BREEDING CHRONOLOGY AND PRODUCTIVITY OF BLACK-LEGGED KITTIWAKES *RISSA TRIDACYTLA* AT BLUFF, ALASKA, 1975–2008: ASSOCIATIONS WITH REGIONAL ENVIRONMENTAL INDICES AND DISTANT COLONIES

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SUMMARY

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Breeding chronology and productivity of Black-legged Kittiwakes *Rissa tridactyla* at Bluff, Alaska, were documented nearly annually during 1975–2008. Nest numbers and productivity were highest, and hatching was earliest, when spring conditions were warmest. Comparing Bluff with five other colonies in the Bering and Chukchi Seas with long-term data sets, breeding began relatively early along the Alaskan coast compared with the Pribilof Islands (St. Paul and St. George), and progressively much earlier relative to sea ice retreat at more northern coastal colonies. Average annual productivity was significantly higher at Bluff and Cape Lisburne than at Cape Peirce, owing perhaps to higher intraspecific competition for food or higher predation on eggs and chicks at Cape Peirce. Breeding chronology was positively correlated at Bluff and Cape Peirce, and productivity was positively correlated between Bluff and both capes Peirce and Lisburne; these colonies are in the flow field of Alaskan Coastal Water. Both breeding chronology and productivity on St. Paul Island in the Middle Shelf Domain were strongly and independently correlated with timing and productivity not only at nearby St. George Island but also at Bluff, possibly reflecting stronger couplings to continental-shelf food webs on St. Paul than St. George. Both breeding chronology and productivity were significantly correlated between Cape Peirce and both St. Paul and St. George islands, suggesting commonalities across water masses that have very different patterns and processes of seasonal food web development. Productivity on St. George Island was highest in years when winter sea ice concentration was highest, in apparent contrast to Bluff; however, productivity at both St. George and Bluff was higher in years of earlier ice retreat. Positive correlations in both timing and productivity among colonies in disparate oceanic regimes could be due to similarities in pre-breeding condition of adults if they winter or stage in early spring in the same or similar areas.

Key words: Alaska regional perspective, Bering Sea, breeding chronology, breeding productivity, Chukchi Sea, food web, kittiwake, *Rissa tridactyla*

INTRODUCTION

The Black-legged Kittiwake *Rissa tridactyla* (BLKI) is one of the most abundant and widely distributed seabirds in Alaska (e.g. Hatch *et al.* 1993). Accordingly, its breeding performance has been studied annually or periodically at numerous Alaskan colonies. Studies at Bluff in the northeastern Bering Sea (Fig. 1) began in 1975 and continued annually through 2008, except in 1992–1994. Summarizing results through 1989, Murphy *et al.* (1991) reported high annual variation in breeding chronology, numbers of nests and productivity that correlated with sea ice concentration (SIC) in mid-May and spring air temperatures: breeding was earliest and nest numbers and productivity were highest when spring conditions were warmest. Here, we update and re-evaluate these relationships using data collected through 2008, the last year of fieldwork at Bluff.

The first comprehensive breeding study of Alaskan BLKIs was conducted at Cape Thompson on the eastern Chukchi Sea coast during 1959–1961 (Swartz 1966; Fig. 1); additional BLKI studies were conducted there during 1976–1995 (e.g. Roseneau *et al.* 2000). In 1976, BLKI studies were initiated at both Cape Lisburne (e.g. Roseneau *et al.* 2000), also on the eastern Chukchi Sea coast, and Cape Peirce (e.g. Haggblom & Mendenhall 1993), on the southeastern Bering Sea coast (Fig. 1). Bluff and these colonies are in the northward flow of Alaskan Coastal Water, a relatively warm, low-salinity water mass that originates in the Gulf of Alaska and is fed by major rivers entering from western Alaska (Coachman *et al.* 1975, Coachman 1986).

BLKI studies were initiated on St. Paul Island in 1975 and St. George Island in 1976, in the Pribilof Island group, southeastern Bering Sea (e.g. Byrd *et al.* 2008; Fig. 1). These offshore islands are on the continental shelf, about 100 km and 45 km from the shelf break (200 m isobath), respectively. Additionally, they are near the outer edge (100 m isobath) of the Middle Shelf Domain, between the 50 m and 100 m isobaths (e.g. Kinder & Schumacher 1981a, Hunt *et al.* 2008). Byrd *et al.* (2008) reported that BLKIs on St. Paul nested earlier when winter and spring sea-surface temperatures (SSTs) were colder; on St. George BLKIs nested earlier when winter SSTs were colder, and their productivity was higher when winter SICs were higher and spring SSTs were colder. These patterns contrast with the relationships at Bluff, where breeding was earlier and productivity was higher in warmer years (Murphy *et al.* 1991).

We compare our findings at Bluff with those obtained at other BLKI colonies, noted above, studied extensively during the same timeframe (1975–2008). We expected to find positive correlations in timing of breeding and productivity of BLKIs between Bluff and the other coastal colonies associated with Alaskan Coastal Water. In contrast, we expected to find either no correlations or negative correlations between Bluff and the Pribilof Island colonies because breeding chronology was earliest and productivity was highest at Bluff following warm springs and low SIC in mid-May (Murphy *et al.* 1991), and because Byrd *et al.* (2008) reported weak or opposite relationships on the Pribilof Islands.

STUDY AREAS AND METHODS

Bluff

Bluff (64°34′N, 163°45′W to 163°40′W) is a mainland BLKI colony on the north shore of Norton Sound (Fig. 1) with up to about 12 500 pairs in recent decades (highest boat-based count of adults on the cliffs was 12,459 in 1987). Fieldwork was carried out in 1975–1991 and 1995–2008. In 1975–1978, fieldwork spanned the entire breeding season from pre-nesting into the fledging period. Studies in each season from 1975 to 1978 have been summarized by Drury (1976), Steele & Drury (1977), Biderman *et al.* (1978), and Ramsdell & Drury (1979), respectively. In 1987–1991 and 1998, fieldwork started at the pre-nesting stage and ended as fledging was beginning. In all other years, fieldwork started after most eggs had been laid and ended before any chicks had fledged. Field methods were described in detail by Murphy *et al.* (1991). Nests were defined as "substantial mud platforms with evidence of activity in the current season" (Ramsdell & Drury 1979); thus, our counts include partial and incomplete nests, as well as completed nests with well-formed cups. Field crews mapped and counted nests on "reproductive plots" and observed those plots every few days to determine contents (eggs, chicks) of nests. We also recorded instances when no adult was attending the nest. In most years field crews monitored five reproductive plots (8, 10, 13, 14 and 17); in 1986 and 1995 no observations were conducted on reproductive plot 17. Chick ages were estimated using criteria developed by Ramsdell & Drury (1979:651). In 1978–1981, 1983, 1987, 1988 and 1990, we also used a small boat to access three other nesting areas where we recorded numbers of eggs and chicks in all visible nests and weighed chicks in all accessible nests.

We computed the growth rate of each chick that had been weighed two or more times between 50 g and 350 g (the linear growth phase) as the slope of the linear regression equation of weight on date for that chick and used median values for each colony-year sample in our analyses. We also used a regression equation from hatching to 350 g to estimate the date that the chick would have weighed 35 g, the typical hatching weight of chicks, to estimate the hatching date of each weighed chick.

In years when we weighed sufficient numbers of chicks, we estimated median hatching dates from estimated hatching dates of all weighed chicks that were either the larger of the two chicks in two-chick (2-C) nests or the single chick in one-chick (1-C) nests. In years when we did not weigh chicks but fieldwork spanned the entire hatching period (1990, 1998), we estimated median hatching dates from direct observations, using the midpoint between the last date we observed eggs and the first date we observed at least one chick in each nest if that period was ≤10 d. For the six years when we weighed chicks and observations spanned the hatching period, these two estimates of median hatching dates were within 2.5 d, and observed values averaged 1.1 d later. Since the sample size for this comparison was small, we made no adjustment when using one or the other, but report which one we used in our analyses (Appendix 1, available on the website, Table A1).

When fieldwork started after hatching had begun (1979–1981, 1983–1986, 1995–1997, 1999–2008), we estimated hatching dates from age classes of chicks, backdating from the median age for each chick's age class to estimate its hatching date. Comparing median hatching dates based on growth rates and age classes of chicks for the seven years we had data for both, we found that the median based on age classes averaged 3 d later and ranged from 3 d earlier to 11 d later; i.e. on average, ages were underestimated by 3 d using age classifications. We have no data to evaluate the validity of Ramsdell & Drury's (1979) age classifications. Assuming they are accurate, the inconsistencies are likely due, at least in part, to the wide range in days for each age class, particularly the older ones, e.g. age class 4a ranges from 21 to 30 d of age. Thus, estimates of median hatching dates using age classes are likely relatively imprecise. As they may also be biased late on average, we note which estimate we used in each year for our analyses (Table A1).

In 1982, 1985 and 1986, data were obtained only for the first date of hatching, and we estimated median dates based on the difference between first and median dates (seven days) in the 14 years when

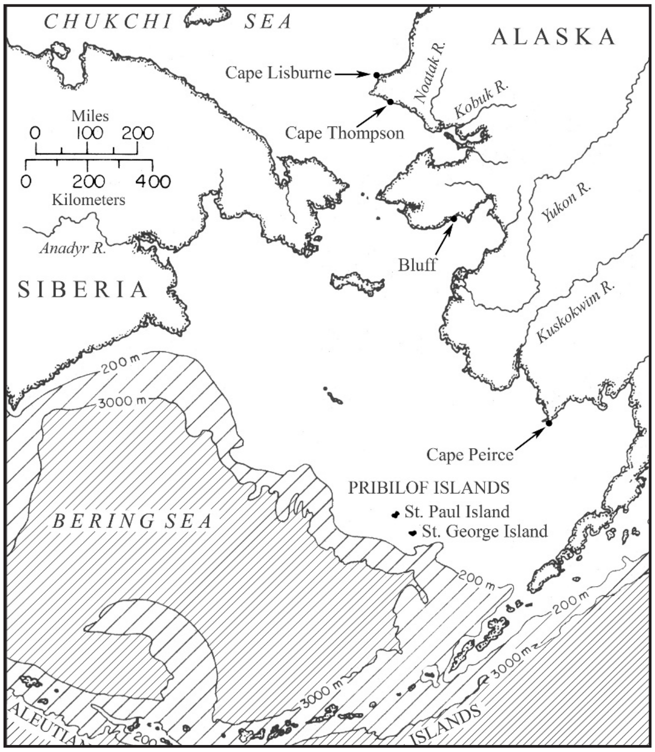

Fig. 1. Locations of the six BLKI colonies in the Bering and Chukchi seas that were compared in this study (Bluff, capes Peirce, Thompson, and Lisburne, and St. Paul and St. George islands).

we obtained data for both. We could not estimate hatching dates in 1984, as fieldwork ended on 20 July, before any eggs had hatched.

In most years, we obtained data on chick numbers in individual nests on the reproductive plots on several days. Using maximum likelihood methods (Rotella *et al.* 2004; also see Rotella 2007), we used these data to compute survival rates of single chicks in 1-C broods and older chicks in 2-C broods. We then estimated the probability that they would survive to the age of 35 d, the approximate fledging age (e.g. Baird & Gould 1986; S.A. Hatch & V. Gill, pers. comm.) using the daily survival estimates and estimated ages of chicks when they were last observed. For nests in which eggs still were being incubated when the nests were last observed during the hatching period, we assumed those eggs would likely hatch in the next several days, so we added seven days to the 35-d exposure period and used the same daily survival rates as for chicks in that year to estimate their probability of fledging.

Because survival rates of second chicks in 2-C broods are typically much lower than those of first chicks (e.g. Braun & Hunt 1983), we separately modelled daily survival rates of second chicks in 2-C broods, following the same procedure as above, to estimate their survival to fledging age. We define productivity as the estimated number of fledglings per nest, including empty nests in the denominator. For 1982, too few eggs had hatched before fieldwork ended to compute daily survival rates of chicks, so we used the mean daily survival rates of broods (0.977) and second chicks (0.890) in all other years to estimate numbers surviving to fledging in that year. We used PROC GENMOD, SAS Version 9.0 (SAS Institute 2004) for these analyses. Using the 95% Wald confidence limits for the estimate of daily survival, we also computed upper and lower limits on the estimates of numbers fledging. We report these in Table A1 only to provide a sense of the uncertainty in the modelling exercise. This does not address underlying assumptions of this approach, e.g. constant daily survival rates.

Our estimates assume that daily survival rates to fledging were the same (1) during our observations and (2) between the end of our observations and fledging. To evaluate the validity of this assumption, we first examined complete brood loss by date in 1987–1991 and 1998 (years of nearly full-season observations) and found periods of elevated brood loss only in 1990 and 1998 during periods of severe storms with high winds and heavy rain (see Results below); on one day during each of those periods average wind speeds exceeded 32 km h^{-1} (8.9 m s^{-1}). Therefore, we examined daily weather records for Nome in 1975–2008 and listed days when average daily wind speeds exceeded 8.9 m s^{-1} during the chick period in that year, which we estimated by adding 49 d to the median date of hatching (35 d for fledging of chicks hatching on the median date plus 14 d for later hatching chicks). For years when severe storms occurred between the end of our observations and the end of the fledging period, we estimate percentage of broods <35 d of age at the time of the storm using the frequency distribution of hatching dates plus 35 d; our calculations of daily survival rates likely overestimated numbers fledging in those years. In contrast, if our observations included periods of severe storms with high chick mortality but the period between the end of our observations and fledging of the latest hatching chicks did not, then our calculations likely underestimated numbers fledging in that year. This issue is especially relevant to our estimates of daily survival rates of second-hatched chicks, because they are far more susceptible to death during storms with high winds than their older and larger siblings (Braun & Hunt 1983). Additionally, the estimates of survival to fledging assume that we accurately determined ages of chicks. As noted above, ages estimated using Ramsdell & Drury's (1979) age classes may be biased a few days younger than actual ages. In the years when we estimated ages using only this method (1995–2008, except 1998 and 2001; see Table A1), our estimates of numbers of chicks surviving to fledging may be somewhat low to the extent that we underestimated ages and thus overestimated the number of days remaining to fledging.

Other colonies

We compared annual variability in breeding chronology and productivity at Bluff to that at three other mainland coastal colonies (capes Peirce, Thompson, and Lisburne) and two offshore island colonies (St. Paul and St. George islands) in the Bering and Chukchi seas (Fig. 1). For each, we note the location, distance from Bluff and estimated numbers of BLKIs (US Fish and Wildlife Service 2012): Cape Peirce (58°33′15″N, 161°46′0″W; 650 km south of Bluff; 11 304), Cape Thompson (68°08′40"N, 165°58′40″W; 400 km north; 29 600), Cape Lisburne (68°53′0″N, 166°13′0″W; 500 km north; 15 000). St. Paul Island (57°10′N, 170°15′W; 900 km southwest; 18 140) and St. George Island (56°35′N, 169°35′W; 980 km southwest, 62 568).

Generally, methods of data collection at these colonies were similar to those at Bluff, but duration of field observations varied widely. At Cape Peirce, field crews determined breeding chronology, numbers of nests and productivity on designated plots in 1976, 1981 and 1984–2008, collecting data from pre-laying through fledging (e.g. Haggblom & Mendenhall 1991, 1993, M. Winfree, Togiak National Wildlife Refuge, pers. comm.). Similarly, field crews recorded breeding chronology, numbers of nests and productivity on St. Paul Island in 1975–1979, 1984–1990, 1992–2008 and on St. George Island in 1976–2008, also typically from pre-laying through fledging; we use mean values of hatching dates and productivity reported in Thomson *et al.* (2015) for St. Paul Island and Tappa *et al.* (2015) for St. George Island in our analyses below. Although fieldwork has continued at all of these colonies since 2008, we restrict our analyses to the period 1975–2008, corresponding to the period of fieldwork at Bluff.

Field methods to determine BLKI breeding chronology and performance differed at capes Thompson and Lisburne, where relatively few nesting ledges can be viewed safely from cliff-top vantage points. At these colonies, field crews typically placed ladders on the beach below ledges where BLKIs were nesting, counted eggs and weighed and counted chicks in accessible nests, and recorded contents of inaccessible nests that could be viewed using a mirror on a long pole. In each year that nests were mapped and observed repeatedly during the chick period but observations ended before fledging, we calculated daily survival rates of broods and of second chicks in 2-C broods using the methods described above at Bluff. For Cape Lisburne, we computed mean daily survival rates from field notes for the years 1978–1981, 1983, 1987, 1993, 1995 and 1997–1998, years when data were recorded repeatedly on a nest-by-nest basis. We used the means of those values to estimate survival to fledging in 1984–1986, 1993 and 1999–2008, years when nest contents were recorded on only one date or data were not recorded on a nest-by-nest basis. We specify whether we used colony means or year-specific values of daily survival rates in Table A2 and report basic statistics for growth rates in Table A3 (in Appendix 1). Also, our estimates of productivity at Cape Lisburne are lower (mean difference = 0.27 fledglings nest^{-1}) than those that have been reported either in tables (e.g. Dragoo *et al.* 2012) or graphically (e.g. Dragoo *et al.* 2011), reports that did not include estimates of egg and chick mortality between the end of observations and fledging.

Climatic and oceanic indices

For air temperature, we used monthly weather data recorded at Nome (US Weather Service); we used mean air temperatures for April (Nome$_{\text{April}}$) and May (Nome$_{\text{May}}$) since we had previously noted significant ($P < 0.05$) correlations of BLKI breeding chronology and productivity with spring air temperatures (Murphy *et al.* 1991). We used maps of SIC on 15 May or the closest available date to calculate percent of the northeastern Bering Sea, including Norton Sound, that was ice-free in mid-May (Ice-FreeMay, 57°N–66°N, 160°W–170°W). If the closest map date was three or more days different from 15 May, we averaged values using maps on the closest dates before and after 15 May (range = 10–20 May). To calculate this index, we overlaid a matrix of dots on the map and tallied dots that were at least half-covering an area of ice versus those over open water. Numbers of dots ranged from 95 to >300, depending on the scale of the map. From 1975 through 1994, the Naval Fleet Weather Facilities in Suitland, Maryland, produced hard-copy maps. For 1997–2008 these data are available on the National Ice Center website (www.natice.noaa.gov/products/weekly_products.html). We were unable to obtain maps for 1995 or 1996, when the National Ice Center was transitioning from hard-copy to digital maps. For the period 1979–2008, data on SIC at a resolution of 25 km × 25 km grid cells were also available from the National Snow and Ice Data Center. For the same region (57°N–66°N, 160°W–170°W), we obtained data on mean SIC on 15 May (SIC$_{\text{NB15May}}$) each year (nsidc.org/data/nsidc-0079). We included both indices in our analyses, since the missing years differ.

We also used the following indices maintained by the National Oceanic and Atmospheric Administration (see www.beringclimate.noaa.gov/data/index.php for detailed descriptions and data): Ice Cover Index (ICI, average ice concentration, January through May, in the area 56°–58°N, 163°–165°W, available for 1979–2008 only); Ice Retreat Index (IRI, number of days after 15 March when the average ice concentration reached <10% in the area 56°–58°N, and 163°–165°W, available for 1978–2008 only); average SST in the southeastern Bering Sea (54.3°–60.0°N, 161.2°–172.5°W) in May (SST$_{\text{SE-May}}$); average SST at Mooring 2 (57°N, 164°W), in the Middle Shelf Domain, southeastern Bering Sea, 15 January–15 April (SST$_{\text{M2-JanApr}}$); and normalized SST anomalies in the area 52.5°–57.5°N, and 167.5°–172.5°W, near the Pribilof Islands, in January through March (SST$_{\text{Prib-JanMar}}$).

We also included the data set for SICs and SSTs used by Byrd *et al.* (2008) in their analyses from 1975 through 2005: SIC in December through February in the regions 57°–62°N, 180°–160°W (SIC$_{\text{DJF5762}}$) and 55°–60°N, 180°–160°W (SIC$_{\text{DJF5560}}$, centered on the Pribilof Islands) and SSTs in the region 52°–57°N, 175°–165°W for winter (SST$_{\text{Prib-DecFeb}}$), spring (SST$_{\text{Prib-MarMay}}$) and summer (SST$_{\text{Prib-JunAug}}$). These data are from the United Kingdom Meteorological Office (see Byrd *et al.* 2008 for details). We were able to update all indices except SIC$_{\text{DJF5560}}$ to include 2006–2008 in our analyses below.

Statistical analyses

We used Pearson product-moment correlation coefficients to examine associations and linear and multiple regression to examine annual variability in numbers of nests, median hatching dates and productivity at Bluff relative to air temperatures, SICs and SSTs. In multiple regression analyses we chose models with the lowest Akaike's information criterion (AICc) and with variance inflation factors (VIF) < 10 (to guard against multicollinearity).

We also used Pearson product-moment correlation coefficients to examine pairwise associations among colonies in hatching chronology and productivity. We examined differences in hatching chronology and productivity among colonies using analysis of variance (ANOVA) followed by Tukey's procedure to evaluate pairwise differences between colonies. We performed the ANOVA on ranks if the assumption of normality or homogeneity of variances was violated (Conover 1999).

Data reported in Thomson *et al.* (2015) for St. Paul Island and Tappa *et al.* (2015) for St. George Island, as well as unpublished data available for Cape Peirce (provided by M. Winfree, Togiak National Wildlife Refuge), included means and standard deviations but not medians. At Bluff, Cape Thompson and Cape Lisburne, we had estimates of median hatching dates for more years than we had mean estimates, and we used medians in our analyses of differences in timing of breeding among colonies. At Bluff, medians averaged 1.0 d earlier than means for the 23 years we had estimates for both, but the difference varied among years, so we made no adjustment for this difference in our analyses. We report medians and means in Tables A1 and A2 for these latter three colonies.

In reviewing data from Bluff and Cape Peirce, we wished to analyze possible differences in predation rates of Common Ravens (C*orvus corax)* on BLKI nest contents, particularly eggs, at the two colonies (see Results). We therefore tested for differences in relative laying dates of BLKIs and Common Murres (*Uria aalge*) at the two colonies, examining their average clutch initiation dates. We backdated 34 d (e.g. Murphy 1995) from average hatching dates of murres and 27 d (Hatch *et al.* 2009) from average hatching dates of BLKIs to estimate average laying dates of both species at both colonies.

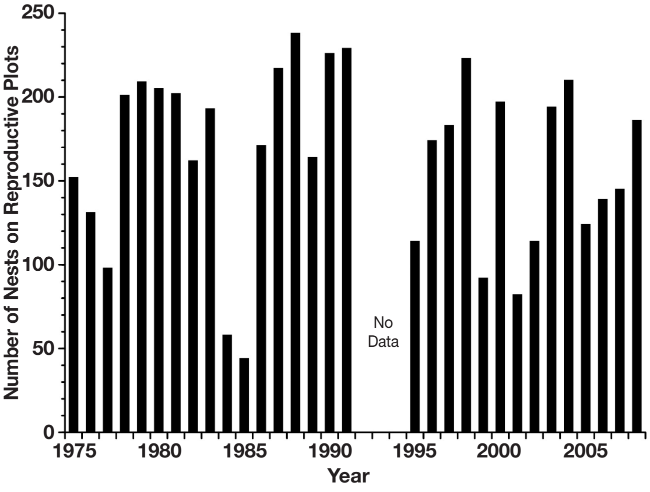

Fig. 2. Total number of BLKI nests on the five reproductive plots at Bluff, Alaska, 1975–2008.

RESULTS

Results for Bluff

Nest numbers, breeding chronology and productivity

Numbers of nests on the five reproductive plots varied markedly among years, ranging from 44 in 1984 to 238 in 1988, and averaged 163.4 (standard deviation [SD] = 52.8, n = 31 years; Fig. 2). There was no linear (Table 1, $P = 0.83$) or quadratic ($P = 0.53$) trend in numbers of nests during the study period.

Breeding chronology also varied markedly among years, with median hatching dates ranging nearly a month, from 11 July (1983) to 8 August (1985, 1986). Median hatching dates showed no trend across years (Table 1). They were significantly correlated, however, with nest counts ($r = -0.595$, n = 29 years, $P = 0.0007$), i.e. breeding chronology was earliest when nest numbers were highest (Fig. 3).

Productivity also varied markedly among years at Bluff; few or no chicks fledged in the study plots during 1976, 1984, 1985, 1989, 1999 or 2001; in contrast, productivity was highest in 1979, when 68% of nests produced one fledgling and 16% of nests produced two fledglings (Fig. 4). Very few nests produced two fledglings in any other year.

During the eight years when we weighed chicks at Bluff (see Table A3 for basic growth-rate data), we first tested for differences in growth rates of first chicks in 2-C broods and sole chicks in 1-C broods. We found no significant differences ($P = 0.39$) and therefore pooled them in subsequent analyses. At Bluff, growth rates varied significantly among years ($F_{7,211} = 5.41$, $P < 0.0001$). Growth rates were significantly higher in 1979 than in 1983, 1987 and 1988, but significantly lower in 1983 than in any other year (Tukey pairwise comparisons, $P < 0.05$). No other pairwise differences were significant.

In 1979, growth rates of second chicks in 2-C broods averaged 20.2 g d^{-1} (SD = 4.6, n = 6), slightly higher than rates of single chicks and first chicks in 2-C broods (19.0 g d^{-1}, SD = 5.0, n = 37). In contrast, growth rates of second chicks in 2-C broods in all other years pooled averaged lower and were much more variable

TABLE 1
Correlations of breeding chronology and productivity of BLKIs at Bluff, Alaska, with year and with local and regional climatic and oceanographic indices

	Pearson correlation coefficient (number of years)			
Index[a]	**Nest count**	**Median hatching date**	**Productivity**	**Total number of fledglings**
Year	-0.041 (31)	-0.296 (29)	-0.090 (31)	-0.126 (31)
Nome$_{April}$	**0.642 (31)**[b]	**-0.658 (29)**[b]	**0.558 (31)**[c]	**0.584 (31)**[c]
Nome$_{May}$	**0.587 (31)**[c]	**-0.688 (29)**[b]	**0.713 (31)**[b]	**0.681 (31)**[b]
Ice-Free$_{May}$	**0.557 (29)**[c]	**-0.621 (27)**[c]	**0.694 (29)**[b]	**0.690 (29)**[b]
SIC$_{NB15May}$	**-0.607(27)**[c]	**0.589 (25)**[c]	**-0.683 (27)**[b]	**-0.653 (27)**[c]
ICI	0.017 (27)	-0.019 (25)	-0.249 (27)	-0.215 (27)
IRI	-0.328 (28)	**0.415 (26)**[d]	**-0.506 (28)**[d]	**-0.460 (28)**[d]
SST$_{SE\text{-}May}$	**0.367 (31)**[d]	**-0.380 (29)**[d]	**0.718 (31)**[b]	**0.682 (31)**[b]
SST$_{M2\text{-}JanApr}$	0.015 (31)	-0.058 (29)	0.344 (31)	0.337 (31)
SST$_{Prib\text{-}JanMar}$	-0.015 (31)	0.048 (29)	0.200 (31)	0.213 (31)
SST$_{Prib\text{-}DecFeb}$	-0.089 (31)	0.150 (29)	0.092 (31)	0.103 (31)
SST$_{Prib\text{-}MarMay}$	0.203 (31)	-0.222 (29)	0.465 (31)d	**0.444 (31)**[d]
SST$_{Prib\text{-}JunAug}$	0.105 (31)	-0.016 (29)	0.301 (31)	0.257 (31)
SIC$_{DJF5762}$	0.145 (31)	**0.016 (29)**[d]	0.033 (31)	-0.040 (31)
SIC$_{DJF5560}$	0.109 (28)	-0.023 (26)	-0.005 (28)	-0.072 (28)

[a] Nome$_{April}$: Mean Air Temperature in Nome in April; Nome$_{May}$: Mean Air Temperature in Nome in May; Ice-Free$_{May}$: Percent of the NE Bering Sea that was ice-free on 15 May; SIC$_{NB15May}$: Mean SIC in the NE Bering Sea on 15 May, ICI: Ice Cover Index; IRI: Ice Retreat Index; SST$_{SE\text{-}May}$: Average SST in SE Bering Sea in May; SST$_{M2\text{- }JanApr}$: Average SST at Mooring 2, SE Bering Sea, 15 January-15 April; SST$_{Prib\text{-}JanMar}$: Average SST near the Pribilof Islands, January-March; SST$_{Prib\text{-}DecFeb}$: Average SST near the Pribilof Islands, December-February; SST$_{Prib\text{-}MarMay}$: Average SST near the Pribilof Islands, March-May; SST$_{Prib\text{-}JunAug}$: Average SST near the Pribilof Islands, June-August; SIC$_{DJF5762}$: SIC anomaly in the area 57°-62°N, 180°-160°W, December-February; SIC$_{DJF5560}$: SIC anomaly in the area 55°-60°N, 180°-160°W, December-February (see Methods for additional details).

[b] $P < 0.0001$.

[c] $P < 0.005$.

[d] $P < 0.05$.

(16.1 g d^{-1}, SD = 7.4, n = 20). However, sample sizes of growth rates of second chicks were small, and the difference between 1979 and all other years pooled was not significant ($P > 0.05$).

Productivity was highest in years when nest numbers were highest ($r = 0.69$, n = 31 years, $P < 0.0001$) and breeding was earliest ($r = -0.73$, n = 29, $P < 0.0001$). The estimated total number of fledglings on the five reproductive plots consequently varied markedly, from zero in several years to 208 in 1979 (Fig. 5), and showed no linear (Table 1, $P = 0.50$) or quadratic ($P = 0.80$) trend from 1975 to 2008.

Periods of high chick mortality

Overall, daily nest survival during the chick period was high and averaged 0.977 for the 22 years of data at Bluff. In 1987–1991 and 1998 (years of nearly full-season observations for which we have detailed data), mortality rates of broods were typically low, with no or few losses between successive observation dates and fairly constant rates throughout the chick period (e.g. Murphy *et al.* 1991). However, there were episodes of high chick and brood disappearances during storms in those years. In 1990, brood loss may have been high between observations before and after a storm with peak winds on 17 August (winds ESE, average speed = 12.5 m s^{-1}, peak = 21.9 m s^{-1}) but relatively little rain (peak = 0.8 cm on 16 August); at least five to eight (three were close to fledging age) of 162 1-C broods disappeared, and eight others either fledged or disappeared. Brood loss also may have been high during another storm with heavy rain and high winds on 25 August (rain = 2.9 cm; winds southeast, average speed = 10.8 m s^{-1}, peak = 17.9 m s^{-1}). Although only two to three chicks younger than fledging age disappeared, 22–23 others either fledged or died before fledging (all of those nests were empty on 1 September). Because most of these disappearances were of chicks that may have fledged, we cannot definitively ascribe most of these disappearances in 1990 to storm-related mortality.

In 1998, 29 (20%) of 145 1-C broods disappeared between observations on 10 and 15 August; rainfall on 11–14 August totaled 8.5 cm, 1.6 cm more than the August average (6.9 cm), and winds peaked on 15 August (SSW, average = 10.6 m s^{-1}, peak = 20.1 m s^{-1}). Further, between observations on 17 and 20 August, an additional 27 broods (23% of the remaining 116 broods, including one 2-C brood) disappeared; on 19 August, rainfall was heavy (4.4 cm) with high SSE winds (average = 11.7 m s^{-1}, peak = 21.0 m s^{-1}). During these storms, wave action at the base of the cliffs drove mists upward to reach high on the cliffs (N. W. Murphy, pers. comm.). Since fledging was just beginning, virtually all of these disappearances were likely storm-induced deaths.

Drury (1976) attributed estimated losses of 16 of 39 chicks at "Stake 1," a west-facing cliff face, between observations on 12 and 30 August 1975 to a storm with peak intensity on 25 August (rain = 3.3 cm; winds south-southwest, average speed = 11.2 m s^{-1},

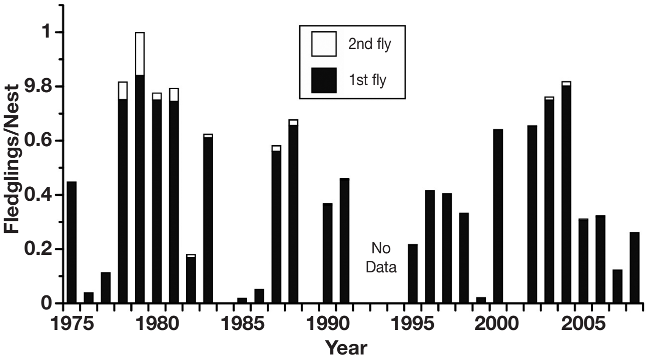

Fig. 4. Estimated BLKI productivity (fledglings $nest^{-1}$) at Bluff, Alaska, 1975–2008. The black portion of each bar represents the number of single chicks in 1-C nests and first chicks in 2-C nests (fledging $nest^{-1}$); the white portion represents number of second chicks (fledging $nest^{-1}$). No data were collected in 1992–1994; complete nesting failures occurred in 1984, 1989 and 2001.

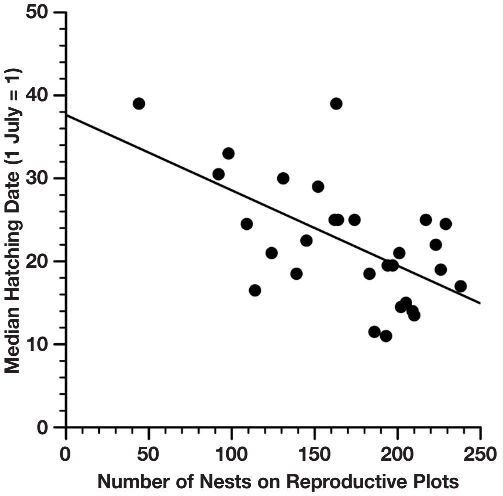

Fig. 3. Relationship of hatching chronology (median hatching date) to number of nests of BLKIs on the five reproductive plots at Bluff, Alaska, 1975–2008.

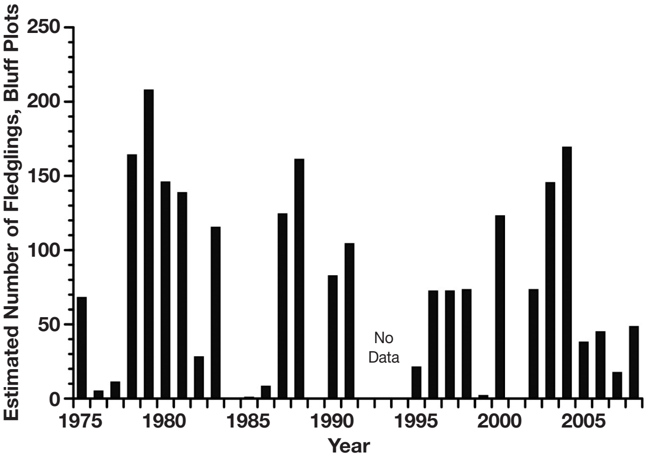

Fig. 5. Estimated total number of BLKI fledglings on the five reproductive plots at Bluff, Alaska, 1975–2008. No data were collected in 1992–1994.

peak = 16.5 m s^{-1}); fledging was just beginning on 30 August. In other years, when our observations ended before the fledging period, we observed elevated mortality only in 1986. During a storm between 8 and 14 August (11 August: rain = 1.0 cm; winds south, average speed = 9.2 m s^{-1}, peak = 11.6 m s^{-1}), 16 of 66 (24%) 1-C broods disappeared; none of the chicks was near fledging age.

When we examined weather records for similar storms between the end of our observations and the end of fledging, which we estimated as 49 d after the median hatching date, we found records of severe storms in several years. In 1986, one year when we documented high chick mortality during a storm, a second storm with high southerly winds occurred in early September (4 September: south-southeast, average speed = 9.7 m s^{-1}; 5 September: southeast, 10.1 m s^{-1}), before any chicks would have reached fledging age. Because mortality was also likely high during this late storm and we had already incorporated the storm-related mortality in mid-August in our calculations of daily mortality rates, our estimate for 1986 is probably unbiased; we estimated that only eight chicks fledged successfully.

Storms occurred late in the chick period in 1977 (2 [6%] to 7 [21%] of broods < 35 d of age), 1979 (11 [7%] of 147 broods) and 2000 (17 [10%] of 171 broods). We highlight 1979 because we estimated exceptionally high productivity and fledging of second chicks that year. In 1979, a storm with peak winds on 25–26 August (25 August: rain = 6.6 cm; winds south, average speed = 9.6 m s^{-1}, peak = 11.6 m s^{-1}; 26 August: rain = 1.0 cm; winds southwest, average speed = 9.7 m s^{-1}, peak = 13.4 m s^{-1}) occurred when 7% of the broods were < 35 d of age. In all three of these years, pre-fledging mortality rates of late-hatching chicks probably rose somewhat during these late-season storms. In 2005, a storm occurred midway through the chick period (23 [47%] of 57 broods < 35 d of age), and pre-fledging mortality rates of later-hatching broods were likely higher than we estimated. We highlight these years in bold in Table A1.

Attendance of adults at nests with chicks

In most years, we recorded at least one adult at all nests with chicks on all days of observations during the chick period. However, both adults were absent from a substantial number of nests on one or more days of observation in 2004 (58 [34%] of 173 broods, two < 10 d of age), 2006 (27 [47%] of 58 broods, one < 10 d), 2007 (41 [79%] of 52 broods, three < 10 d) and 2008 (59 [72%] of 82 broods, four < 10 d). During those observations, we saw no predation attempts on chicks in unattended nests by Glaucous Gulls *Larus hyperboreus* or ravens, although both species are common at Bluff, and no evidence of elevated mortality was apparent on our next visit.

Breeding performance and oceanographic and atmospheric conditions

Numbers of nests were highest in years when spring air temperatures were warmer, SIC in mid-May was lower and SSTs were warmer (Table 1). The highest correlation was with April temperature (linear regression, $F_{1,29} = 20.38$, $P < 0.0001$; $r^2 = 0.52$; Fig. 6). The best two-variable regression model of nest numbers on climatic and oceanographic indices included both April and May temperatures (adjusted $r^2 = 0.59$):

$$\text{Nest numbers} = 186.68 + 6.36 * \text{Nome}_{\text{April}} + 7.07 * \text{Nome}_{\text{May}}$$

Thus, nest numbers were higher in years when April and May air temperatures were warmer; both months entered the model because April and May temperatures were only moderately positively correlated ($r^2 = 0.25$; variance inflation factor (VIF) = 1.46). Collinearity was too high in the best three-variable models to consider them further.

Median hatching dates also were highly correlated with several climatic and oceanographic indices (Table 1) and were earliest

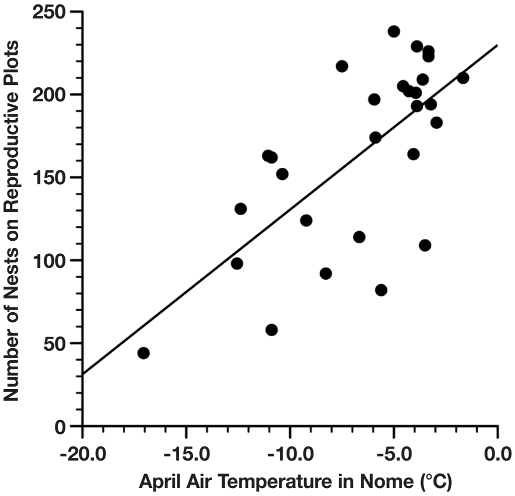

Fig. 6. Relationship of number of BLKI nests on the five reproductive plots at Bluff, Alaska, to April air temperature in Nome. Note that all temperatures are below 0 °C.

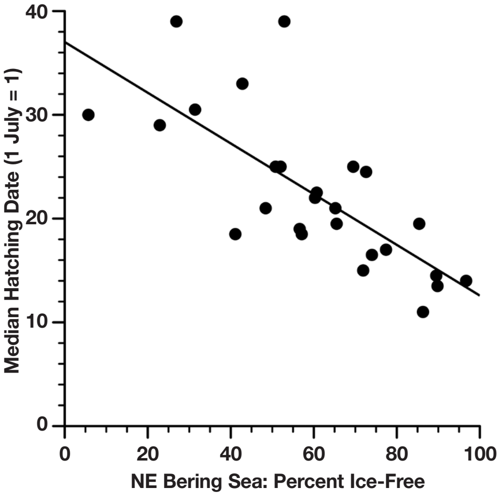

Fig. 7. Relationship of BLKI hatching chronology (median hatching date) at Bluff, Alaska, to the percentage of the northeastern Bering Sea that was ice-free in mid-May.

in years when air temperatures were warmest, ice retreat was earliest and SIC in northeastern Bering Sea in mid-May was least. The highest correlation was with SIC in mid-May (linear regression, $F_{1,25} = 15.67$, $P = 0.0006$; $r^2 = 0.65$; Fig. 7). Similar to nest numbers, the best two-variable regression model for annual variation in hatching dates included May and April temperatures (adjusted $r^2 = 0.76$):

$$\text{Median Hatching Date} = 21.95 - 0.72 * \text{Nome}_{\text{April}} - 1.48 * \text{Nome}_{\text{May}}$$

Correlations of productivity (numbers of fledglings per nest) with the climatic and oceanographic indices closely paralleled those for hatching dates (Table 1). Productivity was highest in years when SIC was least in mid-May ($F_{1,25} = 28.70$, $P < 0.0001$; $r^2 = 0.66$; Fig. 8). In the multiple regression analyses, the best two-variable model included May air temperature and SST in the southeastern Bering Sea (adjusted $r^2 = 0.63$, VIF = 1.31):

$$\text{Productivity} = -0.159 + 0.058 * \text{Nome}_{\text{May}} + 0.169 * \text{SST}_{\text{SE-May}}$$

Correlations of estimated total number of fledglings on the five reproductive plots with climatic and oceanic indices paralleled those for productivity (Table 1). In summary, nest numbers, hatching chronology and productivity were significantly correlated with air temperatures in Nome in April and May, SIC in the northern Bering Sea in mid-May and SST in the southeastern Bering Sea in May. Additionally, hatching chronology and productivity were significantly correlated with the Ice Retreat Index and spring or summer SSTs in Pribilof Island waters. Thus, for BLKIs at Bluff, numbers of nests and productivity were highest and breeding was earliest in years when both air and sea temperatures in late spring were warmest and sea ice retreated earliest.

Breeding chronology and productivity: differences among colonies

Average hatch dates (grand means of annual averages, Table 2) ranged from 9–10 July at Cape Peirce to 29 July at Cape Thompson. Our initial ANOVA for the averages violated the assumption of equality of variances (Levene's test for homogeneity of variances, $F_{5,120} = 4.25$, $P = 0.001$); variance in average hatching dates was highest on the Pribilof Islands, and second highest at Cape Peirce, the southernmost of the mainland coastal colonies (Table 2). Because of the violation of this statistical assumption, we then conducted the ANOVA for ranks of annual averages (Conover 1999), which varied significantly among colonies (ANOVA, $F_{5,120} = 12.67$, $P < 0.0001$). Breeding was significantly earlier at Cape Peirce than at any other colony (Tukey pairwise comparisons, $P < 0.05$). Hatching dates did not differ significantly between St. George and St. Paul or between Bluff and either of those islands. Hatching dates did not differ between capes Thompson and Lisburne, but they did differ significantly between these two colonies in the Chukchi Sea and all colonies in the Bering Sea.

Our initial ANOVA to test for differences in productivity among colonies also violated the assumption of homogeneity of variances, so we also conducted this ANOVA on ranks. Productivity varied significantly among colonies ($F_{5,150} = 3.09$, $P = 0.01$); it was significantly higher at Bluff and Cape Lisburne than at Cape Peirce; no other pairwise differences were significant (Tukey pairwise comparisons, $P < 0.05$).

Breeding chronology and productivity: correlations among colonies

Pairwise correlations among colonies in the Bering Sea (Bluff, Cape Peirce, St. Paul and St. George) in timing of breeding were positive and significant (Table 3), except between Bluff and St. George. Also, the correlation in breeding chronology between Cape Thompson and St. Paul was positive and significant. All other correlations were non-significant ($P > 0.05$) but positive; the correlation in timing of breeding at capes Thompson and Lisburne was high, but studies at those two colonies overlapped in only four years. Correlations were lowest between Cape Lisburne and the other colonies.

Productivity of BLKIs at Bluff was positively and significantly correlated with productivity at capes Peirce and Lisburne, as well as St. Paul, and positively, but not significantly, correlated

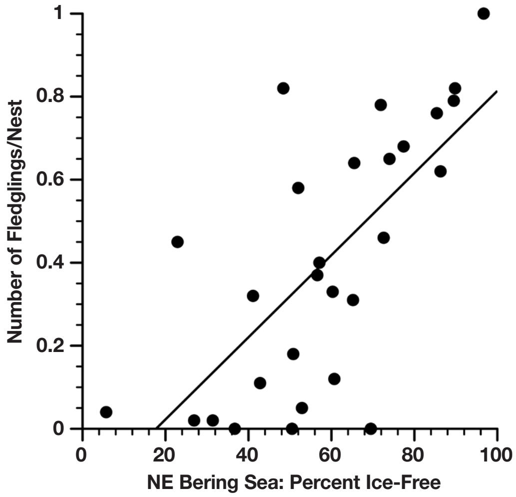

Fig. 8. Relationship of BLKI productivity (fledglings nest^{-1}) at Bluff, Alaska, to the percentage of the northeastern Bering Sea that was ice-free in mid-May.

TABLE 2
Average hatching date and productivity of BLKIs at study colonies in the Bering and Chukchi seas, 1975–2008

Colony (south to north)	Grand mean estimates ± SD (number of years)	
	Hatching date[a]	Productivity
St. George Island	18.4 July ± 10.4 d (26)	0.21 ± 0.20 (33)
St. Paul Island	17.9 July ± 9.6 d (25)	0.28 ± 0.22 (29)
Cape Peirce	9.5 July ± 7.8 d (21)	0.17 ± 0.18 (27)
Bluff	20.6 July ± 4.6 d (23)	0.39 ± 0.30 (31)
Cape Thompson	29.0 July ± 5.6 d (9)	0.45 ± 0.40 (9)
Cape Lisburne	27.5 July ± 6.0 d (22)	0.40 ± 0.33 (27)

[a] St. George Island, St. Paul Island and Cape Peirce: annual means; Bluff, Cape Thompson and Cape Lisburne: annual medians (see text).

with productivity at Cape Thompson and St. George (Table 3). Productivity also was positively and significantly correlated between Cape Peirce and both St. Paul and St. George, and between the two islands (Table 3; as reported by Byrd *et al.* 2008).

At Bluff, very few pairs successfully produced two fledglings in any year except 1979, when two chicks fledged in 16% of nests, and productivity was exceptionally high (Fig. 4). Similarly, very few pairs produced two fledglings except in 1979 (21%) and 1990 (20%) at Cape Thompson and 1979 (25%) and 1998 (24%) at Cape Lisburne. Furthermore, growth rates of second chicks in 2-C broods were high at Cape Thompson (Table A3) and appeared high at Cape Lisburne, where severe storms precluded recording of both first and second weighings of the fastest-growing chicks before they exceeded 350 g (see Table A3), suggesting exceptionally good conditions for breeding at these three colonies in 1979.

At all colonies, BLKIs frequently experienced near or complete reproductive failures (defined here as productivity < 0.05, Table 4). All failures at Bluff (1976, 1984, 1985, 1989, 1999 and 2001) coincided with failures at one or more other colonies. In 1976, a failure also occurred at Cape Thompson. In 1984, failures occurred at all colonies except St. George, where productivity was also low. In 1985, a failure occurred at Cape Peirce. In 1989, failures occurred on the Pribilof Islands and productivity was also low at Cape Peirce. In 1999, failures also occurred at all other colonies except Cape Lisburne, where productivity was moderate. In 2001, failures occurred at capes Peirce and Lisburne, and productivity was low on the Pribilof Islands.

The significant correlations in both breeding chronology and productivity between Bluff and St. Paul suggest associations between these two distant colonies, as well as between St. Paul and St. George (Byrd *et al.* 2008). To examine these relationships further, we first conducted a regression analysis of breeding chronology on St. Paul and chronology at Bluff and St. George, which produced a highly significant model ($F_{2,17}$ = 48.21, P < 0.0001, adjusted r^2 = 0.83, VIF = 1.23):

$$\text{Hatch Date}_{\text{St. Paul}} = -6.53 + 0.59 * \text{Hatch Date}_{\text{Bluff}} + 0.51 * \text{Hatch Date}_{\text{St. George}}$$

Similarly, the regression analysis of productivity on St. Paul and productivity at Bluff and St. George produced a highly significant model ($F_{2,22}$ = 58.99, P < 0.0001, adjusted r^2 = 0.83, VIF = 1.11):

$$\text{Productivity}_{\text{St. Paul}} = 0.01 + 0.34 * \text{Productivity}_{\text{Bluff}} + 0.71 * \text{Productivity}_{\text{St. George}}$$

Thus, both timing of breeding and productivity on St. Paul Island demonstrated strong and statistically independent associations (as shown by the low VIF values) with both St. George and Bluff.

Timing of breeding at Bluff and Cape Peirce: BLKIs versus Murres

Because productivity averaged significantly lower at Cape Peirce than at Bluff, we explored whether predation by Common Ravens could be an explanatory factor. At Bluff, ravens are conspicuous predators of eggs of Common Murres (Schauer & Murphy 1996), but they rarely prey on BLKI eggs (e.g. Ramsdell & Drury 1979). In contrast, at Cape Peirce predation by ravens on BLKIs, especially eggs, appears high (e.g. Haggblom & Mendenhall 1991, 1993), particularly before murres start laying (M. Swaim, US Fish and Wildlife Service, pers. comm.). To investigate a possible reason for this difference, we compared relative laying dates of murres and BLKIs at the two colonies. On average, murre egg-laying dates were 3.2 d (SD = 4.5 d, n = 26 years) earlier than those of BLKIs at Bluff, but 5.3 d later at Cape Peirce (SD = 4.8 d, n = 20; t = 2.18, P < 0.05). At Bluff, estimated laying dates of first eggs averaged 5 d earlier for murres than BLKIs (n = 20). This difference may translate to greater vulnerability of BLKI eggs to predation by ravens at Cape Pierce and thus lower productivity there.

Other colonies: Breeding performance and oceanographic and climatic indices

At Cape Peirce, mean hatching dates were earliest when SIC in the northeastern Bering Sea in mid-May was least, ice retreat in the southeastern Bering Sea was earliest, and SSTs in the southeastern Bering Sea were warmest (Table 5; all similar to Bluff). In contrast to Bluff, however, productivity at Cape Peirce was not significantly correlated with any physical index that we examined (Table 5).

TABLE 3
Average dates of hatching (above diagonal) and productivity (below diagonal) of BLKIs at Bluff and other study colonies in the Alaskan Bering and Chukchi seas

Colony	Pearson correlation coefficient (*n*)					
	Bluff	Cape Peirce	Cape Thompson	Cape Lisburne	St. Paul Island	St. George Island
Bluff		**0.615 (17)**[a]	0.671 (9)	0.366 (19)	**0.631 (23)**[b]	0.403 (22)
Cape Peirce	**0.612 (24)**[b]		0.946 (4)	0.028 (14)	**0.687 (17)**[b]	**0.574 (19)**[a]
Cape Thompson	0.334 (9)	0.246 (5)		0.532 (4)	**0.821 (6)**[a]	0.267 (6)
Cape Lisburne	**0.538 (25)**[a]	-0.037 (22)	0.772 (5)		0.298 (17)	0.180 (17)
St. Paul Island	**0.670 (26)**[b]	**0.689 (25)**[b]	0.251 (7)	0.326 (24)		**0.827 (22)**[c]
St. George Island	0.278 (30)	**0.581 (27)**[b]	-0.090 (9)	0.115 (27)	**0.802 (28)**[b]	

[a] $P < 0.05$.
[b] $P < 0.005$.
[c] $P < 0.0001$.

At Cape Thompson, breeding was earliest when SIC in the northeastern Bering Sea in mid-May was least (Table 5). Productivity at Cape Thompson was not significantly correlated with any index, but sample sizes were small; generally, productivity was highest in years when spring conditions were warmest (Table 5). At Cape Lisburne, breeding was earliest in those years when April air temperatures were warmest and SIC on 15 May in the northeastern Bering Sea was least (Table 5). In addition, productivity at Cape Lisburne was highest in years when April and May air temperatures in Nome were warmest and SIC in mid-May was least (Table 5), also similar to Bluff. These correlations indicate positive relationships in both timing of breeding and productivity with spring temperatures at Cape Lisburne as well as Bluff.

TABLE 4
Annual productivity of BLKIs at study colonies in the Alaskan Bering and Chukchi seas, 1975–2008

Year	Bluff	Cape Peirce	Cape Thompson	Cape Lisburne	St. Paul Island	St. George Island
1975	0.45	ND	ND	ND	0.44	ND
1976	**0.04**[a]	0.25	**0.00**[a]	0.11	0.52	0.62
1977	0.11	ND	0.42	0.23	0.43	0.45
1978	0.82	ND	0.23	0.68	0.36	0.22
1979	1.00	ND	1.02	1.06	0.54	0.40
1980	0.78	ND	ND	0.79	ND	0.38
1981	0.79	0.16	ND	0.47	ND	0.08
1982	0.18	ND	0.70	ND	ND	**0.01**[a]
1983	0.62	ND	ND	0.61	ND	**0.01**[a]
1984	**0.00**[a]	**0.00**[a]	ND	**0.02**[a]	**0.00**[a]	0.08
1985	**0.02**[a]	**0.00**[a]	ND	0.11	0.06	0.05
1986	0.05	**0.00**[a]	ND	0.39	0.29	0.23
1987	0.58	0.06	ND	0.81	0.25	**0.00**[a]
1988	0.68	0.16	0.15	ND	0.53	**0.02**[a]
1989	**0.00**[a]	0.06	ND	ND	**0.03**[a]	**0.00**[a]
1990	0.37	0.21	1.02	ND	0.33	0.28
1991	0.46	0.13	0.51	ND	ND	0.38
1992	ND	0.48	ND	**0.01**[a]	0.25	0.36
1993	ND	0.17	ND	0.47	0.23	0.18
1994	ND	0.07	ND	ND	**0.03**[a]	**0.04**[a]
1995	0.22	0.06	**0.01**[a]	0.46	**0.00**[a]	**0.00**[a]
1996	0.42	**0.01**[a]	ND	**0.00**[a]	0.05	**0.03**[a]
1997	0.40	0.10	ND	0.46	0.29	0.26
1998	0.33	**0.00**[a]	ND	1.03	0.40	0.45
1999	**0.02**[a]	**0.00**[a]	ND	0.46	0.03[a]	**0.00**[a]
2000	0.64	0.30	ND	0.73	0.65	0.59
2001	**0.00**[a]	**0.00**[a]	ND	**0.00**[a]	0.17	0.07
2002	0.65	0.62	ND	**0.00**[a]	0.72	0.71
2003	0.76	0.51	ND	0.61	0.58	0.36
2004	0.82	0.48	ND	0.30	0.56	0.20
2005	0.31	0.12	ND	**0.00**[a]	0.05	**0.04**[a]
2006	0.32	**0.00**[a]	ND	0.06	0.16	0.22
2007	0.12	0.21	ND	0.37	**0.00**[a]	**0.02**[a]
2008	0.26	0.33	ND	0.63	0.23	0.15

ND = no data.

[a] Productivity values (fledglings nest^{-1}) < 0.05 (“failures”).

Breeding chronology on St. Paul Island was not correlated with any of the indices we examined (Table 5). Productivity on St. Paul was negatively correlated with SIC in the northeastern Bering Sea in mid-May and positively correlated with SST in May in the southeastern Bering Sea, similar to Bluff (Table 5); these indices were highly negatively correlated ($r = -0.692$, n = 30 years, $P < 0.0001$).

On St. George, breeding chronology was not significantly correlated with any of the indices, but productivity was highest in years when winter SIC in nearby waters was highest (Table 5; Byrd *et al.* 2008). This result suggests a contrast between Bluff and St. George Island in relationships of productivity to regional SIC; productivity was highest at Bluff when SIC in May in the northeastern Bering Sea was least, and productivity was highest on St. George when winter SIC in

TABLE 5

Breeding chronology and productivity of BLKIs and indices of sea ice, sea surface temperature (SST) and air temperature at study colonies in the Alaskan Bering and Chukchi seas

Index[a]	**Pearson correlation coefficient (*n*)**					
	Bluff	**Cape Peirce**	**Cape Thompson**	**Cape Lisburne**	**St. Paul Island**	**St. George Island**
Breeding chronology						
$\mathrm{Nome}_{\mathrm{April}}$	**-0.658 (29)**[b]	-0.161 (21)	-0.552 (9)	**-0.753 (22)**[b]	-0.362 (26)	-0.171 (26)
$\mathrm{Nome}_{\mathrm{May}}$	**-0.688 (29)**[b]	-0.254 (21)	-0.485 (9)	-0.257 (22)	-0.030 (26)	0.250 (26)
$\mathrm{Ice\text{-}Free}_{\mathrm{May}}$	**-0.621 (27)**[c]	**-0.460 (19)**[d]	**-0.721 (8)**[d]	-0.359 (21)	-0.315 (25)	-0.165 (25)
$\mathrm{SIC}_{\mathrm{NB15May}}$	**0.589 (25)**[d]	**0.503 (19)**[d]	0.029 (6)	**0.477 (20)**[d]	0.030 (22)	-0.058 (23)
ICI	-0.019 (25)	0.264 (20)	-0.507 (6)	-0.175 (20)	-0.263 (22)	-0.261 (23)
IRI	**0.415 (26)**[d]	**0.508 (20)**[d]	0.069 (7)	-0.010 (21)	0.080 (23)	0.023 (24)
$\mathrm{SST}_{\mathrm{SE\text{-}May}}$	**-0.380 (29)**[d]	**-0.551 (21)**[d]	-0.062 (9)	-0.037 (22)	0.128 (26)	0.196 (26)
$\mathrm{SST}_{\mathrm{M2\text{-}JanApr}}$	-0.058 (29)	-0.385 (21)	-0.285 (9)	0.227 (22)	0.091 (26)	0.161 (26)
$\mathrm{SST}_{\mathrm{Prib\text{-}JanMar}}$	0.048 (29)	-0.320 (21)	-0.470 (9)	-0.101 (22)	0.106 (26)	0.255 (26)
$\mathrm{SST}_{\mathrm{Prib\text{-}DecFeb}}$	0.150 (29)	-0.176 (21)	-0.328 (9)	0.105 (22)	0.182 (26)	0.350 (26)
$\mathrm{SST}_{\mathrm{Prib\text{-}MarMay}}$	-0.222 (29)	-0.426 (21)	-0.144 (9)	-0.048 (22)	0.067 (26)	0.226 (26)
$\mathrm{SST}_{\mathrm{Prib\text{-}JunAug}}$	**-0.461 (29)**[d]	**-0.508 (21)**[d]	-0.068 (9)	0.172 (22)	-0.317 (26)	-0.264 (26)
$\mathrm{SIC}_{\mathrm{DJF5762}}$	-0.016 (29)	0.150 (21)	0.566 (9)	0.136 (22)	0.064 (26)	-0.009 (26)
$\mathrm{SIC}_{\mathrm{DJF5560}}$	-0.023 (26)	0.180 (18)	0.591 (9)	-0.098 (19)	0.109 (23)	-0.046 (23)
Productivity (fledglings nest^{-1})						
$\mathrm{Nome}_{\mathrm{April}}$	**0.558 (31)**[c]	0.294 (27)	0.238 (9)	**0.461 (27)**[d]	0.165 (29)	0.014 (33)
$\mathrm{Nome}_{\mathrm{May}}$	**0.713 (31)**[c]	0.090 (27)	0.047 (9)	**0.404 (27)**[d]	0.122 (29)	-0.110 (33)
$\mathrm{Ice\text{-}Free}_{\mathrm{May}}$	**0.694 (29)**[b]	0.360 (25)	0.566 (8)	**0.402 (25)**[d]	0.328 (27)	0.014 (31)
$\mathrm{SIC}_{\mathrm{NB15May}}$	**-0.683 (27)**[b]	-0.355 (26)	0.022 (6)	-0.318 (24)	**-0.459 (25)**[d]	-0.248 (30)
ICI	-0.249 (27)	0.064 (26)	-0.373 (6)	0.202 (24)	-0.044 (25)	0.214 (30)
IRI	**-0.506 (28)**[d]	-0.087 (26)	-0.245 (7)	-0.197 (25)	-0.363 (26)	**-0.384 (31)**[d]
$\mathrm{SST}_{\mathrm{SE\text{-}May}}$	**0.718 (31)**[b]	0.260 (27)	0.388 (9)	0.252 (27)	**0.382 (29)**[d]	0.106 (33)
$\mathrm{SST}_{\mathrm{M2\text{-}JanApr}}$	0.344 (31)	-0.144 (27)	0.438 (9)	0.083 (27)	-0.004 (29)	-0.237 (33)
$\mathrm{SST}_{\mathrm{Prib\text{-}JanMar}}$	0.200 (31)	-0.123 (27)	0.478 (9)	-0.072 (27)	-0.034 (29)	-0.182 (33)
$\mathrm{SST}_{\mathrm{Prib\text{-}DecFeb}}$	0.092 (31)	-0.301 (27)	0.429 (9)	-0.023 (27)	-0.244 (29)	-0.315 (33)
$\mathrm{SST}_{\mathrm{Prib\text{-}MarMay}}$	**0.465 (31)**[d]	-0.070 (27)	0.431 (9)	0.184 (27)	0.001 (29)	-0.161 (33)
$\mathrm{SST}_{\mathrm{Prib\text{-}JunAug}}$	0.301 (31)	0.205 (27)	0.412 (9)	-0.033 (27)	0.101 (29)	0.117 (33)
$\mathrm{SIC}_{\mathrm{DJF5762}}$	0.033 (31)	0.190 (27)	-0.573 (9)	0.070 (27)	0.309 (29)	**0.520 (33)**[c]
$\mathrm{SIC}_{\mathrm{DJF5560}}$	-0.005 (28)	0.192 (24)	-0.524 (9)	0.089 (24)	0.302 (26)	**0.560 (30)**[c]

[a] See Table 1 for definitions of acronyms.

[b] $P < 0.0001$.

[c] $P < 0.005$.

[d] $P < 0.05$.

nearby waters was highest. However, productivity at both Bluff and St. George Island was highest in years of earliest ice retreat (Table 5).

DISCUSSION

Bluff

Annual variability in numbers of nests, breeding chronology and productivity

At Bluff, during 1975–2008, annual variation in all aspects of breeding was high; in years when nest numbers were high, breeding was early and productivity was high, and success at early stages translated into success at later stages (see also Renner *et al.* 2014). Nest numbers and productivity were highest, and hatching was earliest, in years when SIC in mid-May was least and spring air temperatures were warmest, continuing the pattern documented for 1975–1989 (Murphy *et al.* 1991). Two extremes were demonstrated in 1984 and 1979. In 1984, the number of nests was low (Fig. 2), and breeding failed colony-wide. Spring air temperatures were cold that year; the monthly May air temperature (-0.5 °C) was the coldest during the study period. Further, SSTs in Norton Sound were anomalously cold from late June to mid-August due to an unusual eastward intrusion of cold Anadyr-Bering Shelf water (Springer *et al.* 1987).

In 1979, breeding was relatively early (median hatch date = 14 July), and productivity was the highest during the 1975–2008 period. This was the only year when we estimated that substantial numbers of pairs fledged two chicks (Fig. 4), and growth rates of second chicks averaged slightly higher than those of first chicks (Table S3). It also was one of only two years at both capes Thompson and Lisburne when substantial numbers of pairs fledged two chicks and growth rates of second chicks were high (Table A3). In 1979, ice retreat in the northeastern Bering Sea was exceptionally early; SIC in mid-May was the lowest during the study period. Also, winter/spring SSTs in the eastern Bering Sea in 1979 were the warmest on record during the period 1948–2010 (Brown & Arrigo 2013).

Only one year, 1983, exhibited a notable exception to the pattern of earlier breeding and higher productivity following earlier ice retreat and warmer spring temperatures. In 1983 spring conditions were very warm, nest numbers were high and breeding was the earliest we observed; the median hatching date was 11 July. However, productivity was mediocre, and growth rates of chicks were significantly lower than in any other year in which we weighed chicks. Although chick diets appeared typical (Springer *et al.* 1987), the slow growth rate of chicks indicates that either food availability near the colony was low, necessitating longer parental foraging commutes, or that peaks in timing of food availability and needs of growing nestlings were mismatched (e.g. Both *et al.* 2006). Also, the very strong El Niño of 1982-1983 — which may have led to BLKI breeding failures at several colonies in the Gulf of Alaska and on St. George Island, as well as die-offs of BLKIs across a large region of the Gulf of Alaska and the southeastern Bering Sea in August and September 1983 (Hatch 1987) — may have affected food webs as far north as Norton Sound.

Key prey of BLKIs breeding at Bluff, the largest BLKI colony in Norton Sound, include Pacific sandlance *Ammodytes hexapterus* and saffron cod *Eleginus gracilis* (Springer *et al.* 1987). These and other forage fishes of BLKIs, however, have received little study in Norton Sound. In 1976 and 1977 sandlance dominated catches in beach seines in waters near Bluff and also in nearby Golovnin Bay (Barton 1979). In July 2002, sandlance and larval Pacific herring *Clupea pallasi* were the most abundant fishes caught in mid-water trawls near Bluff (Dragoo 2006). Although the coupling of productivity of BLKIs to abundance of sandlance is well-documented in the British Isles (e.g. Frederiksen *et al.* 2004, 2005; Rindorf *et al.* 2000, Wanless *et al.* 2007), little is known about annual variability in sandlance abundance and availability in Alaskan waters, where there is no commercial fishery. However, the appearance of sandlance nearshore in the eastern Chukchi Sea has been linked to warming water temperatures in summer and the development of zooplankton prey populations (Springer *et al.* 1987). Timing of breeding of BLKIs advanced and BLKI productivity increased from one year to the next in the late 1970s at capes Thompson and Lisburne in conjunction with increases in the numbers and body size of sand-lance in their diets and earlier retreat of sea ice (Springer *et al.* 1984).

In summers following warm springs, key prey species of BLKIs, particularly sandlance, are apparently much more abundant near the colony, appearing earlier and persisting longer. For example, foraging flocks of BLKIs, presumably taking sandlance, were observed near the colony throughout July and early August in 1978, a year when breeding was early and productivity was high, but not until August in 1977, a year when breeding was delayed and productivity was low (Drury & Ramsdell 1985).

As demonstrated by numerous highly significant correlations of both breeding chronology and productivity with climatic and oceanographic indices (Table 1), BLKIs at Bluff responded strongly and quickly to environmental conditions in late spring each year. We did not find a biennial pattern in timing of breeding or productivity, as documented for BLKIs and other species of seabirds on the Pribilof and Aleutian islands, possibly due to the competitive impact of pink salmon *Oncorhynchus gorbuscha* on prey availability there (Springer & van Vliet 2014; see also Zador *et al.* 2013). Also, we found no trend in timing of breeding at Bluff in 1975–2008. In contrast, breeding became progressively earlier on both St. Paul and St. George islands during this period (Byrd *et al.* 2008).

Chick survival during severe storms

In two years on Middleton Island, Alaska, growth and survival of BLKI chicks were largely unaffected by storms with high winds, with speeds up to about 8 m s^{-1} (Elliot *et al.* 2014). During a storm with high winds and rain in late August 1990, when we recorded numerous disappearances of nearly fledged chicks at Bluff (but could not ascribe those losses to successful fledging or mortality), winds at Cape Thompson peaked at 22–25 m s^{-1} on 26–27 August but had no impact on survival of nearly fledged chicks (Sharp 1993). Similarly, during the severe storms in August 1998, when high numbers of nearly fledged chicks died at Bluff, there was no elevated mortality of BLKI chicks in study areas at Cape Lisburne, although winds also were extreme there on the same days (DGR, pers. obs.). Our findings of high chick mortality during storms at Bluff seem to contradict observations at other colonies. In 1976, losses of eggs and chicks at Bluff were high but generally not associated with storms, suggesting low food availability for breeding adults; however, nest success was highest in protected areas (e.g. mainland side of sea stacks), suggesting direct effects of storms on breeding success as well (Steele & Drury 1977). The shoreline at Bluff generally faces south, and most cliffs face west, south or east. Wind direction in the severe storms during the chick period varied between southwest and southeast, so most cliff faces and nests at Bluff may be more directly exposed to driving rain, winds and ocean spray than those at other colonies.

The elevated mortality rate of chicks during severe storms contradicts our assumption that daily survival rates during the chick period were the same (1) during the period of our observations and (2) between the end of our observations and fledging in the years when our observations ended before the fledging period. In 1977, 1979, 2000 and 2006 no severe storms occurred during our observations. However, storms did occur between the end of our observations and the completion of fledging. For those years, we likely somewhat overestimated survival to fledging of later-hatching broods. No other severe storms occurred between the end of observations and end of fledging, except in years when breeding failures were already complete (1984, 1985, 1999 and 2001); thus, we believe our assumption of constant rates of brood mortality in estimating fledging numbers generally was justified, particularly for most years when there were no severe storms with high winds and rain throughout the chick period.

Braun & Hunt (1983) documented increased mortality of second chicks in 2-C broods during storms. Thus, our estimates of survival of second chicks to fledging would be biased high if storms occurred after our departure and before fledging. However, very few second chicks were still alive when our observations ended in most years (Table A1). In 1979, the only year when we estimated that high numbers of second chicks fledged, a storm on 25–26 August occurred between the end of our observations and the end of the fledging period. Although this storm could have increased mortality rates of second chicks in the latest-hatching broods, it is also possible that parents were preferentially feeding second chicks late in the chick period in that year (Robertson *et al.* 2015), as growth rates of second chicks were high, equaling those of first chicks, during our observations.

Adult attendance at nests during the chick period

Throughout the chick period, BLKI parents typically alternate their attendance at the nest, one parent attending while the other is foraging. Parents may not be absent at all during the nestling period, or their absence may start when chicks are about two weeks old, progressively increasing until fledging. Brood neglect is more frequent when the chicks are undernourished (Coulson & Johnson 1993, Roberts & Hatch 1993, Wanless & Harris 1989, 1992). Gill *et al.* (2012) experimentally demonstrated that well-fed parents did not leave their broods unattended but that control parents left their broods unattended for progressively more time starting 15 d after hatching. Kitaysky *et al.* (2001) implanted adult and nestling BLKIs with corticosterone to match conditions during food shortages and found that treatment adults spent more time away from the nest, leaving their broods unattended.

From cliff-top vantage points at Bluff on days of good visibility, we typically saw several foraging flocks of BLKIs near the colony, presumably feeding on sandlance, during the chick period in years of moderate to high productivity. We also rarely recorded unattended broods during our nest observations in those years. However, on days of widespread absences in 2004–2008, we observed no foraging flocks even when visibility was excellent, suggesting those absences were due to food shortages near the colony; productivity was low to moderate in 2005–2008, although high in 2004 (Fig. 4).

Differences among colonies in breeding chronology

Although hatching chronology varied significantly among colonies, the magnitude of the differences was remarkably low, given that arrival dates of BLKIs at northern colonies are likely several weeks later than at the Pribilof Islands. BLKIs are present near the Pribilof Islands around the spring equinox (Orben *et al.* 2014, 2015). BLKIs first arrived at St. Lawrence Island, northern Bering Sea, on 9 May 1953 and 11 May 1954 (Fay & Cade 1959) and at Little Diomede Island, Bering Strait, on 15 May 1953 and 14 May 1958 (Kenyon & Brooks 1960). At Cape Thompson BLKIs arrived on 21 May1960, were first seen on the cliffs on 25 May, and first eggs were recorded on 21 June; in 1961 BLKIs were first seen on the cliffs on 22 May and first eggs were recorded on 25 June (Swartz 1966). Swartz (1966) reported first hatching on 17 July 1960, a day earlier than the earliest recorded in 1976–1995, and on 22 July 1961. Although there are no other published records of arrival dates at these and other northern colonies, personnel at Cape Lisburne often saw BLKIs near the colony in early May in the 1990s and early 2000s (pers. comms. to DGR), suggesting that arrival usually occurs in early May, not only at northernmost Cape Lisburne, but also at Cape Thompson and Bluff. Nonetheless, arrival dates in early May would represent a delay of about six weeks compared with arrival dates on the Pribilof Islands, yet the differences in breeding chronology between the Pribilof Islands and Cape Lisburne averaged only 10 d.

Extent and pattern of retreat of the pack ice likely drive patterns in arrival dates. The southern edge of the continental shelf typically defines the maximum extent of sea ice in the region. During 1953–1981 the ice edge, defined as the maximum extent of 50% SIC, extended beyond St. George Island in <25% of those years. During the same period, the ice edge extended well south of Cape Peirce in 75% of those years (LaBelle *et al.* 1983). Although we have not found a similar analysis for the period 1975–2008, these patterns suggest that BLKIs likely arrive at Cape Peirce a few weeks later than at the Pribilof Islands, yet nesting averaged significantly earlier at Cape Peirce. Similarly, sea ice retreat is about four weeks later near Bluff than at Cape Peirce (LaBelle *et al.* 1983), but breeding lagged only 11 d on average. Thus, breeding began relatively early along the Alaska mainland coast compared to the Pribilof Islands, and progressively earlier relative to ice retreat at more northern colonies along the Alaskan coast of the Bering and Chukchi seas.

Differences in productivity among colonies

At St. Paul and St. George islands and Cape Peirce, observations extended through the fledging period each year, resulting in robust measures of productivity. In contrast, there were relatively few years when observations extended into the fledging period at Bluff, none at Cape Lisburne, and only two (1988 and 1990) at Cape Thompson. Consequently, our estimates of productivity using estimated ages of chicks and daily survival rates until fledging are relatively imprecise for those colonies. At Bluff, we likely somewhat overestimated productivity in 1977, 1979, 2000 and 2006, years when severe storms occurred late in the fledging period. On the other hand, we probably slightly underestimated productivity in the years 1995–2008 (except 1998 and 2001), when we estimated ages using Ramsdell & Drury's (1979) age classifications. This method, on average, underestimated ages by 3 d relative to ages estimated from growth rates, and thus overestimated the number of days remaining until fledging. However, this bias did not appear to be consequential in our comparisons of productivity among colonies, as estimated productivity averaged relatively high at Bluff (Table 2).

Annual productivity was significantly higher at Bluff and Cape Lisburne than at Cape Peirce. The difference between Bluff and Cape Peirce could be due to higher intraspecific competition for food at Cape Peirce because there are several other large BLKI colonies nearby (see Hunt *et al.* 1986, Ainley *et al.* 2003, but also see Frederiksen *et al.* 2005); estimated numbers of individuals at nine neighboring colonies within 50 km of Cape Peirce total 97 155, whereas 79% of the BLKIs in Norton Sound are at Bluff (US Fish and Wildlife Service 2012). Additionally, the difference in relative egg-laying dates of murres and BLKIs at Cape Peirce, where BLKIs breed earlier, and Bluff, where murres breed earlier, may lead to higher predation on BLKI eggs by ravens at Cape Peirce. Thus, both higher intraspecific competition for food and higher predation on eggs at Cape Peirce could contribute to lower productivity there. Similarly, either lower predation rates on eggs and chicks of BLKIs or higher *per capita* food availability could account for higher productivity at Cape Lisburne than at Cape Peirce, but studies there to date provide no basis to favor either option.

Although we found no significant difference in productivity of BLKIs breeding on St. Paul and St. George islands using the ANOVA of ranks, Renner *et al.* (2014:258) reported significantly higher nest success (fledging of one or more chicks) on St. Paul using a generalized linear mixed model (GLMM) analysis. On the Pribilof Islands, there are no breeding ravens and Glaucous-winged Gulls *L. glaucescens* have all but disappeared (Kenyon & Phillips 1965), so the differences in productivity between these two islands are most likely food-related. For example, the difference could be due to different foraging environments or higher *per capita* competition on St. George, where numbers of piscivorous seabirds vastly outnumber those on St. Paul.

Production processes and BLKI reproduction at coastal and offshore colonies

Differences between coastal and offshore colonies in patterns of BLKI productivity could be related to differing production processes in Alaska Coastal Water compared with those in the Middle Shelf Domain. Water depths in the Alaska Coastal Water zone are shallow, generally <30 m (Coachman *et al.* 1975, Kinder & Schumacher 1981a,b). In this zone, small-bodied copepods and meroplankton are the dominant zooplankton, and the key prey of sandlance (Cooney 1981, Springer *et al.* 1987). Their secondary production is decoupled from the spring bloom and dependent on warming water temperatures in early summer for reproduction and growth (Cooney 1981, Springer *et al.* 1989, Springer & McRoy 1993). In turn, sandlance is a key prey species of BLKIs at all coastal colonies (Springer *et al.* 1984, 1987, A.M. Springer, unpubl. data). Thus, secondary production is likely higher in years of earlier ice retreat and warming in this zone. Geographic continuity and coupling of production processes in Alaska Coastal Water are enhanced because this water mass retains its integrity as it flows north from the southern Bering Sea to the northern Chukchi Sea, advecting plankton entrained in its flow (e.g. Springer *et al.* 1989). Consequently, we would expect earlier breeding and higher productivity of BLKIs at all of these widespread coastal colonies in years of earlier warming.

At all four coastal colonies (Bluff, capes Peirce, Thompson and Lisburne), breeding chronology of BLKIs was earlier in years when sea ice retreated earlier and spring temperatures were warmer; at Bluff and Cape Lisburne, productivity also was higher in those years (Table 5). In addition, positive correlations in timing of breeding between Bluff and Cape Peirce and productivity between Bluff and both Cape Peirce and Cape Lisburne (Table 3) suggest widespread continuity and commonality in seasonal development of food webs and foraging opportunities in Alaska Coastal Water for breeding BLKIs.

St. Paul and St. George islands are in a much different oceanographic zone, near the outer edge of the Middle Shelf Domain with water depths of 75–100 m. Hunt *et al.* (2011) proposed that secondary productivity in this zone is higher in cold years, when sea ice retreats late and the spring bloom occurs at the ice-edge, than in warm years, when ice retreats early and the bloom occurs in open waters. In cold years, production and energy density of larger herbivorous zooplankton, particularly calanoid copepods *Calanus* spp. and euphausiids *Thysanoessa* spp. are higher (Baier & Napp 2003, Coyle *et al.* 2011, Eisner *et al.* 2014). In turn, *C. marshallae* and euphausiids are keys to the transfer of carbon and energy to higher trophic levels, such as walleye pollock *Gadus chalcogramma*, a staple in the diets of BLKIs at the Pribilof Islands (Coyle *et al.* 2011, Heintz *et al.* 2013, Hunt *et al.* 1981, Paredes *et al.* 2012, 2014, Renner *et al.* 2012). This pattern provides a plausible causal basis for earlier breeding and higher productivity of BLKIs on the Pribilof Islands when winter and spring SSTs are colder and winter SIC is higher (Byrd *et al.* 2008). However, Brown & Arrigo (2013) found that the spring bloom in this region consistently occurred in early to mid-May and that primary productivity was higher in years of early ice retreat when the spring bloom occurred in warmer, open water. Although their analyses did not include evaluation of the importance of under-ice or ice-algal production that would be enhanced in years of late ice retreat, Brown & Arrigo (2013) suggested the relationships proposed by Hunt *et al.* (2011) should be re-evaluated.

On St. George Island, BLKI productivity was higher in years when winter SIC was higher (Byrd *et al.* 2008, Table 5). Also, Byrd *et al.* (2008) reported that breeding was later on both St. Paul and St. George when winter SSTs were warmer and on St. Paul when spring SSTs were warmer, using "detrended" values (residuals of quadratic regression analyses on year) for timing of breeding. Thus, these analyses suggested that timing of breeding was later and productivity lower when winter and spring conditions were warmer, in apparent contrast to the relationships for Bluff.

Strong positive correlations of both timing of breeding and productivity of BLKIs on St. Paul Island and at Bluff appear to contradict the expectation of earlier breeding and higher productivity in warmer conditions at coastal colonies and in colder conditions at the Pribilof Islands (Byrd *et al.* (2008). However, on St. Paul breeding chronology was not correlated with the environmental indices we considered, and productivity was higher in years when SIC in the northeastern Bering Sea in mid-May was lower and May SST in the southeastern Bering Sea was warmer, similar to Bluff. Both timing and productivity of BLKIs on St. Paul were strongly, positively and independently (statistically) correlated with timing and productivity on St. George and at Bluff. St. George is much closer to the shelf break (~45 km from the 200 m isobath) than St. Paul (~100 km). This results in different foraging opportunities in shelf, shelf edge and basin habitats for BLKIs breeding on these two islands. For example, in 2008–2010, BLKIs on St. Paul foraged more in shelf waters and less in basin waters beyond the shelf break than those on St. George, and in shelf waters they foraged predominantly on age-1 walleye pollock and sandlance; foraging ranges of BLKIs breeding on the two islands did not overlap (Paredes *et al.* 2012, 2014). BLKIs on St. Paul relied more on nearby shelf waters than on more distant shelf edge or basin waters; this may contribute to the positive and significant correlations of timing and productivity with BLKIs at Bluff.

Recent studies have suggested that breeding chronology and productivity of BLKIs on the Pribilof Islands may not be coupled to winter and spring conditions following the patterns shown in Byrd *et al.* (2008). Satterthwaite *et al.* (2012) found no relation between BLKI productivity on the Pribilof Islands and SIC, and they suggested that either the different time periods (1984–2008 versus 1975–2005 in Byrd *et al.* [2008]) or the different SIC metrics the two studies used could account for this difference. Satterthwaite *et al.* (2012) used the same Ice Cover Index (ICI) as we did in this study, and we also found no correlations between ICI and breeding chronology and productivity for the Pribilof Islands, or any other colony, during the period 1975–2008 (Table 5). For the periods when we have data for SIC indices used in both of these studies, ICI was significantly ($P < 0.005$) correlated with both $\mathrm{SIC_{DJF5762}}$ and $\mathrm{SIC_{DJF5560}}$, the SIC indices used by Byrd *et al.* (2008) but did not account for substantial variability in either ($r^2 = 0.15$ and $r^2 = 0.33$, respectively). This indicates that the different metrics of SIC used in these two studies provided conflicting insights.

Satterthwaite *et al.* (2012) also found a weak positive association between productivity of BLKIs on the Pribilof Islands and their SST index (Summer Pacific Decadal Oscillation) and suggested that BLKI productivity may be higher when SSTs in nearby waters are warmer; Byrd *et al.* (2008) found no significant correlations between BLKI productivity and summer SST (also see Table 5). Renner *et al.* (2014) found positive correlations ($P < 0.10$) of BLKI productivity on St. Paul Island with their spring SST index and of productivity on both islands with their summer SST index; they suggested the patterns reported by Byrd *et al.* (2008) should be evaluated further. Our study extended the analysis period from 2005 through 2008 for indices used in Byrd *et al.* (2008). We found no significant associations of either hatching chronology or productivity of BLKIs on the Pribilof Islands with their, or any other, SST indices we examined, but we also found higher BLKI productivity on St. George Island in years of higher winter SIC ($\mathrm{SIC_{DJF576}}$; Table 5), as reported in Byrd *et al.* (2008).

Renner *et al.* (2014) also used a GLMM analytical approach to model lagged associations of BLKI productivity on the Pribilof Islands and found that productivity was higher when productivity the previous year was higher. Zador *et al.* (2013) used a different analytical approach and first computed principal component (PC) scores for timing of breeding and productivity of BLKIs, Red-legged Kittiwakes *R. brevirostris*, Common Murres and Thick-billed Murres *U. lomvia* breeding on the two islands. They then examined relationships of PC1 (interpreted as an index of timing of all four species and productivity of murres on both islands) and PC2 (an index of productivity of both kittiwake species on both islands). For PC1 (timing) they found significant same-year relationships only with their wind-mixing index: breeding was later when wind-mixing was stronger. Timing also was significantly correlated with bottom temperatures and SSTs, but with a lag: breeding chronology was later one to two years after SSTs and bottom temperatures were warmer. PC2 (kittiwake productivity) was significantly correlated with the IRI two years earlier: productivity was lower when IRI was later two years earlier. In years of later ice retreat, the spring bloom occurs at the ice edge (Brown & Arrigo 2013, see above), leading one year later to high abundance of age-1 pollock (Coyle *et al.* 2011, Hunt *et al.* 2011) and thus high productivity of kittiwakes (Zador *et al.* 2013). Because age-1 pollock can be a key prey for successful breeding of kittiwakes on the Pribilof Islands, and age-2 pollock are too large for kittiwakes to capture and consume, this result suggests carryover effects from one breeding season to the next in adult physiological condition. That is, in a year when age-1 pollock are more abundant, kittiwakes are more likely not only to breed successfully but also to enter the next breeding season in superior condition (Zador *et al.* 2013, Renner *et al.* 2014).

These studies suggest complex and possible multi-year environmental effects on timing of breeding and productivity of BLKIs on the Pribilof Islands. Thus, apparent contrasts in the responses of BLKIs to environmental conditions between the Pribilof Islands and Alaskan coastal colonies may be overstated, including the contrast between St. George and Bluff in the relationship of BLKI productivity to SIC. However, this still leaves us with no explanation for the positive correlations between the Pribilof Islands and coastal Alaskan colonies in both breeding chronology and productivity, as found in this study.

Why are breeding chronology and productivity correlated among colonies?

Both timing of breeding and productivity were significantly and positively correlated across colonies in the Bering Sea, except between Bluff and St. George, where the correlations were positive but non-significant (Table 3). These correlations cannot be explained on the basis of common correlations at these colonies with any of the environmental indices we examined (Table 5). However, all correlations between hatching chronology and environmental indices that were significant at Bluff (except May air temperature) were also significant at one or more other coastal colonies (Table 5). Furthermore, each correlation between productivity and environmental indices that was significant at Bluff (except spring SST in the Pribilof Islands region) was also significant at either Cape Lisburne, St. Paul Island or St. George Island (Table 5).

One possibility that could account for these results is if colder conditions over the deeper shelf are coupled with warmer conditions in the coastal zone. However, that is not the case; generally, colder years are colder and warmer years are warmer across the entire eastern Bering-Chukchi shelf. For example, considering the indices used in this study, SIC in the northeastern Bering Sea on 15 May was significantly and negatively correlated with SST in the southeastern Bering Sea in May ($P < 0.0001$) and with SSTs in the Pribilof Island waters in March–May ($P < 0.02$) and June–August ($P = 0.0002$). In winter, sea ice commonly covers most or all of the continental shelf. In large measure, the timing and rate of retreat of sea ice in spring drive couplings in seawater temperatures across the entire continental shelf of the Bering Sea (Stabeno *et al.* 2012).

BLKI productivity was higher at both Bluff and St. George Island in years when ice retreated earlier, suggesting that there may be unexpected commonalities in seasonal production processes across water masses. The $SIC_{DJF5762}$ and IRI indices were uncorrelated (r = -0.120, n = 31 years, P = 0.52), likely because this SIC index is centered on January and SIC typically peaks much later, in March, shortly before ice retreat begins. Although correlations between productivity at other colonies and the IRI were non-significant, all were negative (Table 5), suggesting that BLKI productivity in years of earlier ice retreat may be higher throughout the entire region. Although these results are consistent with Brown & Arrigo's (2013) findings of higher primary productivity in years of earlier ice retreat across the continental shelf of the eastern Bering Sea, they seem to be inconsistent with patterns of secondary production in the Middle Shelf Domain (see above).

Carryover effects of the physiological condition of the adults from one season to the next also could account for positive correlations in breeding chronology and productivity at coastal and offshore colonies, as Renner *et al.* (2014:263) concluded: "Adult condition and foraging conditions during the non-breeding season may be important datasets for understanding drivers of kittiwake and murre reproductive success at the Pribilofs." Field experiments on BLKIs have documented impacts of successful breeding not only on subsequent over-winter survival but also on breeding propensity and performance in the next year (Golet *et al.* 1998, Golet & Irons 1999); in other words, long-term carryover effects of body condition. Thus, shorter-term carryover effects of body condition in late winter on subsequent breeding performance seem likely. Consequently, the positive correlations in timing of breeding and productivity of BLKIs between the Pribilof Islands and mainland coastal colonies could be due to similar physiological condition of pre-breeding adults, rather than to commonalities in seasonal patterns of food web development. If this hypothesis is correct, then we would expect positive correlations in condition indices of pre-breeding adult BLKIs at all of these colonies shortly before breeding, but no relevant studies have been conducted to date. Overlapping wintering areas, however, could lead to convergence in physiological condition of BLKIs breeding at colonies throughout the Bering and Chukchi seas.

There have been no studies of wintering areas used by BLKIs breeding at Bluff and more northern colonies; however, BLKIs from these colonies migrate south to the ice edge or beyond. Divoky (1991) documented high densities of BLKIs in March and April along the southern edge of the pack ice on the outer continental shelf, indicating pre-breeding staging in this region in early spring. With respect to wintering locations, BLKIs nesting on the Pribilof Islands, recently investigated during one year, exhibited considerable individual variation, with some BLKIs ranging widely; no appreciable overall difference was evident between BLKIs from the two islands. BLKIs from both islands wintered primarily in the central northern North Pacific Ocean south of the Aleutian Islands, and relatively few individuals wintered in the basin of the Bering Sea (Orben *et al.* 2014, 2015). If BLKIs from more northern colonies move to the same or similar areas, either during winter or in early spring, they would likely be in similarly poor or good physiological condition shortly before breeding, depending on conditions that winter. Such similarity in pre-breeding condition could lead to positive correlations in timing of breeding across water masses. Moreover, those similarities in physiological condition would likely weaken as the period lengthens between staging in late March and arrival at more northern breeding colonies. This could account for the relatively low and non-significant correlations in breeding chronology of BLKIs breeding at Cape Lisburne with those breeding at colonies in the Bering Sea.

CONCLUSION

Annual variation in breeding chronology and productivity of BLKIs at Bluff was strongly associated with annual variability in spring air temperatures, SIC and SST, suggesting BLKIs are highly responsive to regional and local conditions when they return to this colony in spring. No other colony showed such a high coupling with these climatic or oceanographic indices, some of which are focused on Bluff, suggesting that appropriate regional indices focused on other colonies could provide additional insights.

Generally positive correlations in both timing of breeding and productivity of BLKIs at Alaskan coastal colonies in the Bering and Chukchi seas likely reflect, at least in part, commonalities in food web development in Alaska Coastal Water. Similarly, strong positive correlations in both timing and productivity of BLKIs on St. Paul and St. George islands suggest couplings within the Middle Shelf Domain. Breeding is earlier and productivity is higher following warm springs with early retreat of sea ice at coastal colonies, but this pattern appeared to be reversed on the Pribilof Islands, particularly St. George. We therefore expected to find either weak or negative correlations between coastal and island colonies in both timing and productivity. However, both timing and productivity were positively correlated between coastal and offshore island colonies in the Bering Sea. These correlations could be due to commonalities in the pre-breeding physiological condition of the birds or the seasonal development of the prey base of BLKIs in these very different marine systems. Neither of these possibilities can be evaluated based on studies to date.

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