Barbraud and Weimerskirch, 2003). For terrestrial birds, changes in phenology have clearly shown demographic consequences; several authors have shown declines in productivity associated with earlier breeding, attributed to a “mismatch” between the timing of prey availability and offspring production (Both et al., 2006). In marine systems, fewer studies have been conducted, though similar mismatches have been suggested for marine birds off British Columbia, Canada (Bertram et al., 2001). Furthermore, Cushing (1990) and others (Beaugrand, 2004) have demonstrated the importance of phenological mismatches to recruitment probabilities in other top-level predators in the marine food web (predatory fish).

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Seabirds have high energy requirements and are therefore sensitive to changes in marine ecosystems that affect prey availability. Additionally, because they are central place foragers during the nesting season, as a group, seabirds have a strong dependence on local marine food webs. Therefore, seabirds can provide early signals for oscillations in the marine environment (Montevecchi, 1993) that are otherwise difficult or expensive to measure (e.g., bird diets at colonies are easier to measure than forage fish concentrations over a wide geographic area). Establishing fundamental patterns in reproductive timing and success in relation to environmental factors is a necessary first step in understanding how climate change alters seasonal cycles of predators and prey (Durant et al., 2004). Phenology of nesting indicates yearly variation in response to environmental conditions, and productivity is a metric that integrates conditions throughout the breeding season largely mediated through the marine food web.

Polar regions of the world are predicted to be affected by climate change sooner and to a greater extent than temperate or tropical regions (IPCC, 2001). In the northern hemisphere, major changes have been documented in sub-arctic systems, particularly in the past three decades, including increased interannual variation in the maximum extent and timing of melt in the spring of winter sea ice in the eastern Bering Sea (see Niebauer, 1998; Overland et al., 2002; Overland and Stabeno, 2004; Sasaki and Minobe, 2005). Atmospheric oscillations at multiple time scales from interannual to interdecadal also can affect ice melt and sea temperatures (Minobe, 1999, 2000). The timing and location of spring melt can have direct effects on marine food webs (Hunt et al., 2002). For example, in the northern Bering Sea, due to recent reductions in ice cover and earlier melt, there appears to be a fundamental change from a system dominated by benthic biomass to one dominated by pelagic organisms (Grebmeier et al., 2006). Ecosystem controls are not well understood, but Hunt et al. (2002) suggested that both nutrient-driven (bottom-up) and predation (top-down) controls may determine ecosystem form and function, and that control mechanisms may vary by climate regime. Thus, overall productivity over the eastern Bering Sea shelf (and elsewhere) is strongly influenced by ice extent and the timing of ice retreat (Hunt et al., 2002; Ottersen et al., 2004).

The influence of these physical and lower trophic-level biological changes on top predators is of particular interest, yet has been inadequately investigated. Conservation concerns for marine mammals, particularly Steller's sea lion (*Eumetopias jubatus*), and northern fur seal (*Callorhinus ursinus*) have led to new efforts to understand coupled climate–ecosystem fluctuations, and the effects of secular climate change, on populations of these depleted species (Trites et al., 2006). One of the longest-running research programs on a suite of top predators in the eastern Bering Sea is that of the US Fish and Wildlife Service—Alaska Maritime National Wildlife Refuge (AMNWR; Dragoo et al., 2006), with a focus on marine birds. The AMNWR seabird program covers several sites in the Bering Sea, including the Pribilof Islands. Built on the early work of others (Hunt et al., 1981; Johnson, 1985; Lloyd, 1985), this ongoing annual program in the Pribilof Islands now spans three decades, from 1975 to 2005. Information on timing of breeding and demographic attributes, such as annual productivity, has been obtained to promote understanding of seabird population dynamics. The primary species of fish-eating seabirds (piscivores) nesting on the islands are surface-foraging black-legged and red-legged kittiwakes (*Rissa tridactyla* and *Rissa brevirostris*, respectively) and deep-diving common and thick-billed murres (*Uria aalge* and *Uria lomvia*, respectively). Given the extensive and comprehensive nature of this dataset, it is also of considerable value for examining the effects of temporal environmental variation on seabird timing and

productivity on multiple time scales, from interannual to interdecadal.

Herein, we test the hypothesis that timing of breeding events and productivity of seabirds in the Pribilof Islands is related to variation in ocean climate, as indexed by changes in sea-ice concentrations (SICs) and sea-surface temperature (SST). Others (Lloyd, 1985; Decker et al., 1995; Hunt et al., 1996; Hunt and Byrd, 1999) have considered aspects of this research topic in the Pribilof Islands, although previous work was based on a more limited data set than ours. We are not aware of other studies evaluating relationships between timing of breeding and SST or specific relationships between SIC and seabird breeding biology in the Pribilof area.

Although physical variables such as currents and wind are theoretically of interest, SIC and SST were selected initially as a step in developing an understanding of ocean climate and seabird responses in the region because these variables are responsive to warming, a recent major research theme in the region (Anonymus, 2004; North Pacific Research Board, 2005).

This work is significant as seabirds have been proposed to be useful ecosystem indicators, primarily responding by changes in demographic parameters like breeding success to fluctuations in availability of prey (Cairns, 1987; Montevecchi, 1993; Furness and Camphuysen, 1997). The potential for this application in the eastern Bering Sea is dependent on establishing relationships between seabird breeding parameters and measurements of ocean climate or conditions that affect ecosystem function.

2. Study area

The Pribilof Archipelago, comprised of four islands (St. George, St. Paul, Otter, and Walrus) and several adjacent small islets (e.g., Sea Lion Rock), is located in the southeastern Bering Sea (~57°N, 169°W) near the edge of the continental shelf (Fig. 1). St. Paul is approximately 65 km farther north from the edge of the continental shelf than is St. George. The Pribilof Islands are situated in the Middle Shelf Domain, where water is approximately 100 m deep (Kinder and Schumacher, 1981). Dynamic physical oceanography in the region (Stabeno et al., 1999) contributes to an extremely productive ecosystem, referred to as the “Green Belt” (Springer et al., 1996). Along the shelf break, an along-shelf current that interacts with tides and the shelf break creates a frontal system, which facilitates the vertical flux of nutrients and consequent production (Stabeno et al., 2008; Sullivan et al., 2008; Mizobata et al., 2008).

SIC plays an important role in Pribilof area primary productivity, though the mechanism is not well known (see BEST, <http://www.arcus.org/bering/>). Prior to the regime shift in the eastern

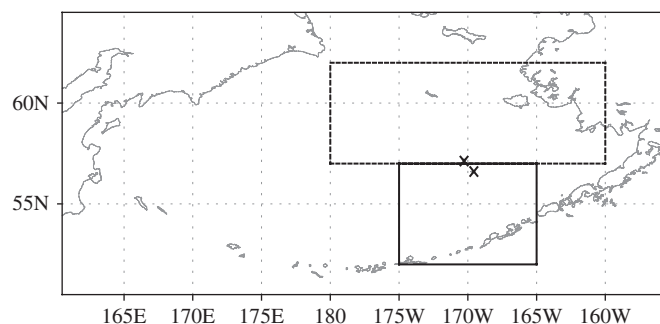


Fig. 1. Map of Bering Sea and areas where sea-surface temperature (solid rectangle, 175–165°W, 52–57°N) and sea-ice concentration (dashed rectangle, 180–160°W, 57–62°N) time series are calculated. Crosses indicate locations of St. George and St. Paul islands.

Bering Sea in the mid-1970s (Mantua and Hare, 2002), sea ice reached the Pribilofs in most winters (Stabeno et al., 1999); however, since about 1976, the annual maximum extent of the ice pack has varied considerably and has remained north of the Pribilofs more frequently (Niebauer, 1998; Overland and Stabeno, 2004). This change in the historical position of the Bering Sea ice pack at its southern terminus makes the Pribilof Islands particularly well situated for assessing ice-related, climatic effects on sub-arctic ecosystems.

The importance of the Pribilof Islands to piscivorous marine birds and marine mammals (e.g., northern fur seal) was documented historically (Elliot, 1875; Preble and McAtee, 1923; Kenyon and Phillips, 1965) and was quantified more thoroughly in the mid-1970s during the Outer Continental Shelf Environmental Assessment program for offshore oil leases (Hickey and Craighead, 1977; Hunt et al., 1981; Craighead and Oppenheim, 1985; Troy and Baker, 1985). Besides the large numbers of seabirds and marine mammals, the region has large populations of commercially valuable fish (National Research Council, 1996). Prevalent pelagic fish in the area (see Brodeur et al., 1999; Sinclair et al., 1999) that are important in the diets of piscivorous seabirds are juvenile walleye pollock (*Theragra chalcogramma*) and lantern fish (Myctophidae; Hunt et al., 1981, 1997). Sand lance (*Ammodytes hexapterus*), large zooplankton (euphausiids), and squid (e.g. *Gonatopsis*, *Berryteuthis*) also are important in some years (Hunt et al., 1981; Loughlin et al., 1999; Sinclair et al., 2008).

Black-legged and red-legged kittiwakes and common and thick-billed murres are the most abundant species of piscivorous seabirds in the Pribilof Islands, where they aggregate in one of the largest breeding concentrations in the North Pacific region, estimated at more than 2 million individuals (Hickey and Craighead, 1977). These islands are particularly important for red-legged kittiwakes (more than 80% of the world's population nests there; Byrd et al., 1997) and for murres (St. George is probably the largest colony in the Bering Sea; Sowls et al., 1978). Although native arctic foxes (*Alopex lagopus*) prey on a small percentage of nests that are accessible to them, typically significant seabird nest predators like large gulls (e.g., *Larus glaucescens*) and common raven (*Corvus corax*) are relatively scarce in the Pribilofs (Kenyon and Phillips, 1965); hence any loss of reproductive potential for kittiwakes and murres is largely prey related. The two islands are similar in total land area, but kittiwake and murre cliff nesting habitat on St. George is much more extensive (spanning nearly 50 km of coastline and elevations up to more than 300 m tall) than on St. Paul (11 km of coastline and up to 115 m high). Accordingly, St. George Island has approximately an order of magnitude more ledge-nesting seabirds than St. Paul Island (Hickey and Craighead, 1977).

3. Materials and methods

3.1. Data collection

Nesting phenology and productivity were estimated each year by recording the status (i.e. presence of nest structure, egg, or chick) of nests on systematically selected plots within the viewable population (see Hunt et al., 1981; Byrd, 1989). Data collection consisted of photographing or drawing each plot and numbering nest sites on the photograph so that individual sites could be followed throughout the nesting cycle. For kittiwakes, numbered sites were structures to which new plant material was added each year (our definition of an active nest), but for murres (which do not build nests), the appearance of an egg constituted an active site. Therefore, the proportion of nest sites where eggs were laid could not be estimated for murres as they were for

kittiwakes). Numbered sites typically were checked every 3–5 days throughout the incubation and chick-rearing periods to estimate hatch dates (i.e. mid-points between the date the egg was last seen and the date the chick was first observed) and loss of reproductive potential during the laying (for kittiwakes), egg, and chick stages of the nesting cycle.

Time series data SIC and SST were from the United Kingdom Meteorological Office (the Met Office Hadley Center SIC and SST dataset version1 HadISST1) [<http://www.metoffice.gov.uk/research/hadleycentre.html>] and were produced on a monthly 1° × 1° grid (Rayner et al., 2003). The effects of SIC during late winter/early spring were evaluated when sea ice was at its maximum coverage in the Eastern Bering Sea, and effects of SST were evaluated for three seasons: winter (DJF), spring (MAM), and summer (JJA). SIC is defined as percentage of grid area covered by sea ice. To determine the areas where SICs were likely to be influential to kittiwakes and murres, correlation maps were produced between seasonally averaged SIC anomalies and productivity averaged for all kittiwakes given the similar tendencies shared by kittiwakes; the correlation map analysis was repeated for murres. The same analysis was applied for SSTs as well. Generally, SICs north of the Pribilof Islands and SSTs south of the islands were related to the seabird parameters, and the areas shown in Fig. 1 were used to calculate area-averaged seasonal time series of SICs and SSTs.

3.2. Data analysis

Because of the presence of trends for some of the seabird datasets, residuals from quadratic regressions were used to “detrend” the data for interannual comparisons with climate variables. Detrending emphasizes high-frequency (interannual) variability by suppressing low-frequency (interdecadal) variability. Both detrended and non-detrended data were used to evaluate relationships among biological and climate variables.

Table 1

Spearman correlation matrix (rho values) for mean hatch dates of kittiwakes and murres at St. George and St. Paul islands, Pribilof Islands, Alaska, 1975–2005

	SGBL ^{a,b}	SPBL	SGRL	SPRL	SGCM	SPCM	SGTM
SPBL	0.84***						
SGRL	0.91***	0.90***					
SPRL	0.81***	0.83***	0.88***				
SGCM	0.28	0.34	0.13	0.07			
SPCM	0.05	0.36*	0.12	−0.00	0.80***		
SGTM	0.50**	0.65***	0.39*	−0.40*	−0.84***	−0.78***	
SPTM	−0.18	−0.26	−0.42*	−0.42*	−0.62***	−0.45**	−0.38*

^a Codes: SG = St. George, SP = St. Paul, BL = black-legged kittiwake, RL = red-legged kittiwake, CM = common murre, TM = thick-billed murre.

^b Levels of significance: * < 0.1, ** ≤ 0.05, *** ≤ 0.01.

Table 2

Spearman correlation matrix (rho values) for productivity of kittiwakes and murres at St. George and St. Paul islands, Pribilof Islands, Alaska, 1975–2005

	SGBL ^{a,b}	SPBL	SGRL	SPRL	SGCM	SPCM	SGTM
SPBL	0.89***						
SGRL	0.78***	0.58***					
SPRL	0.80***	0.67***	0.89***				
SGCM	0.01	0.20	0.13	0.12			
SPCM	0.17	0.37	0.03	0.05	0.70***		
SGTM	0.11	−0.03	0.21	0.14	0.68***	0.56**	
SPTM	0.22	0.30	0.04	0.10	0.70***	0.78***	0.40*

^a Codes: SG = St. George, SP = St. Paul, BL = black-legged kittiwake, RL = red-legged kittiwake, CM = common murre, TM = thick-billed murre.

^b Levels of significance: * ≤ 0.1, ** ≤ 0.05, *** < 0.01.

Annual mean hatch dates and productivity (i.e. proportion of nests fledging chicks based on nests for kittiwakes and eggs for murre; the latter do not construct nests) were estimated from samples of nests on cliff sections scattered throughout seabird nesting areas (Byrd, 1989). For each time series (e.g., hatch date for common murre at St. Paul) linear and polynomial (quadratic) regression analysis was used to investigate trends during the study period. Cross-correlation analysis (Spearman's rho) was used to test each parameter for relationships among species, islands, and climate variables.

4. Results

4.1. Co-variation amongst species and sites

There was significant co-variation in the timing of breeding for kittiwakes between islands and species (i.e. hatching dates were significantly correlated, all $r_s \geq 0.81$, all $p < 0.001$, Table 1). Similarly, there was significant co-variation for murre (Table 1), though the relationship for thick-billed murre at St. Paul was generally weaker (r_s as low as 0.38, $p < 0.100$, Table 1). Annual mean hatch dates varied more for kittiwakes (SD ranged 8–11 days among the four species–island cases) than for murre (SD ranged 4–7 days, calculated from Appendices A and B, respectively). Co-variation between murre and kittiwakes for hatch dates was generally weak (Table 1).

There was pronounced co-variation in kittiwake productivity between species and islands (all $r_s \geq 0.58$, $p < 0.001$, Table 2), and similar correlations were found for productivity between the

species of murre and between islands (all $p < 0.100$ level, Table 2; five of six species–island combinations, $r_s \geq 0.56$, $p < 0.050$). Annual mean productivity estimates were much more variable among years for kittiwakes (range of CVs: 67–83%) than for murre (range of CVs: 23–31%; calculated from Appendix C), and there was little evidence of co-variation between genera.

4.2. Temporal trends in phenology and productivity

Hatching dates for both species of kittiwakes at both islands became progressively earlier over the study period. We found significantly negative linear slopes (all $p < 0.010$), which varied from -0.57 to 0.88 d/yr (Figs. 2A–D) over the 30-yr period. Overall, Pribilof kittiwakes are now breeding about 20 days earlier

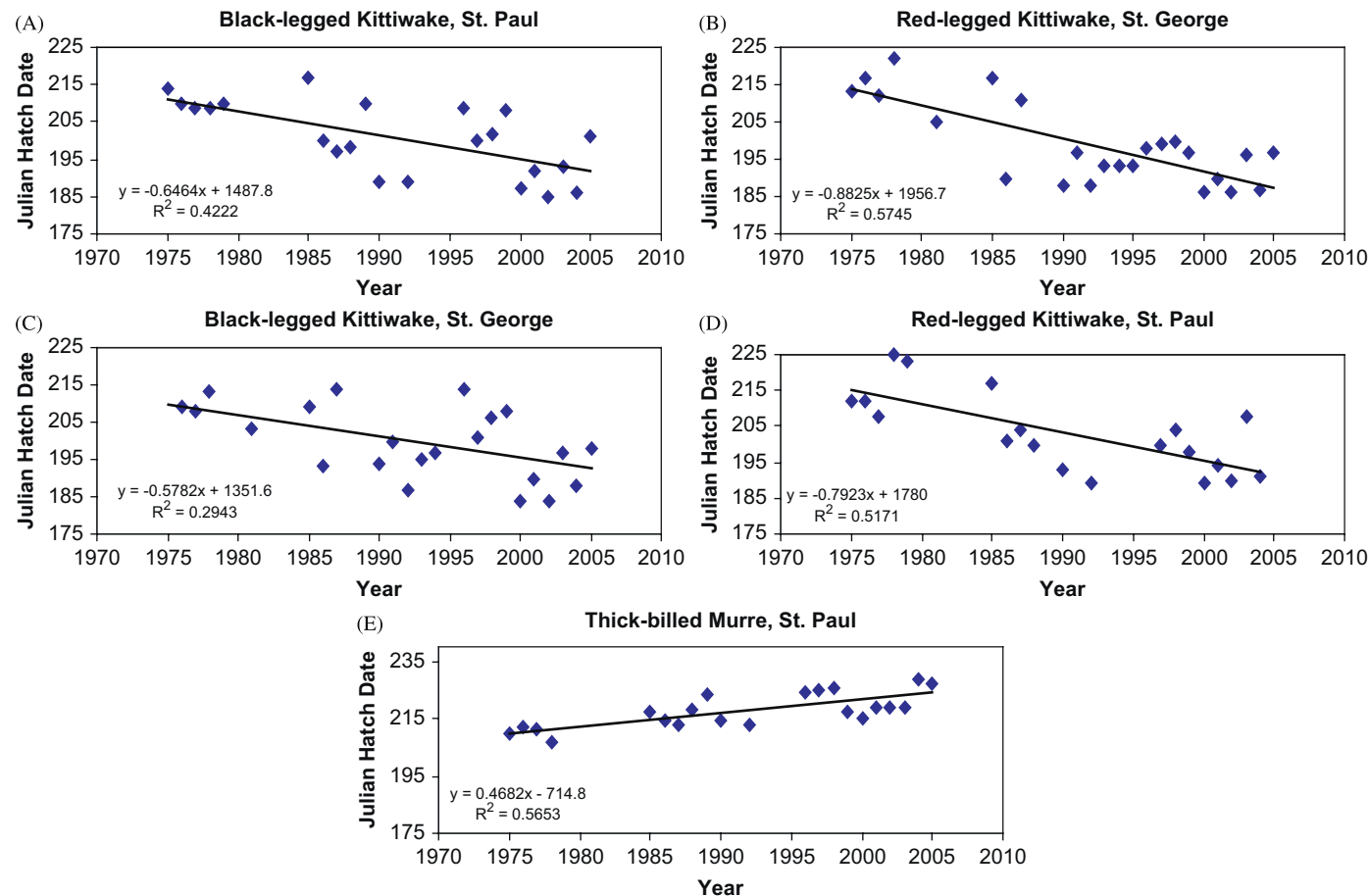


Fig. 2. Trends in kittiwake and murre hatch dates at the Pribilof Islands, 1975–2005.

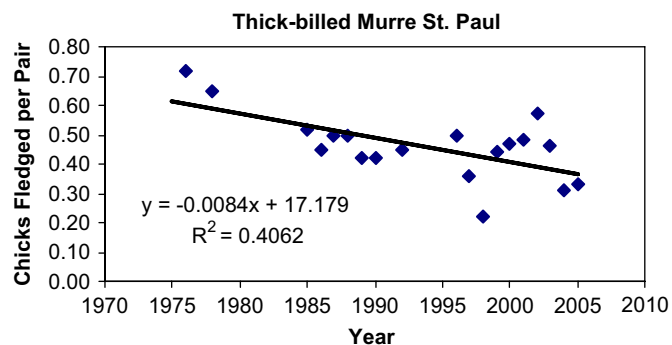


Fig. 3. Trends in thick-billed murre productivity at St. Paul Island, 1975–2005.

than they were in the mid-1970s. For murres, the only statistically significant trend in hatching dates was for thick-billed murres at St. Paul, which hatched progressively later ($p < 0.050$) through the period (Fig. 2E).

No trends in kittiwake productivity were found during the study period, although there were sustained periods with relatively low success (e.g., early to mid-1980s, Appendix C) and relatively high success within the time series. Productivity declined progressively over the study period for thick-billed murres at St. Paul (Fig. 3), but no significant trends were detected for thick-billed murres at St. George or for common murres on either island (Appendix C).

4.3. Relationships between phenology and productivity

Using both raw and detrended series, relationships between timing of nesting and productivity were negative (Fig. 4). For both murre species at St. Paul, relationships were stronger using the raw series, than after detrending. This indicates that the phenology–productivity relationship for thick-billed murres, at least, was due to the trends observed in both of these parameters

at this site. Significant relationships were found between the parameters for black- and red-legged kittiwakes at St. George using the detrended (isolating the interannual time scale) series, indicating that the phenology–productivity relationship was operating interannually. Overall, the body of evidence for all species and sites suggests that productivity is higher in years when timing of nesting is earlier.

4.4. Relationships with SIC

Detrended (i.e. interannual) kittiwake hatching dates were related negatively with SIC (Fig. 5, $r_s = -0.28$ to -0.57), indicating nesting occurred earlier in years with more extensive ice cover. There were no relationships between SIC and murre phenology using either raw or detrended data.

Kittiwake productivity was related positively to SIC for three of four species–island pairs ($r_s = 0.25$ to 0.50 , for detrended data). These relationships held whether examining raw or detrended time series, although detrended relationships were stronger (Fig. 5). In contrast, there were no statistically significant relationships between SIC and murre productivity.

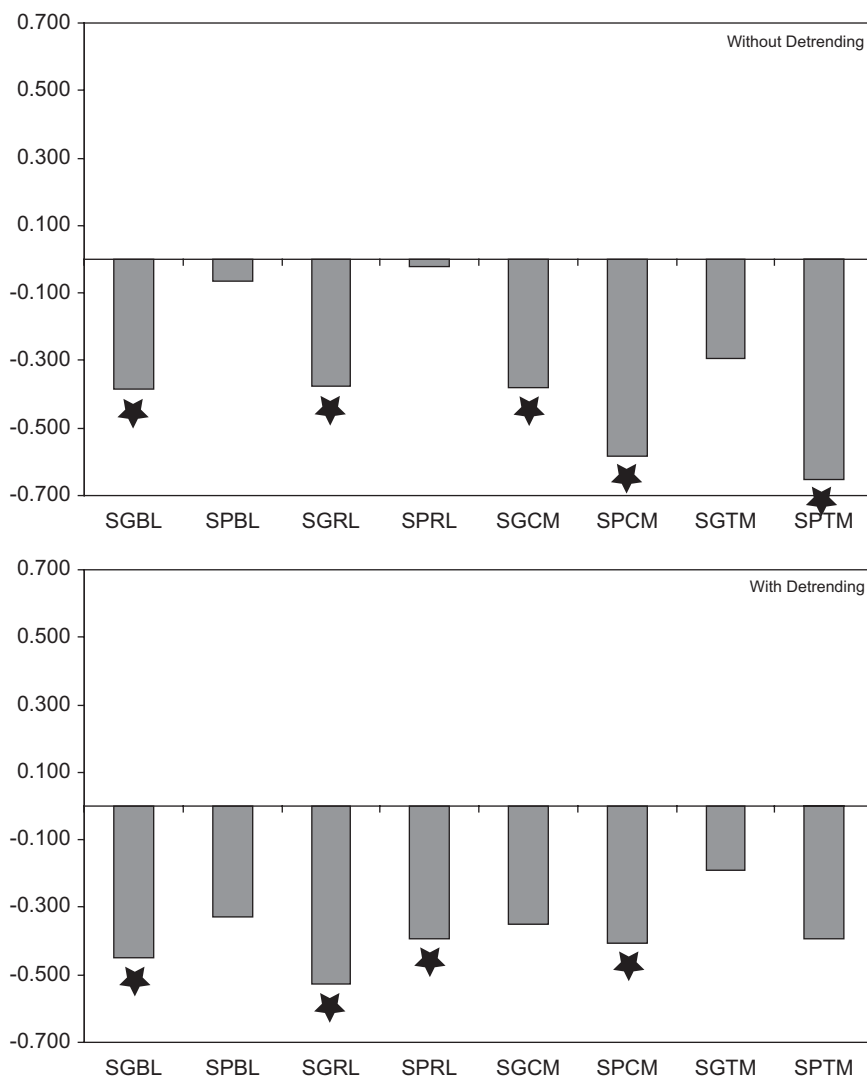


Fig. 4. Spearman's rank correlation between mean annual hatch dates and productivity for kittiwakes and murres in the Pribilof Islands, 1975–2005, without detrending (top) and with quadratic detrending (bottom). Stars above the bars indicate that the correlations are significant at the 90% confidence level. Abbreviations are the same as those used in Table 1. SG = St. George, SP = St. Paul, BL = black-legged kittiwake, RL = red-legged kittiwake, CM = common murre, TM = thick-billed murre.

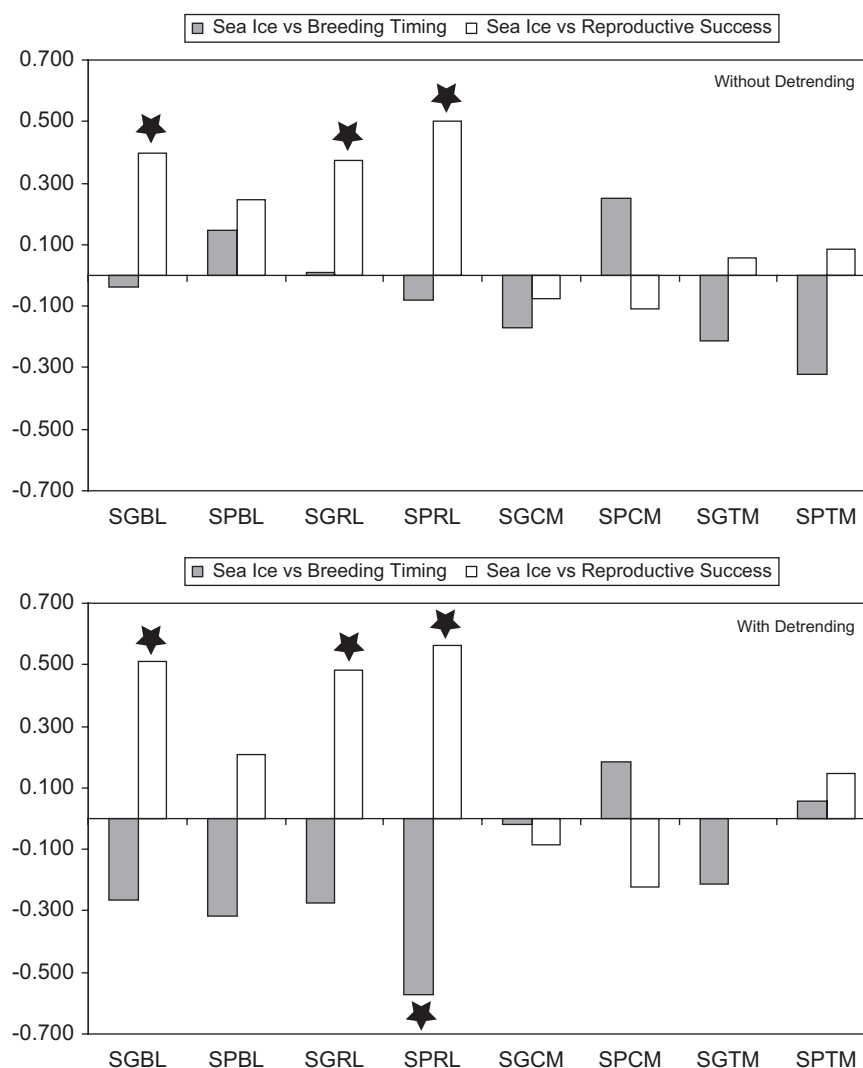


Fig. 5. Spearman's rank correlation between winter (December–February) sea-ice concentrations (SICs) and timing of nesting events or productivity of kittiwakes and murre in the Pribilof Islands, 1975–2005, without detrending (top) and with quadratic detrending (bottom). Stars above the bars indicate that the correlations are significant at the 90% confidence level. Abbreviations are the same as those used in Table 1. SG = St. George, SP = St. Paul, BL = black-legged kittiwake, RL = red-legged kittiwake, CM = common murre, TM = thick-billed murre.

4.5. Relationships with SST

4.5.1. Winter

Winter SST was positively correlated with kittiwake phenology and was strongest ($r_s = 0.38–0.59$, all $p < 0.100$) for the detrended kittiwake data (Fig. 6). For murre, although relationships all appeared positive (Fig. 6), the only significant correlation was for thick-billed murre (detrended) at St. George ($r_s = 0.42$, $p < 0.050$).

Evidence of only weak negative relationships was found between winter SST and both kittiwake and murre productivity (the strongest relationship being with the detrended red-legged kittiwake, St. Paul series, $r_s = -0.40$, $p < 0.050$, Fig. 6).

4.5.2. Spring

For kittiwakes, detrended data suggested relationships between timing of breeding and spring SST were all positive, but only two of the correlations were significant (both species on St. Paul Island; Fig. 7). No clear relationships were found between spring SST and murre timing (Fig. 7).

For kittiwake productivity, relationships with spring SST were negative (three of four species–island pairs having significant correlations with detrended data, $r_s = -0.34$ to -0.43 , all

$p < 0.100$), indicating that higher success was associated with cooler springs. These relationships are of similar strength as the relationships between winter SST and kittiwake productivity. For murre, although all the relationships between productivity and spring SST were negative (Fig. 7), the only significant correlation was for thick-billed murre at St. George ($r_s = -0.46$, $p < 0.050$ for raw data).

4.5.3. Summer

Once trends were removed, neither the timing of breeding for kittiwakes nor their productivity was related to summer SST (Fig. 8). For murre (Fig. 8), timing of breeding was not correlated with summer SST. In contrast, murre productivity was correlated negatively with summer SST ($r_s = -0.37$ to -0.60 , most species–island pairs with $p < 0.10$) whether the data were detrended or not (Fig. 8), indicating higher success when ocean temperatures were cooler.

5. Discussion

Herein, we established some relationships among piscivorous seabirds and ocean climate variables that have been elusive in the past at the Pribilof Islands (Decker et al., 1995; Hunt et al., 1996).

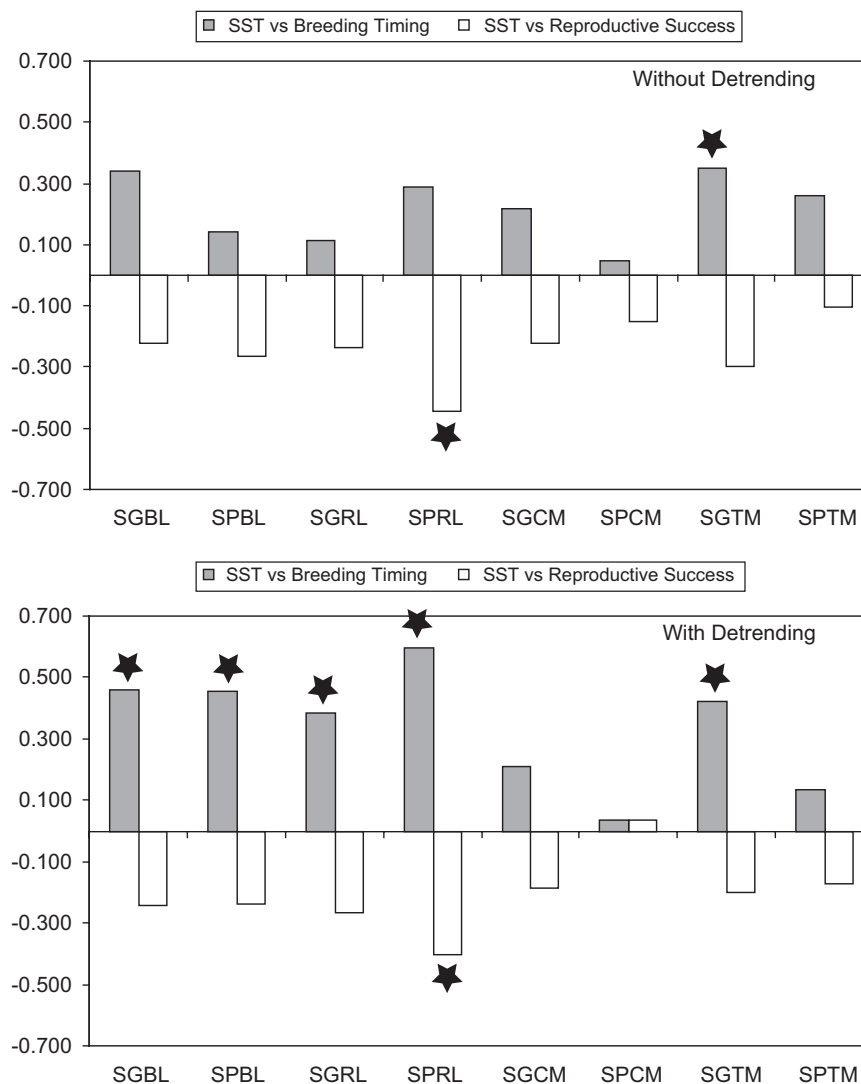


Fig. 6. Spearman's rank correlation between winter (December–February) sea-surface temperatures (SSTs) and hatch dates or productivity for kittiwakes and murre in the Pribilof Islands, 1975–2005, without detrending (top) and with quadratic detrending (bottom). Stars above the bars indicate that the correlations are significant at the 90% confidence level. Abbreviations are the same as those used in Table 1. SG = St. George, SP = St. Paul, BL = black-legged kittiwake, RL = red-legged kittiwake, CM = common murre, TM = thick-billed murre.

Specifically, we found relationships between climate variables (SIC and SST) and timing of reproduction (a key life history characteristic in the study of global change biology (Parmesan, 2006)). We also found a co-varying demographic rate (annual productivity) within seabird genera (*Rissa* spp. and *Uria* spp.) and between islands (St. Paul vs. St. George), which suggests that kittiwakes and murre were responding to environmental conditions operating at scales broader than individual islands, and perhaps reflecting ecosystem and food web changes across a broader region of the eastern Bering Sea. Additionally we found differing correlative relationships for murre and kittiwakes, which we discuss in further detail below. Our analyses differed from earlier studies by: (1) using detrending procedures to isolate interannual variability from lower-frequency variability, (2) investigating a sequence of seasonally based environment indices (winter SIC and winter, spring, and summer SST), and (3) augmenting previous time series with about 10 years of new information.

5.1. Ice effects

Winter SIC, and hence the potential effect of ice cover on marine ecosystem dynamics in the vicinity of the Pribilof Islands,

varies at interannual and decadal temporal scales. A combination of physical factors, including currents, water-mass intrusions, air temperature, and the direction and amplitude of winds, determines ice characteristics in the region (Niebauer, 1998; Wyllie-Echeverria and Wooster, 1998; Minobe 1999, 2000, 2002; Napp et al., 2000; Stabeno et al., 2001; Luchin et al., 2002; Hunt and Megrey, 2005; Sasaki and Minobe, 2005). The relationships among ice extent, the timing of ice retreat, and marine food web dynamics in the EBS are poorly known and a subject of debate, but are certainly likely to have profound effects on both pelagic and benthic food webs (Hunt et al., 2002; Grebmeier et al., 2006).

Sea ice extended as far south as the Pribilofs in >70% of winters from 1972 to 1997 (Overland and Stabeno, 2004); it has been highly variable but generally less frequently prevalent near the Pribilofs since (Zhang and Rothrock, 2003). We found that both red-legged and black-legged kittiwakes nested earlier (inverse correlation) and with higher breeding success (positive correlation) when SIC was greater in the EBS. Elsewhere in the world, ice has been shown to be a key determinant of marine ecosystem and seabird productivity (Croxall et al., 2002; Gaston et al., 2005). For Pribilof kittiwakes, the relationships between annual productivity and SIC were similar when examining either

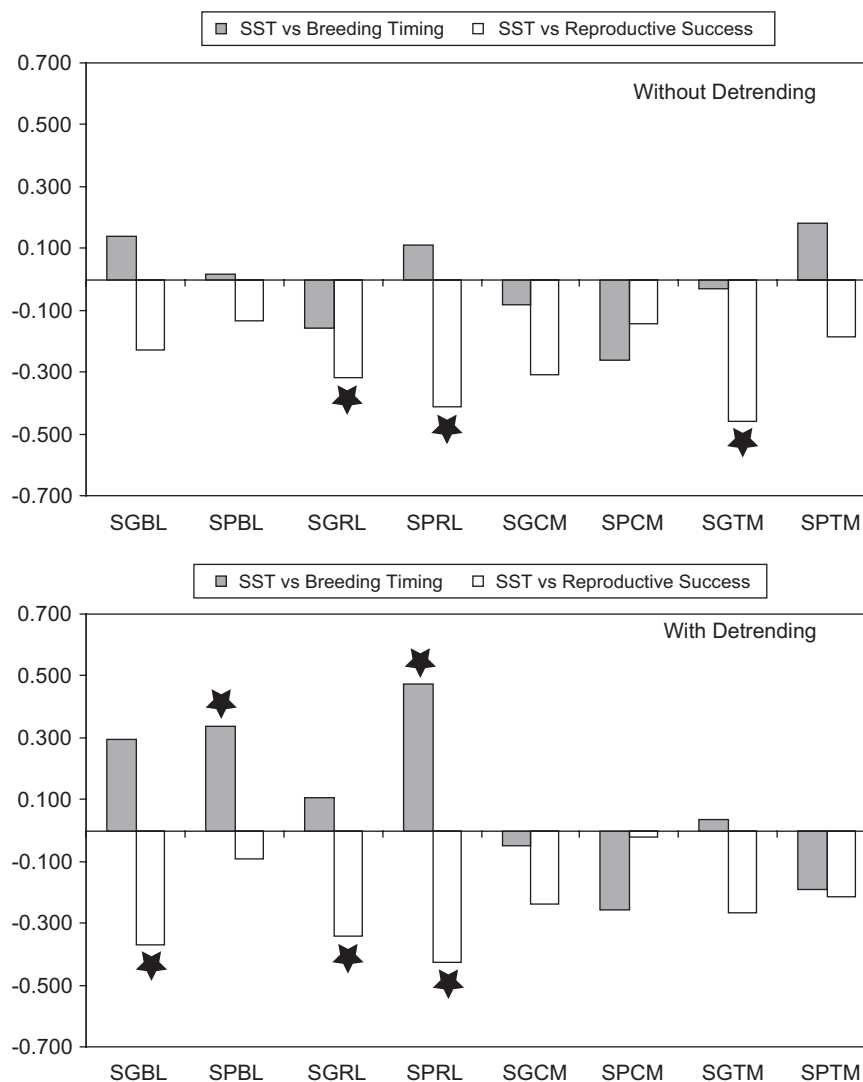


Fig. 7. Spearman's rank correlation between spring (March–May) sea-surface temperature (SST) and hatch dates or productivity for kittiwakes and murre in the Pribilof Islands, 1975–2005, without detrending (top) and with quadratic detrending (bottom). Stars above the bars indicate that the correlations are significant at the 90% confidence level. Abbreviations are the same as those used in Table 1. SG = St. George, SP = St. Paul, BL = black-legged kittiwake, RL = red-legged kittiwake, CM = common murre, TM = thick-billed murre.

raw or detrended time series, indicating that both interannual and lower-frequency temporal environmental variability in ice cover was important to these species. This is intuitive as there were no significant trends in kittiwake productivity, yet there were obvious multi-year periods of either high or low kittiwake productivity (Appendix C).

The effect of SIC on kittiwakes was likely mediated through prey availability, although we have a poor understanding of this mechanism. The implication is that kittiwake prey (e.g., age 0 and age 1 walleye pollock, myctophids, and euphausiids; Sinclair et al., 2008) were also positively related to ice cover, but we do not know if increasing SIC results in greater abundance and/or greater availability of prey. It seems reasonable to assume that ice somehow relates to prey availability in the upper water column since kittiwakes forage near the ocean's surface. In contrast, we found no relationships between SIC and murre (*Uria* spp.) timing of breeding or productivity. This result differed from the findings of Gaston et al. (2005), who documented ice effects on timing of nesting and reproductive success for thick-billed murre in the eastern Canadian arctic.

One explanation for the contrasting responses of murre and kittiwakes at the Pribilofs to ice is that murre initiate nesting up to 4 weeks later than do kittiwakes (derived from Appendices A and B; usually in early July when sea ice has receded far north of the Pribilofs). Another possibility is that SIC has less effect on the deeper water column and benthic food webs that murre depend upon. However, a current leading hypothesis about food web dynamics in the region supports the notion that ice affects both pelagic and benthic food webs (Hunt et al., 2002). When ice retreats later each year, the ice edge bloom purportedly sinks to the bottom, promoting benthic food webs, whereas when ice retreats earlier within each season, the pelagic food web is stimulated by a match between the timing of pelagic phytoplankton abundance and zooplankton reproduction. On the surface, neither the lack of relationships between murre and SIC, nor the positive relationship between SIC and kittiwake productivity apparently supports this hypothesis, though there is certainly more to be explored (e.g., other ice characteristics that may determine pelagic vs. benthic food web dynamics).

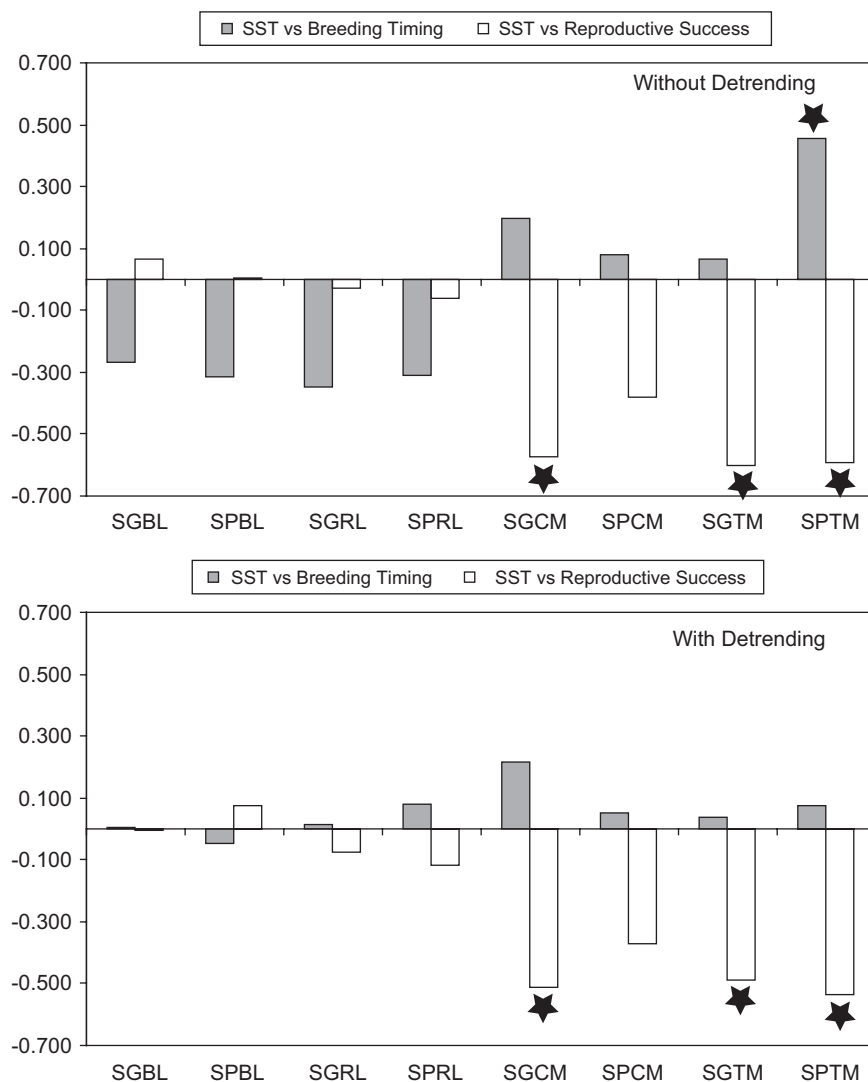


Fig. 8. Spearman's rank correlation between summer (June–August) sea-surface temperature (SST) and hatch dates or productivity for kittiwakes and murres in the Pribilof Islands, 1975–2005, without detrending (top) and with quadratic detrending (bottom). Stars above the bars indicate that the correlations are significant at the 90% confidence level. Abbreviations are the same as those used in Table 1. SG = St. George, SP = St. Paul, BL = black-legged kittiwake, RL = red-legged kittiwake, CM = common murre, TM = thick-billed murre.

5.2. SST and timing

Because kittiwakes are restricted to surface foraging, they are likely to be more sensitive than murres to variations in sea temperatures (and ice) that affect the vertical distribution of prey (Fredericksen et al., 2004). Kittiwakes (Fredericksen et al., 2004), and to a lesser extent, murres (Gaston et al., 2005), and other seabirds (Abraham and Sydeman, 2004) vary timing of breeding in relation to environmental conditions. As noted above for ice effects, this difference between genera might be related to variation in timing of laying.

5.3. SST and productivity

The seasonal variation we observed in the relationships between seabird productivity and SST (i.e. inverse correlations between kittiwake productivity and SST in winter and spring, inverse correlation between murre productivity and summer SST) could have been related to the differences in timing of nesting for kittiwakes and murres. Alternatively, our metric for productivity included different components for the two genera (i.e. fledglings per nest for kittiwakes compared to fledglings per egg for murres, which do not build nests), potentially reducing our ability to

detect effects on murres prior to laying. Differences in prey (Hunt et al., 1981) or foraging strategies (Takahashi et al., 2008) also may explain why the significant relationships observed between productivity and SST were with winter and spring SST for kittiwakes and with summer SST for murres.

5.4. Implications for climate change

For both species of kittiwakes nesting in the Pribilofs, it appears that productivity is higher when nesting begins earlier, when ice is abundant near the islands/foraging grounds, and when SST is relatively cool in winter and spring. For murres, productivity is higher when summers are cooler.

Consistent with our results, Lloyd (1985) found a positive relationship between relatively cool conditions and higher seabird productivity in the southeastern Bering Sea. More recent studies in the Antarctic and in the California Current have found similar relationships (Loeb et al., 1997; Croxall et al., 2002; Abraham and Sydeman, 2004).

The relationships between environmental variables and seabird responses are more complex than the simple relationships we detected. Illustrating this is the linear advance in breeding dates

for kittiwakes in the Pribilofs over the study period, indicating a response to more than just SIC and SST (because neither of those variables has changed in linear fashion over the period). Nevertheless, climate fluctuations very likely influence the marine ecosystem in ways that affect the timing–productivity relationship for kittiwakes and the productivity of murre in the Pribilof Islands. Many studies have pointed out that the response of seabirds to fluctuations in climate is usually mediated through the marine food web, i.e. prey availability (Murphy et al., 1991; Durant et al., 2003; Gjerdrum et al., 2003; Gaston et al., 2005), and we interpret our results from the Pribilofs similarly.

Our results from the Pribilof Islands appear contrary to what would be predicted for the EBS ecosystem if most of the phytoplankton produced at the ice edge in springs, when the ice is relatively far south (i.e. near the Pribilofs), falls to the bottom, thereby nourishing the benthic food web (Hunt et al., 2002; Grebmeier et al., 2006). Such conditions would presumably create unfavorable conditions in early spring for mid-water zooplankton predators such as forage fish, which in turn should negatively influence seabirds. Therefore, we question whether that part of the hypothesis is correct. Although there are indications that the system “resets” each year (Hunt et al., 2002), it is possible that the effects of primary production on the forage fish food web could be set by conditions during the previous year. For instance, Lewis et al. (2001) found that in the North Sea, kittiwakes preyed on age 0 sand lance early in the breeding season, but switched to age 1 sand lance later; in this case, production in two different years (years x and year $x-1$) were important to the bird’s productivity. To make this assessment for Pribilof seabirds, more information is needed on the age classes of forage fish consumed (see Sinclair et al., 2008 for historic data).

If the effects of climate change are mediated through the food web by a loss of ice-related productivity (bottom up), the impacts may be relatively subtle because ice is not the only productivity-enhancing feature in the vicinity of the Pribilofs. For example, the shelf break south of St. George Island is part of the highly productive “green belt” (Springer et al., 1996). High productivity is also associated with nearby canyons (Brodeur, 2001) and structural fronts (Coachman, 1986), which concentrate prey for seabirds (Decker and Hunt, 1996; Kokubun et al., 2008). Conversely, if the effect of climate change results in a reduction in the influence of sea ice on sea temperatures, particularly the “cold pool” in the Bering Sea, the result might be increased competition for prey with predatory fish like pollock as the system is dominated by top-down control of the food web (Wyllie-Echeverria and Wooster, 1998; Napp et al., 2000; Hunt et al., 2002). In either case, based on the relationships detected, any sustained increase in temperatures will most likely result in reduced productivity for seabirds in the Pribilof Islands.

Although responses of marine organisms to fluctuations in climate are well documented, piscivorous seabirds may respond differently in different marine ecosystems. For example, in contrast to the Pribilofs, kittiwakes at Bluff in the northern Bering Sea experienced delayed nesting and lower productivity in relatively cold springs (they also failed in an exceptionally warm year, Murphy et al., 1991). Additionally, in the Okhotsk Sea (northwestern Pacific) Kitaysky and Golubova (2000) found that puffins (*Fraterecula* spp.) had lower productivity in cold years. In contrast, at colonies in the California Current ecosystem, seabirds tend to have higher success in colder years (Bertram et al., 2001; Lee et al., 2007).

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Appendix A

Mean annual hatch dates for kittiwakes in the Pribilof Islands, Alaska, 1975–2005

Year	Black-legged kittiwake						Red-legged kittiwake					
	St. Paul Island			St. George Island			St. Paul Island			St. George Island		
	Mean	n	SD	Mean	n	SD	Mean	n	SD	Mean	n	SD
1975	2 Aug	33	4.7				31 July	3	0	1 Aug	19	7
1976	29 July	23	2.8	28 Jul	17	6.1	31 July	41	4.7	5 Aug	35	6.3
1977	28 July	60	4.9	27 July	63	4.6	27 July	10	6.7	31 July	93	8.3
1978	28 July	39	5	1 Aug	32	5	13 Aug	7	11.9	10 Aug	25	10.1
1979	29 July	19	4.3				11 Aug	12	3.8			
1981				22 July	43	4				24 July	14	6.8
1985	5 Aug	62	5.5	28 July	41	3.7	5 Aug	6	5.1	5 Aug	15	7.8
1986	19 July	229	6.1	12 Jul	81	4.9	20 July	19	10.1	9 July	81	6
1987	16 July	148	6.5	1 Aug ^a	24	8.2	23 July	2	2.1	30 July	44	13.6
1988	17 July	113	6.3				19 July	17	11			
1989	29 July	30	6.1	30 July ^a	10	5.2				22 July ^a	25	8.5
1990	8 July	189	5.6	13 July	43	6.7	12 July	11	5.3	7 July	119	7.9
1991				19 July	47	3.2				16 July	149	6.8
1992	8 July	333	6.1	6 July	57	5.9	8 July	21	4.4	7 July	113	7.5
1993				14 July	33	6.2				12 July	140	5.8
1994				16 July	16	7.6				12 July	90	6.2
1995				18 July ^a	10	8.4				12 July	30	11.4
1996	28 July	37	4.8	2 Aug	20	7.5	25 July	2	12.7	16 July	35	8.7
1997	19 July	133	4.8	20 July	38	4.1	19 July	11	4.9	18 July	74	7.1
1998	21 July	199	4.8	25 July	42	5.2	23 July	22	6.3	19 July	103	7.7
1999	27 July	31	6.4	27 July	6	5.7	17 July	18	5.3	16 July	75	5.2
2000	6 July	236	NR ^b	3 July	77	6.7	8 July	23	4.8	5 July	151	6.6
2001	11 July	86	5.5	9 July	15	4.6	13 July	13	7.4	9 July	107	5.1
2002	4 July	210	5.4	3 July	71	5.4	9 July	16	6.6	5 July	115	7.1
2003	12 July	201	5.7	16 July	48	4.5	27 July	5	7.2	15 July	76	7.9
2004	5 July	273	5.6	7 July	41	8.2	10 July	20	6.7	6 July	86	7.7
2005	20 July	52	8.5	17 July	11	12.0	10 July	5	3.3	16 July	31	11

^a Two or less eggs hatched; hence dates estimated from laying dates and average incubation period (27 days for black-legged kittiwake and 30 days for red-legged kittiwake). Data not used in calculations in results.

^b Not reported.

Appendix B

Mean annual hatch dates for murre in the Pribilof Islands, Alaska, 1975–2005

Year	Common murre						Thick-billed murre					
	St. Paul Island			St. George Island			St. Paul Island			St. George Island		
	Mean	n	SD	Mean	n	SD	Mean	n	SD	Mean	n	SD
1975	17 Aug	3	1.2				29 July	23	6.6			
1976	2 Aug	3	6.9	3 Aug	9	3.7	31 July	83	6.4	3 Aug	26	9.1
1977	14 Aug	14	6.0	4 Aug	10	7.0	30 July	34	5.7	5 Aug	43	8.3

1978	25 July	7	4.7	2 Aug	13	9.9	26 July	50	4.8	29 July	36	5.0
1981				30 July	19	6.5				26 July	44	6.3
1985	2 Aug	5	5.4	2 Aug	5	9.8	5 Aug	16	4	3 Aug	86	5.7
1986	2 Aug	33	6.5	3 Aug	8	4.5	2 Aug	72	7.1	1 Aug	160	5.4
1987	28 July	39	5.3	2 Aug	5	5.4	1 Aug	260	5.7	1 Aug	241	6.7
1988	31 July	116	7.2				6 Aug	45	6.6			
1989	9 Aug	165	7.2	10 Aug	35	9.8	11 Aug	205	4.5	5 Aug	203	8.5
1990	29 July	NR ^a	NR				2 Aug	NR	NR	27 July	170	5.5
1991										28 July	194	7.5
1992	29 July	74	5.8	30 July	55	6.8	1 Aug	220	6	26 July	219	6.5
1993				29 July	79	6.2				26 July	241	6.3
1994				8 Aug	53	7.3				2 Aug	205	6.0
1995				4 Aug	54	4.7				29 July	145	5.5
1996	10 Aug	55	6.1	6 Aug	36	5.5	12 Aug	204	6.2	4 Aug	134	5
1997	10 Aug	30	5.7	9 Aug	15	5.4	13 Aug	133	5.7	2 Aug	138	8
1998	15 Aug	10	7.5	17 Aug	14	4.9	14 Aug	66	6.4	9 Aug	92	5.7
1999	8 Aug	97	6.0	6 Aug	31	5.8	5 Aug	241	6.6	1 Aug	162	6.3
2000	1 Aug	107	5.4	1 Aug	40	6.2	3 Aug	321	3.4	29 July	168	7.3
2001	1 Aug	103	4.7	3 Aug	75	5.9	7 Aug	52	6.8	30 July	218	6.4
2002	6 Aug	82	4.9	1 Aug	30	5.8	7 Aug	153	5.2	27 July	151	5.5
2003	29 July	51	7.7	1 Aug	24	4.3	7 Aug	145	6.9	28 July	99	6.0
2004	10 Aug	40	11.1	10 Aug	41	8.4	17 Aug	192	7.1	3 Aug	82	8.6
2005	18 Aug	34	4.9	9 Aug	25	10.3	15 Aug	106	6.1	4 Aug	207	10.1

^a Not reported.

Appendix C

Summary of productivity data for kittiwakes (proportion of nests fledging chicks) and murres (chicks fledged/egg laid) in the Pribilof Islands, Alaska, 1975–2005

Year	Black-legged kittiwake		Red-legged kittiwake		Common murre		Thick-billed murre	
	St. George	St. Paul	St. George	St. Paul	St. George	St. Paul	St. George	St. Paul
1975		0.44		0.34				
1976	0.62	0.52	0.38	0.63		0.56		0.72
1977	0.45	0.43	0.54	0.54			0.43	0.49
1978	0.22	0.36	0.13	0.10	0.70	0.61	0.51	0.65
1979	0.40	0.54	0.18	0.34				
1980	0.38		0.27					
1981	0.07		0.11		0.30		0.15	
1982	0.01		0.01					
1983	0.01		0.01					
1984	0.14	0.06	0.13	0.10				
1985	0.12	0.27	0.07	0.19	0.76	0.69	0.72	0.52
1986	0.27	0.31	0.29	0.25	0.58	0.45	0.38	0.45
1987	0.00	0.24	0.13	0.00	0.75	0.61	0.67	0.50
1988	0.40	0.53	0.54	0.42	0.71	0.67	0.65	0.50
1989	0.00	0.04	0.00	0.00	0.37	0.50	0.52	0.42
1990	0.31	0.35	0.26	0.22		0.49	0.62	0.42
1991	0.46		0.43				0.61	
1992	0.35	0.25	0.47	0.27	0.47	0.55	0.58	0.45
1993	0.19	0.23	0.46	0.35	0.61		0.66	
1994	0.04	0.03	0.24	0.21	0.51		0.52	
1995	0.00	0.00	0.08	0.05	0.59		0.52	
1996	0.12	0.09	0.12	0.00	0.49	0.48	0.48	0.50
1997	0.27	0.29	0.26	0.24	0.33	0.40	0.47	0.36
1998	0.47	0.44	0.50	0.49	0.21	0.15	0.49	0.22
1999	0.01	0.04	0.28	0.26	0.53	0.46	0.61	0.44
2000	0.57	0.62	0.52	0.49	0.65	0.52	0.61	0.47
2001	0.06	0.18	0.22	0.13	0.54	0.64	0.53	0.48
2002	0.65	0.66	0.44	0.39	0.55	0.70	0.53	0.57
2003	0.32	0.48	0.23	0.08	0.37	0.56	0.43	0.46
2004	0.19	0.43	0.25	0.25	0.58	0.51	0.46	0.31
2005	0.04	0.04	0.02	0.00	0.23	0.30	0.31	0.33
Mean	0.24	0.30	0.25	0.24	0.52	0.52	0.52	0.46
SD	0.20	0.20	0.17	0.18	0.16	0.14	0.13	0.11
n	30	26	30	26	21	19	24	20

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