

# Combined seabird indices show lagged relationships between environmental conditions and breeding activity

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**ABSTRACT:** Ecosystem managers and policy-makers need ecological indicators that have a sound scientific basis and that can inform them about the ecological state of the marine environment. In this study, we integrate existing data on seabird reproductive performance into 2 simplified indices in the eastern Bering Sea and use these indices to test hypotheses concerning the effects of environmental conditions on this suite of predators. We used principal components analysis to integrate 17 data sets on the reproductive effort of common murres *Uria aalge*, thick-billed murres *U. lomvia*, black-legged kittiwakes *Rissa tridactyla*, red-legged kittiwakes *R. brevirostris*, and red-faced cormorants *Phalacrocorax urile*. Two strong patterns were evident in the leading principal components (PC). In general, PC1 represented the hatch timing and reproductive success of diving foragers; PC2 represented kittiwake reproductive success trends. Together, PC1 and PC2 accounted for 65.2% of the variability in the seabird reproductive performance data. Time series analysis of these indices against selected environmental variables showed significant, but in most cases, lagged relationships. Warmer bottom and surface temperatures, greater wind mixing, and higher stratification correlated with delayed and lower productivity for most seabirds up to 2 yr later. Later ice retreat was correlated with lower kittiwake productivity 2 yr later, whereas higher local abundances of age-1 walleye pollock *Theragra chalcogramma* were linked to higher kittiwake productivity the following year. Since the observable impacts of environmental forcing on seabirds may be delayed, oceanographic and prey variables may serve as leading indicators of seabird breeding activity in the eastern Bering Sea.

**KEY WORDS:** Eastern Bering Sea · Pribilof Islands · Principal components analysis · Ecosystem indicators · Common murre · Thick-billed murre · Black-legged kittiwake · Red-legged kittiwake

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## INTRODUCTION

Ecosystem managers and policy makers require ecological indicators that can inform them on the ecological state of the marine environment. Indicators should have a sound scientific basis (Frederiksen et al. 2007). Ideally, indicators should be simple to measure or produce, and mechanisms linking the indicators to other aspects of the ecosystem should be well

understood. One challenge to producing informative indicators is the need to reduce the myriad of environmental data into simpler metrics that convey general information about the status of the environment. This simplicity necessitates a fine balance between the potential to exclude important details and the potential to provide a quick and easy way to gauge ecosystem status, test mechanistic hypotheses, and define thresholds where management action is required.

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Multivariate statistics are often used to extract common signals from multiple, correlated time series in marine systems (Daskalov 2003, Frederiksen et al. 2007). Ordination techniques involve condensing the information contained in the original variables into a smaller set of components or dimensions such that there is a minimal loss of information (Hare & Mantua 2000, McGarigal et al. 2000). The new synthetic components can be used to explain unique patterns in variability, which can then be used to detect changes over time (Hare & Mantua 2000) and to quantify functional relationships between predators and prey (Boyd & Murray 2001, Frederiksen et al. 2007). Here, we investigate the utility of multivariate statistical techniques as a tool for developing a general index or indices of seabird reproductive trends in the eastern Bering Sea, Alaska, by integrating existing reproductive effort data from seabirds.

St. George and St. Paul Islands, which are the largest of the Pribilof Islands, each host a similar suite of breeding seabird species. Among these species are common murre *Uria aalge*, thick-billed murre *U. lomvia*, black-legged kittiwake *Rissa tridactyla*, red-legged kittiwake *R. brevirostris*, and red-faced cormorant *Phalacrocorax urile*. All are largely piscivorous; murre and kittiwakes also forage on invertebrates such as euphausiids and squid (Decker et al. 1995, Renner et al. 2012). These species can be further partitioned by foraging style, with kittiwakes representing surface-foragers, murre representing divers, and cormorants representing epibenthic foragers (also divers). Together, they sample a large swath of the eastern Bering Sea shelf, foraging during the summer breeding season from the nearshore (cormorants, Kotzerka et al. 2011) up to >200 km away (kittiwakes, Sigler et al. 2012). Furthermore, Pribilof seabirds have shown similar temporal trends in several breeding parameters (Byrd et al. 2008), which suggested to us that they would be good candidates for integration into a general seabird index.

Our goal was to create a multivariate index that would capture reproductive trends across species of seabirds that nest in the eastern Bering Sea, and, if successful, to use this index to test whether these trends were responsive to selected environmental indices. To reach these goals, we used principal components analysis (PCA) to identify and extract temporal patterns common to this group of seabird species breeding on the 2 islands. We then tested for within-year and lagged correlations between the strongest seabird temporal patterns and bottom-up environmental forcing factors. We hypothesized that the effects of changes in seabird food supply, or in the

physical environment that likely influence food supply, could be detected in reproductive activity up to 2 yr later based on underlying physiological mechanisms such as food-related stress, as measured by the level of stress hormones in the birds (sensu Kitaysky et al. 2007). For example, we expected that environmental conditions that affect foraging success may affect body condition, which may then affect breeding activity the following year. We deliberately chose not to focus on population data, because with long-lived species, such as seabirds, population trends occur at longer time scales than this 16 yr study would likely detect. Also, we sought to analyze seabird responses to environmental conditions that occur at shorter time scales, on the order of 0 to 2 yr, that could be detected in reproductive data more easily. We discuss what these patterns may signal in the environment and how this may be useful to ecosystem, and in particular, fisheries managers.

## METHODS

We assembled mean hatch dates (to represent phenology) and reproductive success (to represent productivity) for black- and red-legged kittiwakes, common- and thick-billed murre, and red-faced cormorants nesting on St. Paul and St. George Islands from 1996 to 2011 from US Fish and Wildlife Service reports (Klosterman et al. 2011, Thomson & Drummond 2011). This time period was chosen for the completeness of the data records for these species, although cormorant data were only available from St. Paul Island during this time period. Reproductive success values were defined as the proportion of nest sites with eggs from which chicks fledged. Black-legged kittiwakes experienced complete reproductive failure on St. George Island in 2011, so mean hatch dates were not available. For that year, we substituted the mean hatch date of black-legged kittiwakes from St. Paul Island, where they experienced very low reproductive success (0.01). This was justified as the hatch dates of this species on these islands were highly correlated in the other years ( $r = 0.95$ ,  $p < 0.001$ ).

All seabird time series were standardized to a mean of zero and standard deviation of 1 to ensure equal weighting. Hatch dates were inverted to ease biological interpretation of trends (earlier hatch dates scale with higher reproductive success in these time series: we found positive correlation coefficients for all 8 possible correlations,  $p \leq 0.05$  for 3 of these). Pearson product-moment correlation analysis was

used to test each seabird parameter for relationships among species and islands.

PCA and non-metric multi-dimensional scaling (NMDS) are 2 common multivariate ordination techniques used with marine ecological datasets (Daskalov 2003, Litzow 2006). PCA creates linear combinations of the original variables (i.e. principal components) that are oriented in directions that describe the maximum variation. NMDS avoids assumptions of linearity by using only rank order information to create a dissimilarity matrix, but is not robust to incorrect assumptions about initial conditions or dimensionality of the data. NMDS is often used when datasets have many zeros (e.g. Litzow 2000). The standardized Pribilof Island datasets contained only 1 zero and were robust to Euclidean distance; therefore, PCA methods were deemed most appropriate for developing this index.

PCAs were performed using the `prcomp` function in R v.2.15.1 (R Development Core Team 2012). The calculation is done by a singular value decomposition of the centered and scaled data matrix. The signs of the columns of the loadings are arbitrary, and so may differ between different programs for PCA. We considered the 2 leading principal components (PC1 and PC2) successful candidates for combined seabird indices if they explained a sufficient level (>20% each) of the variance in the datasets. Inspection of the time series of breeding parameters loading most strongly on each PC (loading strength  $\geq 0.2$ ) enabled interpretation of the biological meaning of the new index.

Six physical indices were examined: the North Pacific Index (NPI), an ice retreat index, mean bottom and surface temperature on the eastern Bering Sea shelf, wind mixing, and stratification. All indices were chosen based on possible mechanisms mediated through food supply that we hypothesized would influence seabird breeding activity at time scales of 0 to 2 yr. The NPI measures the strength of the Aleutian Low, an indicator of climate forcing of the Bering Sea (Trenberth & Hurrell 1994). It is defined as the area-weighted sea level pressure over the region 30°N to 65° N, 160° E to 140° W; we used winter NPI (November to March average). The ice retreat index is the number of days past March 15 when areal sea ice coverage is >10% across a section of the southeast Bering Sea (56.5 to 57.5°N, 165 to 163°W; Fig. 1). These 2 indices were chosen because of their inclusion as the key physical indices in a list of 10 broad-scale indicators of ecosystem-wide productivity in a recent ecosystem assessment of the eastern Bering Sea (Zador & Gaichas 2010). Mean

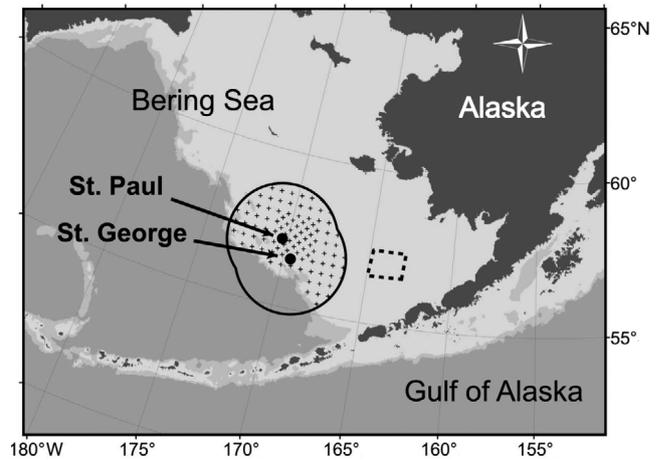


Fig. 1. Study area around St. Paul and St. George Islands in the eastern Bering Sea, Alaska. The solid line encircles the islands at 200 km. The crosses within depict bottom trawl survey locations. The dashed line approximates the area where the ice retreat index is calculated

bottom and surface temperatures are recorded during standard annual bottom trawl surveys conducted by the National Marine Fisheries Service along the eastern Bering Sea shelf during the summer (Acuna & Lauth 2008, described in greater detail below). The extent of survey coverage varies somewhat among years, so water temperatures are weighted by the proportion of the area covered each year. Mean bottom temperature was chosen to represent dynamics of the cold pool of bottom water that forms annually (Stabeno et al. 2001), and has been shown to be influential in the structure and function of the eastern Bering Sea ecosystem (Kotwicki et al. 2005, Mueter & Litzow 2008, Spencer 2008). Mean surface temperature has recently been shown to be influential in survivorship of age-0 walleye pollock *Theragra chalcogramma* (hereafter, pollock) (Mueter et al. 2011), a common prey species for Pribilof seabirds (Decker et al. 1995, Renner et al. 2012). The wind mixing index is the average cubed friction velocity for May calculated for 57.2° N, 169.7° W, near St. Paul Island ([www.beringclimate.noaa.gov](http://www.beringclimate.noaa.gov)). This provides an estimate of the rate of mixing at the base of the upper mixed layer. A stratification index, calculated from temperature and salinity data collected at a mooring located in the southeast Bering Sea shelf (56.9° N, 164.1° W) (Ladd & Stabeno 2012), provides an estimate of the strength of stratification in late summer (August). Stratification is one mechanism by which the large-scale climate forcing patterns may directly influence the ecosystem of the Bering Sea (Ladd & Stabeno 2012), including the foraging patterns of thick-billed murre (Takahashi et al. 2008).

Two measures of prey supply were also examined: the mean survey catch rates of age-1 pollock within 200 km of the islands, and the estimated age-1 pollock recruitment from the eastern Bering Sea pollock stock assessment (Ianelli et al. 2010). Age-1 (as well as age-0) pollock are commonly found in the diets of murres and kittiwakes at the Pribilof Islands (Renner et al. 2012). In the absence of a concurrent time series of age-0 pollock abundance, we estimated catch per unit effort (CPUE) of age-1 pollock, 10 to 19 cm, from standard annual bottom trawl surveys conducted by the National Marine Fisheries Service (Acuna & Lauth 2008). CPUE was calculated kg per ha; area swept (ha) was computed as the distance the trawl net was towed multiplied by the mean net width. The surveys occur during summer, starting between late May and early June and ending in late July or early August. The survey area is designed with fixed stations on a 20 × 20 nautical mile (37.04 × 37.04 km) grid. Since the survey is a combined shellfish and groundfish survey, the station density increases in areas of high historical crab abundance, such as around the Pribilof Islands. We weighted the mean CPUE calculation to reflect the increased density of these survey regions. Fish that are higher in the water column, such as some age-1 pollock, are sampled only on deployment and retrieval of the bottom trawl. Nevertheless, we used the catches of age-1 pollock as indices of their relative abundance and representative of the abundance of forage fish prey for these seabirds.

We used cross correlation functions (CCF) to test for significant relationships between the leading PCs and select environmental variables at lags of ≤2 yr. We did not consider longer lags because of the short length of the time series analyzed. Also, we did not

have proposed mechanisms for potential relationships found at longer lags.

Assessing significance of cross correlation analysis is complicated by both intra-series correlation and multiple tests. We tested each PC time series for autocorrelation. PC1 showed partial autocorrelation at a lag of 1, so we pre-whitened the PC1 time series (Pyper & Peterman 1998). We tested for autocorrelation within the environmental time series, but found none. We compared our analysis with environmental variables with and without the pre-whitened PC1 series, but found no differences, so we present results without pre-whitening. We do not account for the problem of multiple tests in this study because we consider our study to be an exploratory analysis to highlight patterns to be tested in predictive models to be developed (Botsford & Lawrence 2002). Correcting for multiple comparisons, while uncommon for CCFs, may reduce the significance of some of the lags, but the pattern would likely be the same. However, by limiting the lags we tested to ±2 yr of a 16 yr time series (12.5%), we ensured low levels of cross-correlation bias as recommended by Olden & Neff (2001).

## RESULTS

Correlations of reproductive success and mean hatch dates were high among genera and islands (Table 1). All significant ( $p \leq 0.05$ ) correlations were positive.

### Creating the multivariate indices

The PCA showed strong and distinct trends in the first 2 PCs, which together accounted for 65.2% of

Table 1. Pearson's product moment correlation coefficients ( $r$ ) of standardized reproductive success (upper right) and mean hatch dates (lower left) of seabirds breeding on St. George (SG) and St. Paul (SP) Islands, Alaska, during 1996–2011. Bird species codes are: BLKI = black-legged kittiwake, RLKI = red-legged kittiwake, TBMU = thick-billed murre, COMU = common murre; RFCO = red-faced cormorant. Values in **bold** indicate significance at the  $p < 0.05$  level

Hatch date	Reproductive success								
	BLKI SG	BLKI SP	RLKI SG	RLKI SP	TBMU SG	TBMU SP	COMU SG	COMU SP	RFCO SP
BLKI SG		<b>0.93</b>	<b>0.82</b>	<b>0.64</b>	0.27	0.12	0.01	0.09	0.02
BLKI SP	<b>0.96</b>		<b>0.80</b>	<b>0.68</b>	0.25	0.01	0.17	0.24	0.18
RLKI SG	<b>0.81</b>	<b>0.78</b>		<b>0.91</b>	0.49	0.11	0.20	0.01	0.03
RLKI SP	<b>0.74</b>	<b>0.61</b>	<b>0.81</b>		0.38	0.16	0.17	0.01	0.08
TBMU SG	<b>0.56</b>	<b>0.54</b>	<b>0.69</b>	0.39		0.09	<b>0.62</b>	0.26	0.01
TBMU SP	0.45	0.36	<b>0.60</b>	0.35	<b>0.79</b>		<b>0.51</b>	<b>0.73</b>	<b>0.65</b>
COMU SG	0.48	0.42	<b>0.65</b>	0.36	<b>0.94</b>	<b>0.83</b>		<b>0.55</b>	0.37
COMU SP	0.41	0.40	<b>0.59</b>	0.22	<b>0.78</b>	<b>0.83</b>	<b>0.85</b>		0.49

the total variance in the time series. All seabird hatch date and cormorant, common murre, and St. Paul thick-billed murre reproductive success time series were associated (loadings  $\geq 0.2$ ) with PC1, which explained 42.6% of the total variance (Fig. 2). Kittiwake and St. George thick-billed murre reproductive success time series were strongly associated with PC2, which explained 22.6% of the total variance.

The temporal patterns of the 2 indices differed (Fig. 3). Within this timeframe, PC1 exhibited weak evidence of an 8-yr periodicity with partial autocorrelation at 1 yr (Fig. 4). The PC2 index did not have significant autocorrelation but showed a sawtooth pattern with values mostly alternating between increasing and decreasing from previous years as well as overall lower mean values from 2005–2011 (Fig. 3). The sign of PC scores is arbitrary; therefore, we present the inverse of PC1 for intuitive interpretation of biological meaning (higher value equates to higher and earlier reproductive activities).

The temporal patterns of the PCA results were robust to removal of 1 to 3 yr of data at either end of the time series before recalculation. Both the variance explained and the loadings of the datasets onto each PC trend changed little (0 to 3 datasets with loadings that either increased or decreased from 0.2) with the experimental deletions. The exception was

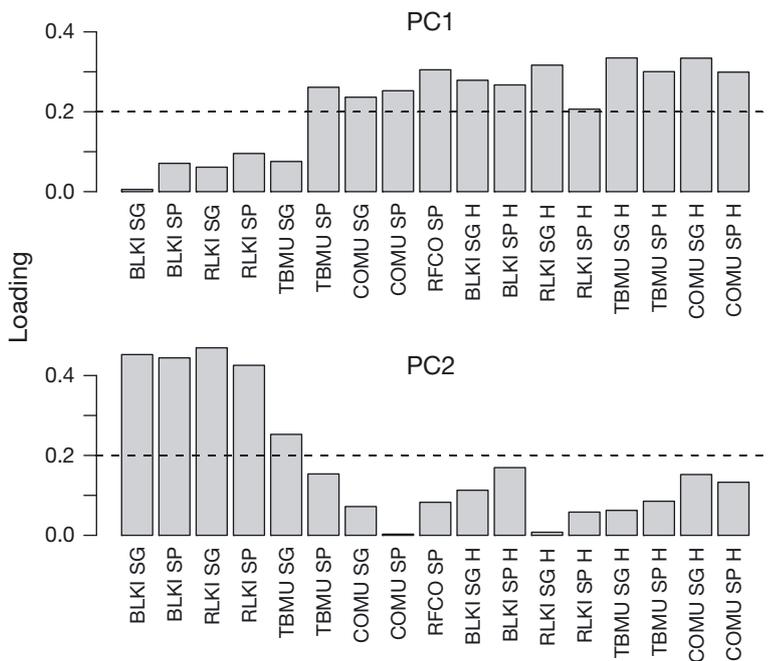


Fig. 2. Loadings (correlations) measuring the strength of association between individual time series and the first (PC1) and second (PC2) principal components. The datasets are labeled with a 4-letter bird species code and a 2-letter island code (see Table 1), and H if it is a hatch date time series

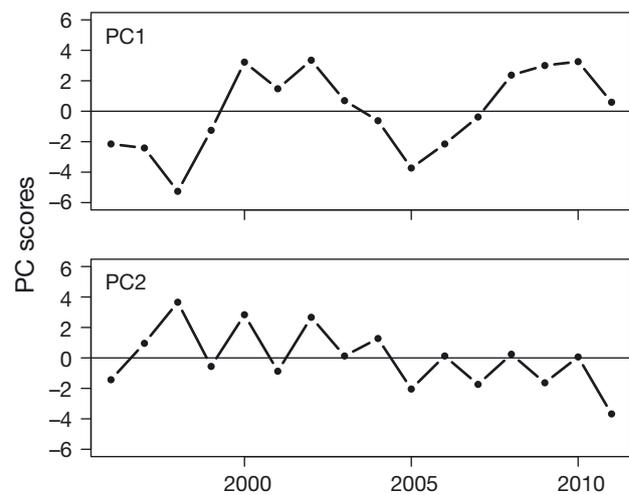


Fig. 3. PC1 and PC2 over time. Higher values of PC1 indicate earlier seabird hatch dates and higher cormorant and murre productivity (except for St. George thick-billed murres). Higher values of PC2 indicate higher kittiwake and St. George thick-billed murre productivity

the 1999–2011 time series, where there was less distinction in the loadings on the PCs. The resulting temporal pattern showed the greatest distinction from the full (1996–2011) PCA during years 2004–2007 in PC2 (Appendix 1). Whereas 2004–2005 appeared to be a break between 2 different mean states in the full PCA, this shift did not occur until 2006–2007 in the 1999–2011 time series. After 2006, there was an overall declining trend in PC2, although the sawtooth pattern remained.

### Time series analysis with environmental variables

The time series of the environmental variables investigated are shown in Fig. 5. The NPI and the ice retreat index were positively correlated ( $p \leq 0.05$ ) with each other and negatively correlated with summer bottom and surface temperature. Bottom and surface temperature were positively correlated ( $p \leq 0.05$ ). The August stratification index and summer surface temperature, but not summer bottom temperature, were also positively correlated ( $p \leq 0.05$ ). The 2011 value for wind mixing was not available at the time of the study, but May wind mixing was

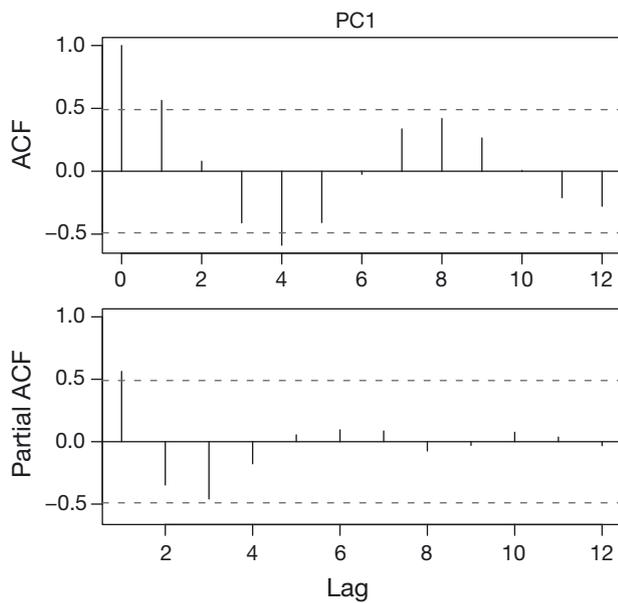


Fig. 4. Autocorrelation (ACF) depicting a weak indication of an 8-yr periodicity in the PC1 series. The partial autocorrelation shows a significant lag at 1. Lines extending beyond the dashed line indicate significance (95 % level) at corresponding lag

not significantly correlated with any of the other series during 1996 to 2010.

All significant relationships in the CCF analysis of the 2 seabird indices against the environmental variables included the seabird indices concurrent with or lagging the environmental state (Fig. 6). None included a seabird index preceding an environmental state, which would have indicated a spurious relationship of the biological variable (PC) influencing the environmental variable. Neither the NPI nor the age-1 pollock recruitment estimates were correlated with either PC at any lag tested.

PC1 was strongly negatively correlated with sea surface temperature the year before and bottom temperature 1 and 2 yr before (Fig. 6). Warmer temperatures were associated with later seabird breeding and lower reproductive success for most diving birds, but this effect was not seen until 1 to 2 yr later (Fig. 7). The wind mixing index was the only environmental variable among the ones we tested that had a significant correlation with a seabird index in the same year (Fig. 6). Higher wind mixing, and presumably deeper mixed layer, was associated with later seabird breeding and lower reproductive success for most diving birds (Fig. 7). The effect was also seen 1 yr later. In both cases, the negative relationship was strongly influenced by a few years with higher than

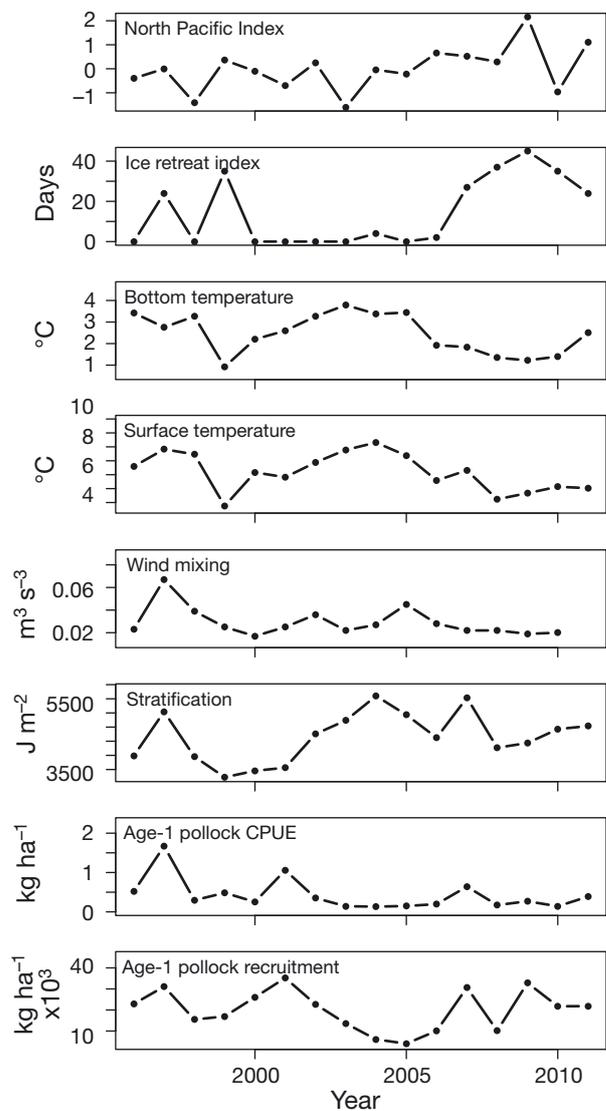


Fig. 5. Time series of the environmental variables included in the analysis with PC1 and PC2. The North Pacific Index is a climatological index that measures the strength of the Aleutian Low. The ice retreat index is the number of days past March 15 when sea ice concentration is >10% in the area contain within 56.5 to 57.5°N and 165 to 163°W. The standardized values of both the ice retreat index and North Pacific Index values are presented. Bottom temperature is the mean bottom temperature recorded during survey trawls conducted by NOAA across the entire eastern Bering Sea shelf. Age-1 pollock CPUE is the catch rate recorded during the NOAA survey bottom trawls within 200 km of the Pribilof Islands (see Fig. 1)

average wind mixing. Stratification was also negatively, albeit weakly, correlated with seabird hatch date and diving species reproductive success 1 yr later (Figs. 6 & 7).

PC2 showed a significant negative correlation with the ice retreat index at a 2 yr lag (Fig. 6), indicating

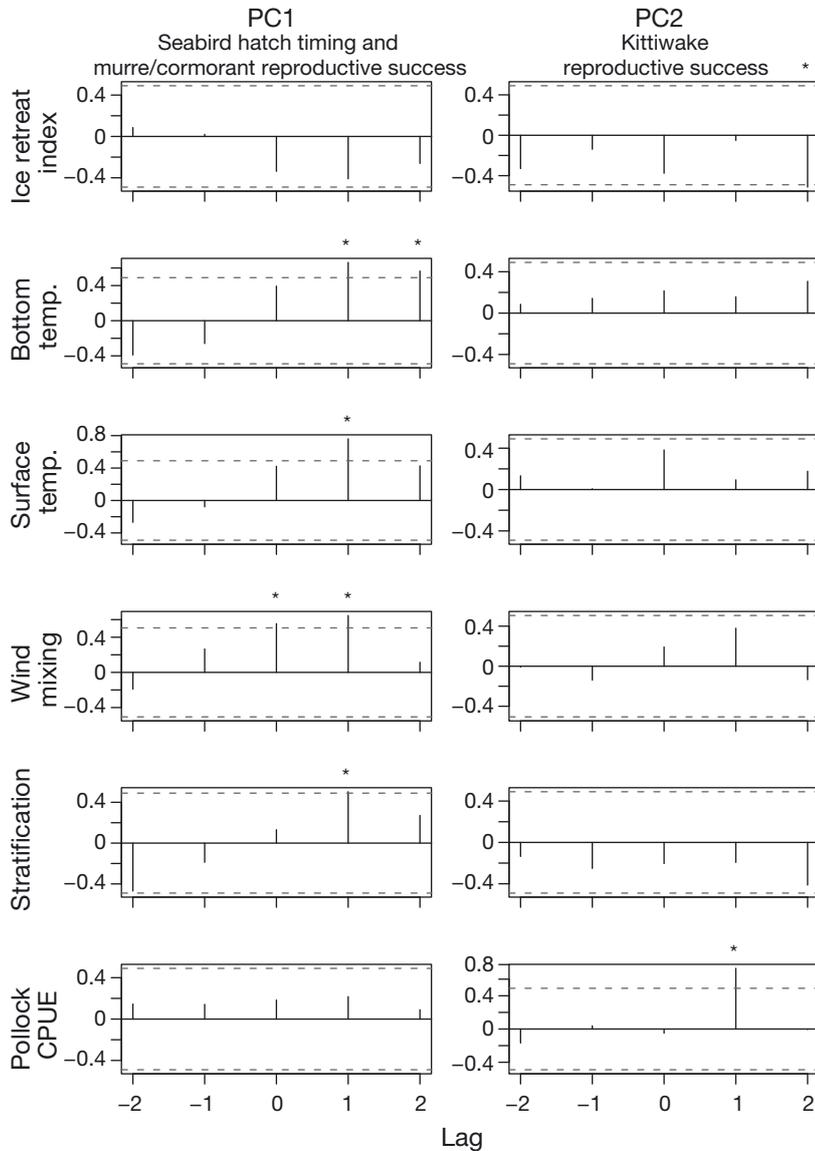


Fig. 6. Cross correlation function analysis of the environmental variables with PC1 and PC2. The x-axis indicates the number of yr (lags) that a correlation with a PC leads (positive number) or follows (negative number) the environmental variable. Lines extending beyond the dashed line indicate significance (95% confidence level) at corresponding lag and are marked with an asterisk. Direction of the line (up/down) indicates a positive or negative correlation. Note that there are no significant correlations where the PC leads the environmental variable. Non-significant results with the North Pacific Index and age-1 pollock recruitment estimates are not shown

that later ice retreat is correlated with poorer kittiwake reproductive success 2 yr later ( $r = -0.56$ ,  $p = 0.04$ ) (Fig. 8). The mean CPUE of age-1 pollock within 200 km showed a strongly significant 1 yr lag with PC2, indicating that the more age-1 pollock caught in the survey, the higher kittiwake reproductive success was the following year ( $r = 0.74$ ,  $p < 0.01$ ).

## DISCUSSION

### The indices and their value

Multivariate, or combined, indices have an important role in indicator-based ecosystem management. Managers are often confronted with an excess of indices representing many different facets of an ecosystem (Zador 2012). Combined indices serve to reduce the myriad data used to track an ecosystem without sacrificing information contained within the trends. They allow for simultaneous analysis of response variables, enabling identification of common patterns among them (Moraes et al. 2012) and reduction of Type I errors incurred by reducing the numbers of statistical tests.

In this study, we produced 2 seabird indices that together capture 65.2% of the variability in 17 seabird reproductive datasets from the Pribilof Islands, Bering Sea, thereby reducing the overall number of time series needed to represent common trends. The 2 new indicators we developed represent distinct groupings of the original datasets, allowing for simple interpretation of their trends. The co-varying trends also suggest that the birds are responding to influences at scales broader than individual islands or species, supporting the findings of Byrd et al. (2008) in their analysis of Pribilof seabird populations. Our study differs from this earlier study by combining time series with similar trends first, then testing for relationships between the underlying trends and environmental variables. Thus, we identify trophic-level species-group responses to environmental forcing, rather than

species-specific responses, which can fail to show relationships to food supply when combined indices do (Frederiksen et al. 2007).

PC1 and PC2 provide information on the reproductive performance of different groups of birds. PC1 represents a trend common to all seabird hatch dates and the reproductive success of the diving species: murre and cormorant. The one exception is the

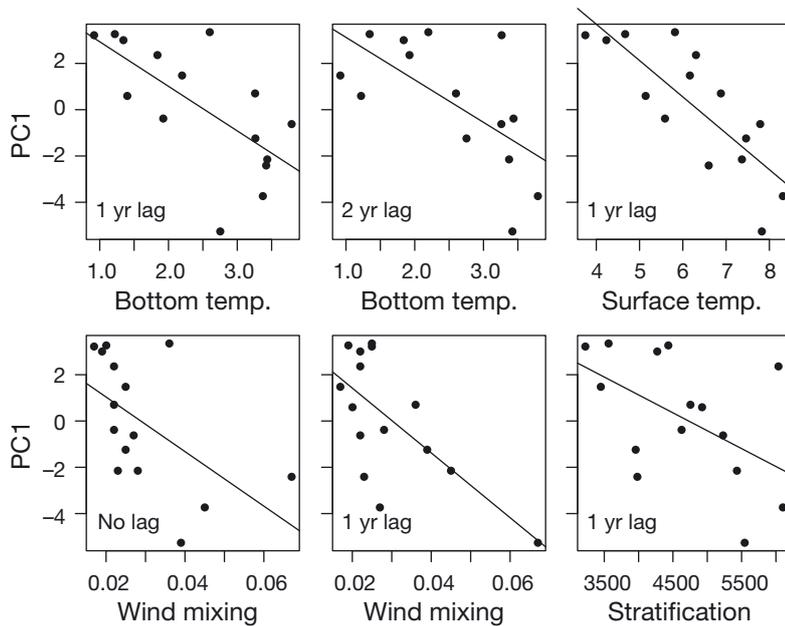


Fig. 7. Significant correlations between PC1 and bottom and surface temperature, wind mixing, and stratification at time lags indicated on plots

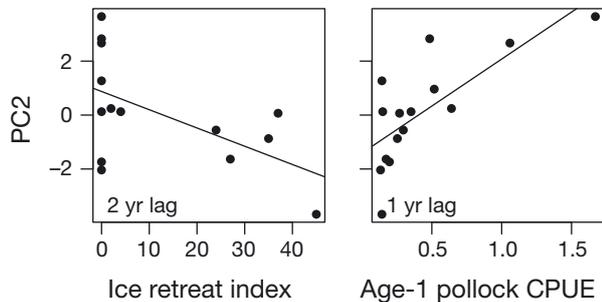


Fig. 8. Significant correlations between PC2 and the ice retreat index and age-1 pollock CPUE at time lags indicated on plots

reproductive success of thick-billed murres that nest on St. George Island, which trend with kittiwake reproductive success in PC2. Thus, we propose that PC1 serves as an index of seabird hatch timing and reproductive success of diving seabird foragers. PC2 represents a reproductive success trend for all kittiwakes and for thick-billed murres that nest on St. George Island. Thus, we propose that PC2 serves primarily as a kittiwake reproductive success index. We hypothesize that the similarity between the St. George thick billed murres and kittiwakes is a result of similarity in summer foraging ranges. Satellite tracks of chick-rearing thick-billed murres show St. George Island birds foraging off the shelf (Harding et al. 2013), similar to the foraging patterns of black-legged kittiwakes nesting on St. George

Island. Black-legged kittiwakes from St. Paul Island forage off the shelf to a limited degree, but thick-billed murres from St. Paul Island appear to forage primarily on the shelf. Also, inter-island differences in diets are more pronounced for thick-billed murres than black-legged kittiwakes (Renner et al. 2012). Tracking data for red-legged kittiwakes are not currently available, but diet data from both islands suggest that they forage off the shelf, too (Decker et al. 1995, Sinclair et al. 2008). We believe that the lack of correlation we found between kittiwake and murre reproductive success reflects the influence of differing foraging ranges and diets in this area, and results in their different PC groupings. In contrast, in the North Sea, Frederiksen et al. (2007) found correlated reproductive success, whose commonalities could be represented within a single PC, among murres and kittiwakes in an area where sandeels *Ammodytes marinus* are the common, principal prey.

We chose our dataset based on completeness of the seabird reproductive record, and this may have had the unintentional consequence of capturing a time period where a combined index was successful. However, a sensitivity analysis of the temporal patterns in the PCA was robust to the experimental deletion of up to 3 yr on either end of the time series. All but one of the significant lags we found indicated that the seabird index follows the environmental state (the exception being a within-year correlation with wind-mixing). We recognize the limits of correlation analysis and that some of the significant correlations we found may be by chance. However, the absence of any significant correlations indicating that the environmental state follows the seabird index leads us to believe our findings are not spurious.

Additionally, we tested for linear relationships, whereas nonlinear relationships between environmental variables and seabird breeding may also occur. In particular, wind mixing and water temperature have been shown to have a dome-shaped relationship to fish recruitment, where values at high or low extremes are related to poor recruitment (Cury & Roy 1989, Mueter et al. 2011). Similarly, we expect that optimal environmental windows may exist for seabird breeding, particularly when mediated through food supply (Cury et al. 2011). Visual

inspection of scatter plots of bottom temperature, wind mixing, and stratification at 0 to 2 yr lags with PC1 and PC2 showed no evidence of dome-shaped or other clearly nonlinear relationships. However, the significant linear relationship between age-1 pollock CPUE and PC2 1 yr later has some indication of an asymptotic form, which is widely seen in the relationship between seabird breeding success and forage fish abundance (Cury et al. 2011) (Fig. 8).

In both PC1 and PC2, most of the significant relationships with environmental correlates were with lags of a year, highlighting the importance of using time series methods to identify delays in relationships among variables that would not be observed if examined only in-phase (Moraes et al. 2012). Our findings are similar to those of Sandvik et al. (2008) who, using a meta-analysis, found that climatic effects most strongly related to seabird breeding success in the Atlantic to be lagged by 0 and 1 yr. In our study, seabird hatch timing and the reproductive success of red-faced cormorants and common murre (PC1) responded to water column properties (sea surface temperature, bottom temperature, wind mixing, and stratification) from the previous year. In contrast, the reproductive success of kittiwakes and St. George thick-billed murre (PC2) responded to the timing of ice retreat 2 yr earlier and to age-1 pollock CPUE 1 yr earlier. We hypothesize that there are at least 2 non-exclusive hypotheses that might explain our results. One involves environmental factors in Year 1 affecting the abundance or availability of prey in Year 2. We also hypothesize that the impacts of stress of breeding in one year, particularly if prey is in short supply, may carry over to the following year, thereby diminishing reproductive performance in the following year. There are good reasons why both of these mechanisms may be at play.

#### **PC1: an index of seabird hatch timing and cormorant and murre reproductive success**

PC1 grouped the hatch timing of all of the species of seabirds investigated, as well as the reproductive success of the red-faced cormorant and the common murre, and showed that 4 measures of water column properties—sea surface temperature, bottom temperature, wind mixing, and stratification—were significant explanatory variables. Warmer bottom and surface temperatures correlated with delayed reproduction for all species and lower reproductive success for most diving species the following 2 yr. These results indicate that although warm years may not

negatively affect seabirds in yr 0, conditions may be set up that then carry over to have negative effects in the following 1 to 2 yr. For example, age-0 pollock and small zooplankton may be abundant in the early summer of a warm year, with little impact on breeding birds, but these age-0 pollock may have low over-winter survival with the consequence that age-1 pollock will be less available to the seabirds in the following year (Hunt et al. 2011).

Spring wind mixing may have a negative effect on the timing of breeding in the same year by disrupting seabird foraging (Dunn 1973, Birkhead 1976). At the Pribilof Islands, Braun & Hunt (1983) hypothesized that the disruption of foraging by storms was the indirect cause of siblicide in black-legged kittiwakes. Kokubun et al. (2008) showed that murre targeted prey below the thermocline in 2005, a year with high wind mixing and low murre reproductive success. Wind mixing may affect hatch timing 1 yr later if it influences the vertical distribution of prey, thus influencing foraging success, body condition, and the timing of breeding in the next year.

The strength of stratification, which influences the amount of mixing that can occur for a given wind strength, is determined largely by the difference in temperature between the upper mixed layer and the bottom layer (Ladd & Stabeno, 2012). Ladd & Stabeno (2012) suggest that correlations between stratification and chlorophyll biomass and pollock recruitment that are consistent among studies (Coyle et al. 2008, Strom & Fredrickson 2008, Ladd & Stabeno 2012) provide supporting evidence of connections between the strength and timing of stratification and the productivity of the ecosystem.

We found that the timing of ice retreat does not appear to correlate with the timing of seabird breeding or the reproductive success of most diving species in the Pribilof Islands. This finding is in line with findings of Byrd et al. (2008), who found no relationship between a measure of sea ice cover and murre hatch timing or reproductive success over a longer time period at the Pribilof Islands. Our findings and those of Byrd et al. (2008) differ from those of Gaston et al. (2005), who found that years of later ice retreat in the eastern Canadian Arctic had negative effects on reproduction of thick-billed murre (delayed egg-laying, lower body condition, and lower nestling growth) and black-legged kittiwakes (delayed egg-laying, lower body condition and lower nestling survival). The timing of sea ice retreat in the southeastern Bering Sea usually occurs before seabirds have begun to occupy nest sites on the Pribilof Islands, and this mis-match in time between the retreat of ice

and the foraging of seabirds tied to nest sites may minimize its influence on hatch timing.

### **PC2: an index of kittiwake reproductive success**

The temporal trend in PC2 shows 2 patterns that may reflect biological-physical interactions occurring at different scales. The first is a general decline in reproductive success after 2005 that coincides with well-documented cycles of warmer conditions during 2001–2005 followed by cold conditions from 2007–2011 (Stabeno et al. 2007, Stabeno et al. 2012). The second is the interannual sawtooth pattern, which we suspect may be influenced by conditions that act upon the prey base.

PC2 grouped the reproductive success of the 2 species of kittiwakes on St. Paul and St. George Islands, as well as the reproductive success of thick-billed murres on St. George Island, and showed that 2 environmental covariates—timing of ice retreat and the CPUE of age-1 pollock—were significant explanatory variables. The timing of ice retreat sets the stage for the production of juvenile pollock, with late retreat and an ice-associated bloom yielding the potential for strong recruitment of age-1 pollock in the following year (Moss et al. 2009, Coyle et al. 2011, Hunt et al. 2011), an important prey for both species of kittiwakes and thick-billed murres (Hunt et al. 1996). Thus, the 2 environmental covariates for PC2 both relate to the abundance of age-1 pollock. The 1 yr lag between the time of measurement of the environmental covariate and its impact on kittiwake and St. George thick-billed murre reproductive success suggests that there is a delayed effect that is mediated through the physiology of the birds (see below), as it is unlikely that the birds capture and eat age-2 pollock due to their size.

Byrd et al. (2008) found significant positive correlations (Spearman's rank correlation at the 90% confidence level) between reproductive success of 3 of the same 4 kittiwake species-island groups used in our study (not St. Paul black-legged kittiwakes) and sea ice concentration in the preceding winter (Dec to Jan, 1975–2005). On the surface, one might expect that higher ice concentrations would lead to later ice retreat, and, thus, the Byrd et al. (2008) results would be contrary to our finding that earlier ice retreat is correlated with higher kittiwake reproductive success 2 yr later. However, the timing of ice retreat is not always closely related to ice cover, as the timing of retreat is largely dependent on the timing and strength of warm winds from the south (Stabeno et al.

2012). Additionally, the area that Byrd et al. (2008) used to calculate their sea ice concentration time series is much larger (20° longitude by 5° latitude, with the southern border at the Pribilofs) than that used for the ice retreat index in our study, and it was chosen based on a correlation map of seasonally averaged sea ice concentration anomalies and averaged reproductive success for all kittiwakes.

Kittiwakes are limited to foraging near the surface, thus limiting access to prey. Their reproductive success has been shown to be more sensitive to variations in food supply than that of diving birds, which presumably have access to prey throughout the water column within their diving range (Piatt & Nettleship 1985, Lewis et al. 2001). Since the patterns in kittiwake hatch timing vary similarly with the diving birds, we suggest that interannual variations in timing of breeding are influenced by conditions prior to the current breeding season, as was evidenced by the significant lagged relationships between water column properties and PC1 described above.

Kittiwake reproductive success was most highly correlated with local survey catch rates of age-1 pollock the year before. Age-0 and age-1 pollock are frequently found in black-legged kittiwake diets and thick-billed murre diets (Renner et al. 2012). In years when age-1 pollock were consumed, they were more prevalent than age-0 pollock in kittiwake, but not murre, diets. Age-1 pollock are important early in the summer, before age-0s are large enough to be suitable prey for the kittiwakes and murres (Hunt et al. 1996). Kittiwakes will feed on age-1 pollock when both age-0 and age-1 are present in the same prey patch (Paredes et al. 2012). Kittiwakes, thus, appear to have a preference for age-1 over age-0 pollock when compared with murres, possibly explaining why we saw a correlation with PC2, and not PC1. Also, wider-ranging kittiwakes may be better than murres at locating near-surface age-1 pollock. Lewis et al. (2001) documented the importance of both age-0 and age-1+ sandeels for kittiwakes during the breeding season; thus, forage fish production in 2 yr (current and previous) influenced reproductive success to some degree.

There is a possible second mechanism that could be responsible for the lagged relationship between environmental correlates and all kittiwake and St. George thick-billed murre reproductive success in PC2. It is likely that reproductive effort in yr 0 influences reproductive success in yr 1 as a result of the cost of reproduction in yr 0. There is extensive literature on the cost of reproduction, and how effort expended in one year may affect the survival or

reproductive success of a bird species in subsequent years (e.g. Roff 1992, Stearns 1992, Nilsson & Svensson 1996, Golet et al. 2004, Milonoff et al. 2004, Goutte et al. 2010a,b). The kittiwake and murre colonies on the Pribilof Islands are large, and there is some indication that prey availability in the vicinity of the colonies is depressed, at least in comparison with other smaller colonies in the Bering Sea where reproductive performance of the same species of seabirds is often higher (Hunt et al. 1996). If kittiwakes and murre breeding on the Pribilof Islands are stressed by insufficient prey availability when attempting to breed, then they may need to exert elevated levels of energy in attempting to fledge their young (Kitaysky et al. 2000). This elevated cost of reproduction may not only decrease over-winter survival following the breeding season. It may also result in a delayed start to the following breeding season (Schoech et al. 2009) and a reduced level of reproductive success (Milonoff et al. 2004).

Both at the Pribilof Islands and elsewhere in Alaska, increased levels of the stress hormone, corticosterone, have been observed when prey was in short supply (Kitaysky et al. 1999, 2007, Buck et al. 2007). Elevated levels of corticosterone are known to cause delayed breeding (Salvante & Williams 2003, Schoech et al. 2009, Goutte et al. 2010a), reduced hatching success (Goutte et al. 2010a), and, thus, overall reduced reproductive success. Satterthwaite et al. (2012) found that relationships between current environmental conditions and nutritional stress, as reflected in corticosterone, were stronger than relationships between current environmental conditions and productivity. We hypothesize that the 1 yr lag between the measure of age-1 pollock abundance and the breeding response of the kittiwakes and the St. George thick-billed murre are at least in part mediated through a stress response to previous breeding efforts in an area where prey may be limited.

The sawtooth pattern in PC2 may reflect prey competition with pink salmon *Onchorhynchus gorbuscha* that suppresses breeding success in years with high pink salmon abundance. Pink salmon are the most abundant salmonid in the North Pacific Ocean and Bering Sea (Ruggerone et al. 2010) and feed on zooplankton, squid, and fish (Davis et al. 2000, Kaeriyama et al. 2004). Their 2-yr life cycle leads to wide annual fluctuations in abundance, with odd-numbered years having higher abundances overall (Ruggerone et al. 2010). High pink salmon abundances have been associated with dietary shifts and reduced size at age in other salmonids (Tadokoro et al. 1996, Ruggerone et al. 2003) and reduced body

condition in seabirds (short-tailed shearwaters *Puffinus tenuirostris* Toge et al. 2011) that have overlapping diets. As kittiwake reproductive success that is reflected in PC2 is lower in odd-numbered years and there is dietary overlap between kittiwakes and pink salmon, we hypothesize that the sawtooth pattern may reflect increased prey competition with pink salmon in those years.

## CONCLUSIONS

The indicators that we have defined can inform us about the effects of past environmental conditions on seabirds nesting at the Pribilof Islands. Furthermore, the documentation of lagged effects of environmental conditions may help to predict impacts of environmental states on seabird hatch dates and reproductive success 1 to 2 yr in advance. Similarly, the hatch dates of Pribilof seabirds have been proposed as a leading indicator of sockeye salmon *Onchorhynchus nerka* returns based on correlations lagged by year of smolt ocean entry (Sydeman et al. 2008). While lagged effects of climate on seabird demography have been documented in several studies, most of these have focused on seabird population size, recruitment, and survival (Thompson & Ollason 2001, Barbraud & Weimerskirch 2003, Jenouvrier et al. 2005, Sandvik et al. 2005, 2012, Crespín et al. 2006), factors which we deliberately chose not to focus on due to the relatively short time span of this study and the relationships we chose to investigate. Others have documented equivocal results from meta-analyses of lagged effects of the North Atlantic Oscillation climate index on seabird breeding success (Sandvik et al. 2008, Sandvik & Erikstad 2008).

An advantage of our study is that we looked for relationships of environmental factors on common trends in seabirds, rather than specific relationships between species-specific individual breeding parameters. Although seabird response to environmental variability is a consequence of behavior at the individual level, by isolating common patterns among seabird populations, we were able to identify relationships to environmental conditions that may not have been detectable at the species level (Frederiksen et al. 2007).

These indices can provide fisheries managers with useful information through both their current state (most recent annual index values) and past relationships with environmental conditions. For example, a current index value indicating low reproductive success and/or late breeding that is assumed to be medi-

ated through poor food supply could indicate future poor recruitment of year classes that seabirds feed on (e.g. pollock), or a poor supply of forage fish that commercially-fished species feed on (e.g. capelin eaten by both seabirds and Pacific cod). Also, better understanding of past relationships between the seabird indices and environmental conditions could help managers to anticipate ecosystem level effects of varying ecosystem states. We see immediate utility of these indices in regional ecosystem assessments (e.g. Zador & Gaichas 2010, Zador 2012) and as part of larger research efforts to elucidate eastern Bering Sea ecosystem dynamics. The responses of Pribilof seabirds to environmental factors identified in this study may be particular to the eastern Bering Sea ecosystem as piscivorous seabirds may respond differently in other ecosystems. However, the method of isolating common trends among species and population parameters and investigating relationships to environmental factors, as shown in this and previous studies (e.g. Boyd & Murray 2001, Frederiksen et al. 2007) are applicable in other marine ecosystems.

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Appendix 1. Sensitivity analysis of the PCA with varying subsets of the input time series

