

Regionalizing indicators for marine ecosystems: Bering Sea–Aleutian Island seabirds, climate, and competitors

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ABSTRACT

Seabirds are thought to be reliable, real-time indicators of forage fish availability and the climatic and biotic factors affecting pelagic food webs in marine ecosystems. In this study, we tested the hypothesis that temporal trends and interannual variability in seabird indicators reflect simultaneously occurring bottom-up (climatic) and competitor (pink salmon) forcing of food webs. To test this hypothesis, we derived multivariate seabird indicators for the Bering Sea–Aleutian Island (BSAI) ecosystem and related them to physical and biological conditions known to affect pelagic food webs in the ecosystem. We examined covariance in the breeding biology of congeneric pelagic gulls (kittiwakes *Rissa tridactyla* and *R. brevirostris*) and auks (murrels *Uria aalge* and *U. lomvia*), all of which are abundant and well-studied in the BSAI. At the large ecosystem scale, kittiwake and murre breeding success and phenology (hatch dates) covaried among congeners, so data could be combined using multivariate techniques, but patterns of response differed substantially between the genera. While data from all sites ($n = 5$) in the ecosystem could be combined, the south eastern Bering Sea shelf colonies (St. George, St. Paul, and Cape Peirce) provided the strongest loadings on indicators, and hence had the strongest influence on modes of variability. The kittiwake breeding success mode of variability, dominated by biennial variation, was significantly related to both climatic factors and potential competitor interactions. The murre indicator mode was interannual and only weakly related to the climatic factors measured. The kittiwake phenology indicator mode of variability showed multi-year periods ("stanzas") of late or early breeding, while the murre phenology indicator showed a trend towards earlier timing. Ocean climate relationships with the kittiwake breeding success indicator suggest that early-season (winter–spring) environmental conditions and the abundance of pink salmon affect the pelagic food webs that support these seabirds in the BSAI ecosystem.

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1. Introduction

Ecological indicators play an important and growing role in understanding and managing terrestrial and aquatic ecosystems. In marine ecosystems, indicators are used to provide key information for assessments of ocean productivity and 'health' (Halpern et al., 2012). Ecosystem indicators play a role in ecosystem-based fisheries management (Cury et al., 2008; Einoder, 2009; Levin et al., 2009). Developing appropriate indicators, however, is a challenge.

In contrast to many large-scale physical indicators (Mantua et al., 1997; Sydeman et al., 2014), most biological indicators are developed at relatively small spatial scales, such as islands or single points along coastlines. Local indicators of ecosystem structure or functions are appropriate for investigating the dynamics of populations and communities within small-scale management units – such as marine protected areas or areas of special fisheries closures – but are often not appropriate to address questions pertaining to large marine ecosystems (Levin et al., 2009). Large-scale indicators are needed for understanding the complexity and regulation of large-scale pelagic food webs, and the effects of climate variability and change on pelagic ecosystem productivity and functions.

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Many, if not most, upper trophic level marine predators, such as piscivorous fish, birds, and mammals, demonstrate greater responses to ocean climate variability than do mid trophic level organisms (Kirby and Beaugrand, 2009; Chust et al., 2014). For this reason, these species may be well-suited as large-scale indicators, especially when parameters co-vary in space and time, and may be combined using multivariate statistical techniques such as Principal Component Analysis (PCA; Jolliffe, 2002). Fisheries landings have often been used as input variables for PCA-derived ecosystem-state indicators (Hare and Mantua, 2000; Beaugrand, 2004; Osterblom et al., 2007), but these data may be compromised by fishing effort, which can explain as much or more of the variability than climate or food web variability (Litzow and Mueter, 2014). Seabirds, on the other hand, are rarely the target of direct human harvest and have been put forth as reliable, near-real-time indicators of the distribution and abundance of pelagic food supplies (Cairns, 1987; Frederiksen et al., 2006; Piatt et al., 2007; Sydeman et al., 2017) and changes in marine ecosystems more generally (Durant et al., 2009; Parsons et al., 2008; Sydeman et al., 2012). As secondary and tertiary consumers, seabirds forage on mesozooplankton, such as krill and large calanoid copepods (e.g., *Neocalanus* spp.), and larger nekton such as cephalopods (e.g., squids and octopuses), small epipelagic and mesopelagic fishes (e.g., sand lance *Ammodytes* spp., capelin *Mallotus villosus*, lanternfish *Myctophidae*), and age-0 and age-1 forms of piscivorous fishes (e.g., pollock *Gadus chalcogrammus*, salmon *Oncorhynchus* spp., cod *Gadus macrocephalus*). Therefore, seabirds may provide information on the availability of these prey species. Multivariate seabird indicators of marine ecosystem health and dynamics have been developed (e.g., Sydeman et al., 2001; Frederiksen et al., 2007a; Lahoz-Monfort et al., 2013; Zador et al., 2013) and are now integrated into annual ecosystem monitoring programs such as the Commission for the Conservation of Antarctic Marine Resources (CCAMLR) ecosystem monitoring program (CCAMLR, 2014) and the Ecosystem Considerations chapter of the Stock Assessment and Fishery Evaluation Report of the North Pacific Fishery Management Council (Zador, 2014; see also <http://access.afsc.noaa.gov/reem/ecoweb/index.php>).

In the Bering Sea–Aleutian Islands (BSAI) ecosystem, Alaska, seabirds are abundant and diverse. Previously-developed multivariate seabird indicators for the Pribilof Islands (Fig. 1), host to one of the largest and most diverse seabird communities in the Bering Sea and the world, identified two modes of variability (Zador et al., 2013). One, which includes change in the phenology (timing of breeding) and breeding success (production per unit effort) of a suite of locally-breeding surface-feeding and diving seabirds, was linked to water column properties. The other represents change in the breeding success of surface-feeding kittiwakes only, was linked to sea ice conditions, and was hypothesized to fluctuate in relation to the abundance of pink salmon (*Oncorhynchus gorbuscha*), a potential competitor for prey resources. In more recent work, Springer and van Vliet (2014) demonstrated an inverse relationship between pink salmon abundance and Alaskan seabird breeding success, and suggested a role for competitive top-down control of prey.

In this study, we extend upon these studies to investigate whether temporal patterns in seabird breeding parameters are coherent across the entire BSAI ecosystem (Fig. 1), and assess whether broad-scale abiotic and biotic conditions explain modes of variability in these parameters. The breeding biology of seabirds, as upper trophic level predators, may be controlled by two processes: bottom-up climatic factors that affect primary production and food availability (Ware and Thomson, 2005), and biotic factors such as predation or competition that may also alter food webs and prey availability (Cury et al., 2000; Frederiksen et al., 2007b). In the North Pacific, recent work suggests that both of these mechanisms

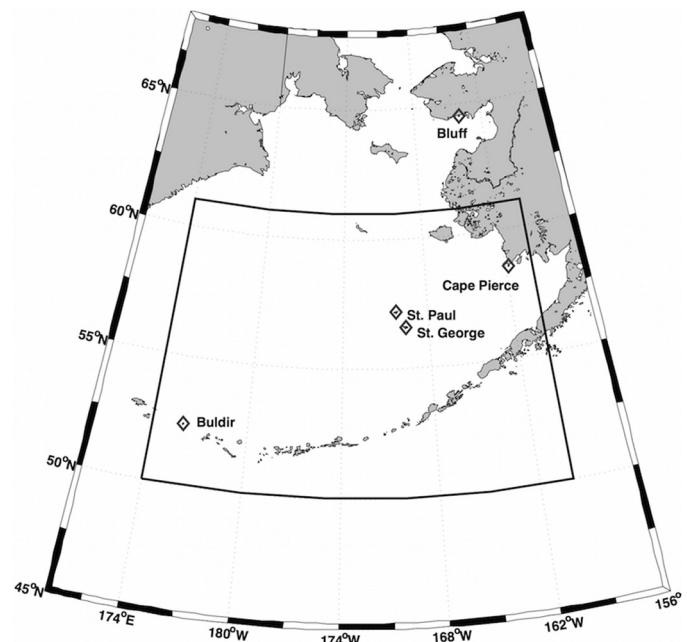


Fig. 1. Map of the Bering Sea–Aleutian Islands study area from Buldir Island in the west to Cape Peirce in the east, and Bluff to the north. The Pribilof Islands (St. Paul and St. George) are on the outer Bering Sea shelf. Monthly environmental data were obtained for the domain 50–60°N and 174°E–160°W (delineated by thin black line). All four seabird species were studied at Buldir and each of the Pribilof Islands, while only common murre and black-legged kittiwakes were studied at Bluff and Cape Peirce. Phenology and productivity were measured at all sites with the exception of Bluff, where only phenology was studied.

operate and may occur simultaneously or out of phase (Hunt et al., 2002, 2011; Litzow and Ciannelli, 2007). Our study area extends from Buldir Island in the western Aleutians, east to Cape Peirce, and north to Bluff, a coastal site in the north-eastern domain of the Bering Sea. The study area does not include the Russian coastline of the western Bering Sea. While the study sites cover a diversity of marine habitats (Piatt and Springer, 2007) affected by regional processes, we hypothesize that common variability in seabird indicators reflects large-scale physical and biological factors that cross regional boundaries. To test this idea, we 1) developed multivariate indicators of seabird reproductive parameters using murres (*Uria* spp.) and kittiwakes (*Rissa* spp.) from five sites, and 2) investigated if interannual variation in these indicators can be attributed to multivariate ocean climatic and/or biological factors. Relative to a previous study (Zador et al., 2013), we test if the apparent effects of pink salmon on seabird indicators described by Springer and van Vliet (2014) are independent or contemporaneous with climatic effects. Zador et al. (2013) also showed that the kittiwake breeding success indicator exhibited quasi-biennial variability, and that murre and kittiwake data could be combined. Here, we test whether the modes of variability described by Zador et al. (2013) are applicable across sites in the BSAI ecosystem.

2. Methods

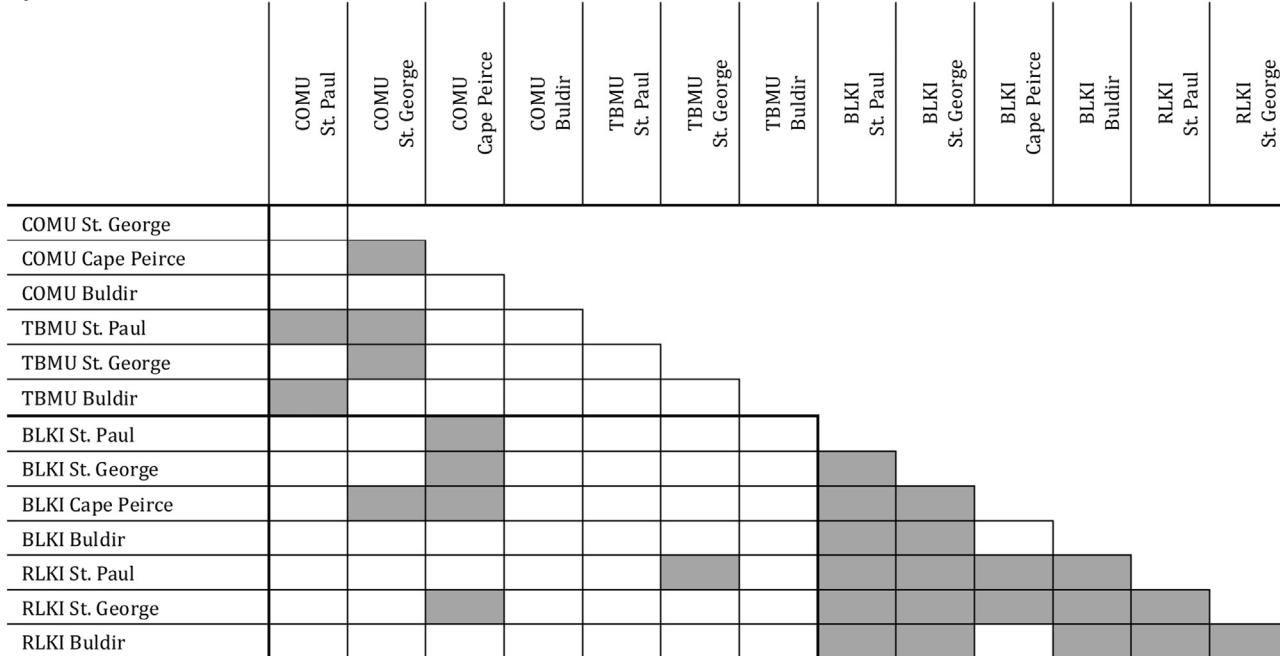
2.1. Biological data

The U.S. Fish and Wildlife Service's (USFWS) Alaska Maritime National Wildlife Refuge (AMNWR) collects and compiles data annually on seabird populations at sites scattered throughout the Gulf of Alaska, Aleutian Islands, Bering Sea, and Arctic Ocean, including information on reproductive biology, phenology (timing of breeding), and food habits (e.g., Dragoo et al., 2014). Using data from the AMNWR program and compiled by Dragoo et al. (2014),

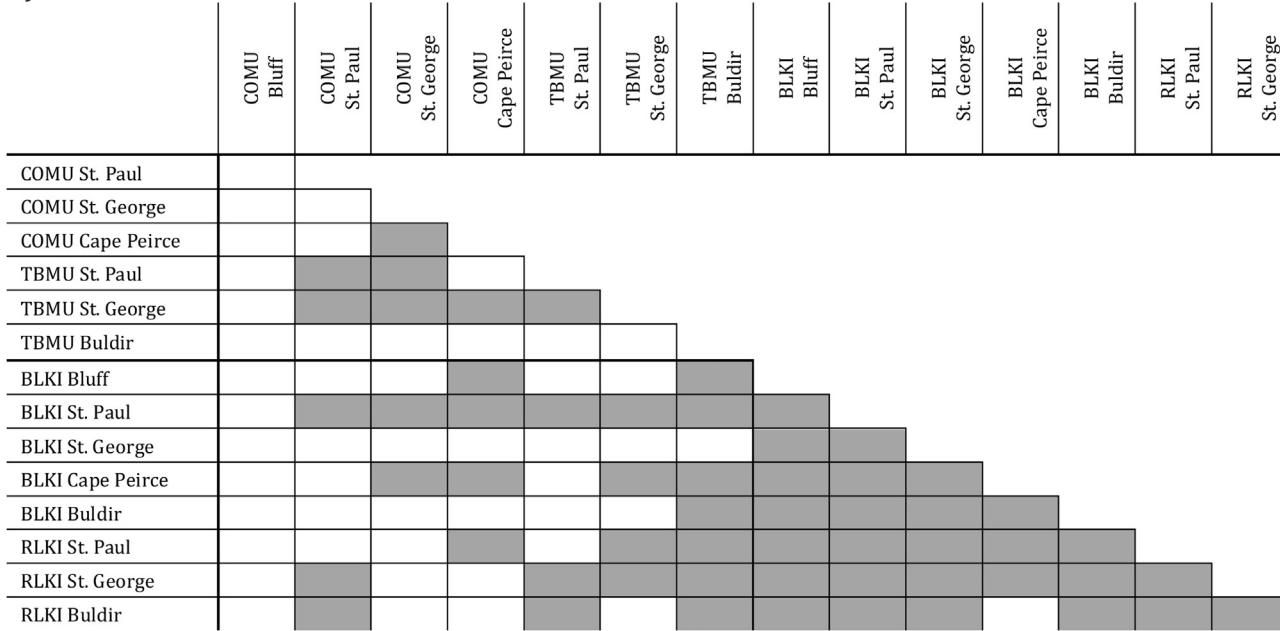
Table 1

Covariance matrix for detrended a) breeding success (1989–2012) and b) phenology (1989–2008) across species and sites, based on Spearman rank correlations. Column and row headers show species and site. COMU: common murre, TBMU: thick-billed murre, BLKI: black-legged kittiwake, and RLKI: red-legged kittiwake. Shaded cells indicate positive correlations of $p < 0.1$.

a)



b)



we modeled breeding success and phenology of four mostly-piscivorous species: common and thick-billed murre (*Uria aalge* and *U. lomvia*) and black-legged and red-legged kittiwake (*Rissa tridactyla* and *R. brevirostris*). Breeding success was defined as the number of young fledged per nest built for kittiwakes, or the number of “jumplings” per all eggs laid for murres (murres take their offspring to sea when half-grown, so this is the latest point in the nesting cycle when breeding productivity can be determined).

These numbers are roughly equivalent to the number of young produced per breeding female per year. Phenology is defined as the mean hatching date of chicks for each species at each colony in each year. Field methods for studies of murres and kittiwakes are described in detail by [Byrd et al. \(2008\)](#), [Zador et al. \(2013\)](#), [Dragoo et al. \(2014\)](#), and references therein. Briefly, individual nest sites or plots containing nesting pairs were monitored by obtaining information on the number of eggs and chicks in each nest on a regular

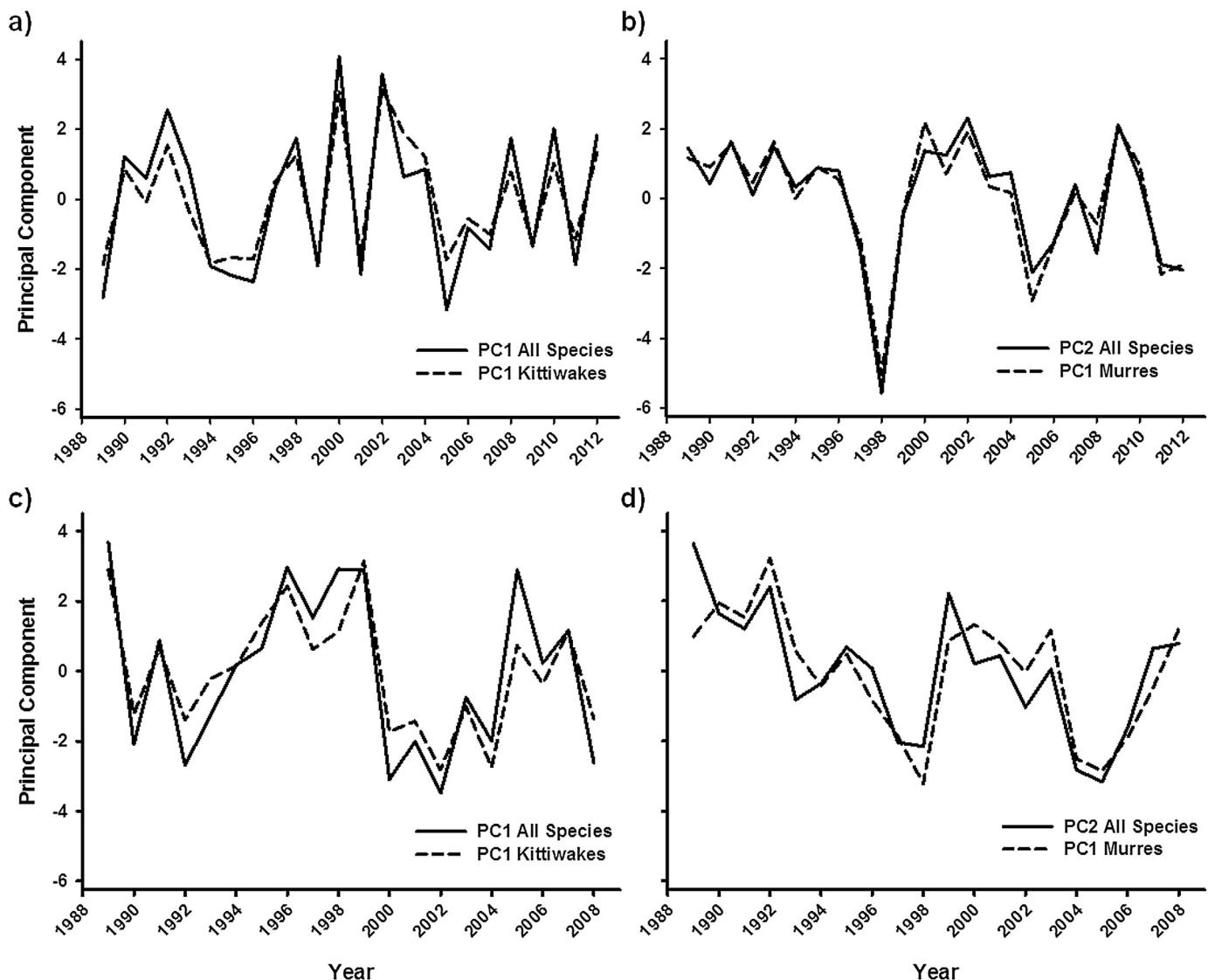


Fig. 2. Time series of seabird PCs: a) breeding success $PC1_{\text{allspecies}}$ and $PC1_{\text{kittiwakes}}$; b) breeding success $PC2_{\text{allspecies}}$ and $PC1_{\text{murres}}$; c) phenology $PC1_{\text{allspecies}}$ and $PC1_{\text{kittiwakes}}$; and d) phenology $PC2_{\text{allspecies}}$ and $PC1_{\text{murres}}$ (sign inverted).

schedule throughout each breeding season. Information on pink salmon abundance (defined as the total number of adult fish caught – assuming constant fishing effort – plus escapement each year; referred to as “run size”) was obtained from the supplementary material of Springer and van Vliet (2014).

We selected sites in the Bering Sea with complete or nearly complete time series. We selected 1989 as our first year because (with the exception of the Pribilof Islands, St. Paul and St. George) data before that year were very limited (Dragoo et al., 2014). This year also corresponds to a putative ecosystem regime shift that began in 1989–1990 in the North Pacific (Hare and Mantua, 2000; Litzow and Mueter, 2014) when fundamental ecosystem relationships may have changed (M. Litzow, pers. comm.). Phenology data were not available in recent years for some sites (i.e., Bluff, Cape Peirce), so our analysis of this parameter ends with data in 2008, the most recent year of a complete data set. However, breeding success data were available and analyzed for all sites through 2012.

For deriving multivariate indicators, we used PCA, but PCA requires no missing values for computation (Jolliffe, 2002). Therefore, for the time periods 1989–2012 and 1989–2008 (breeding success and phenology, respectively), we used multiple imputation (Little and Rubin, 2002) to estimate missing values. A total

of 5% of the breeding success data and 10% of the phenology data were missing. For each time series (e.g., black-legged kittiwake breeding success at Buldir), we conducted 10 imputations for each missing variable (each of 1000 iterations) and used an average of those imputations as our estimate for that year. The completed data matrix on phenology included 20 years of data (1989–2008) for four species and five sites (Fig. 1). The matrix for breeding success included 24 years (1989–2012) for four species and four sites (breeding success data were not available for Bluff; Fig. 1). All data summaries and analyses were performed on these imputed matrices.

2.2. Environmental data

To examine how seabird indicators reflect ocean-climate, we collated monthly environmental data on physical conditions in the Bering Sea known to influence the ecosystem (Hunt et al., 2002, 2011; Coyle et al., 2011; Stabeno et al., 2012; Hermann et al., 2013): sea surface temperature (SST), sea ice cover on the eastern Bering Sea shelf (ICE in % cover), sea level pressure (SLP), and meridional (V) and zonal (U) wind speed. We included wind speed because it affects water column stratification and upwelling, both important

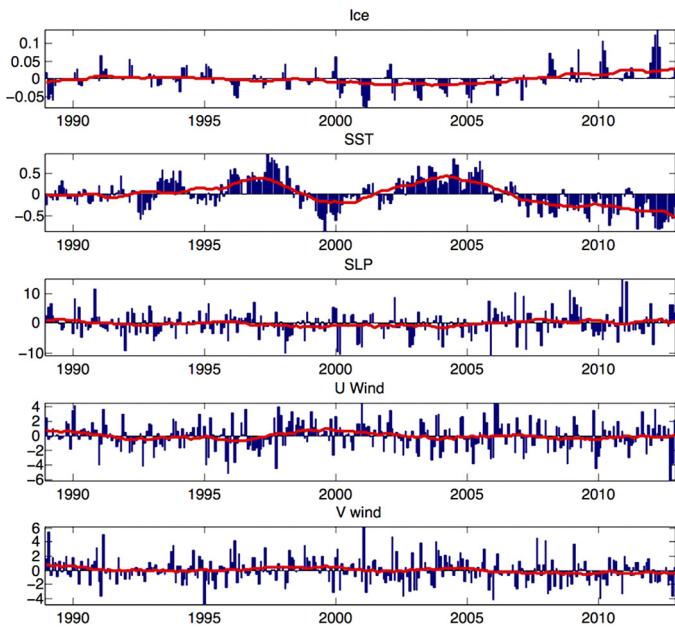


Fig. 3. Time series of monthly anomalies of environmental variables (ICE = ice cover in % cover; SST = sea surface temperature; SLP = sea level pressure; U, V Wind = zonal and meridional wind, respectively), averaged over the area delimited in Fig. 1. Red lines indicate 36-month running means.

determinants of primary production and prey distribution. Even though the seabird data reflect on certain months of the year, we collated monthly environmental data in order to explore which months or seasons correlated most strongly with the seabird data. Due to time lags in the development of robust food webs from environmental forcing to forage fish abundance, we hypothesized that winter and possibly previous fall periods would be important to seabird phenology and breeding success that occur in the spring and summer of each year. Monthly values of each environmental parameter from 1989 to 2012 were averaged for the domain 50–60°N and 174°E–160°W (Fig. 1); this region does not encompass Bluff. Data on SST (°C) and ICE (% cover) were obtained from the Met Office Hadley Center (Exeter, UK) SST reconstruction HadISST data set, with a resolution of 1° (Rayner et al., 2003). SLP data were also obtained from the Met Office Hadley Center's HadSLP2r data set, with 5° resolution and units of hPa (Allan and Ansell, 2006). Wind components (U, V) were obtained from the NOAA National Climate Data Center's iCOADS2.5 data set, with a resolution of 2° and units of m/s (Woodruff et al., 2011). We used a matrix of monthly data by year to create multivariate indicators of environmental conditions to match with our multivariate seabird indicators.

2.3. Data treatment and analysis

As trends in time series can create spurious relationships between environmental and biological variables, initially we tested each data set for non-stationarity (trend) using quadratic regression (of the form: $y = a + \beta x + \beta x^2$, where x^2 is the squared value of x and β are regression coefficients) and Spearman rank correlation; for both techniques, p -values were estimated by Monte Carlo randomizations with 10,000 repetitions (Table S1). To examine covariance between response variables, species, and sites, we de-trended each data set (using the aforementioned quadratic regression) and cross-correlated the residuals using rank correlations. To derive multivariate indices, we conducted PCA on these residuals; PCA on breeding success and phenology data was implemented separately due to the disparity in the time periods available for these variables. For interpreting principal components (here-

after referred to as either "PC1_{descriptor}" or "PC2_{descriptor}"), we selected |0.2| as a cut-off for interpretable loadings (Jolliffe, 2002). To test for robustness of our interpretations, we also analyzed breeding success and phenology residuals within each genus (i.e., two analyses stratified on a) *Rissa* spp. and b) *Uria* spp.). The PCA results generated using data stratified by genus confirmed the patterns of temporal variability obtained when combining genera in a single analysis. We retained the leading (PC1_{allspecies}) and second (PC2_{allspecies}) eigenvector values for analysis against physical environmental conditions and salmon abundance. We also conducted PCA on the monthly environmental variables (24 years × 12 months × 5 variables). Similar to the seabird approach, we detrended the environmental variables prior to synthesizing using PCA (Table S2). For the subsequent analyses, 1989–2012 was used when testing relationships with breeding success, and 1989–2008 was used when testing phenology. Initially, we examined relationships between combined environmental conditions (PC1_{env}, PC2_{env}, PC3_{env}) and seabird indices (PC1_{allspecies}, PC2_{allspecies}) using rank correlation. Next we rank-correlated the seabird indicators with pink salmon abundance (ln-transformed). Finally, we modeled multivariate seabird indices against physical environmental conditions and salmon abundance using forward (and confirmed using backward) stepwise regression.

3. Results

3.1. Trends in seabird and salmon time series

Few seabird time series showed significant temporal trends in phenology or breeding success (Table S1). There were also no overall trends in pink salmon abundance, but as their abundance shows bi-annual variation with every other year being characterized by higher or lower abundance (Ruggerone et al., 2010; Springer and van Vliet, 2014), one needs to consider even and odd years separately. In contrast to Springer and van Vliet, who suggested that odd year Kamchatka stocks have been increasing in abundance, we found no significant trends; no doubt because we analyzed data over a shorter time period, 1989 to 2012 (odd years: $n = 12$, $p = 0.50$, $p = 0.10$; even years: $n = 12$, $p = 0.18$, $p = 0.58$).

3.2. Covariance in seabird phenology and breeding success

There was substantial covariance in kittiwake breeding success time series between species and sites (90% of correlations were significant; Table 1). In contrast, there was less covariance between murre species and sites (24% of correlations were significant), and few correlations between *Uria* and *Rissa* genera (12% of the correlations were significant). Notably, all significant relationships were positive, indicating temporal coherence. For phenology, all but one of the kittiwake species-site correlations were significant (Table 1). For murres, some species-sites pairs were correlated (33%), and almost half (43%) of the correlations between murre and kittiwake species-sites were significant. All of the significant relationships for phenology were positive. Between breeding success and phenology, all but two of the significant correlations were negative, demonstrating that later mean hatching dates were associated with decreasing breeding success (Table S3). Most of these relationships were found when comparing breeding success and phenology at the same site.

3.3. Deriving multivariate seabird indicators

The first and second principal components for breeding success explained 31% and 22% of the variance, respectively (Table 2a). All kittiwake time series loaded strongly on PC1_{allspecies}, while all murre time series with the exception of common murres from

Table 2

PCA on a) breeding success and b) phenology for all species and sites combined, and individual eigenvectors for each species/site combination. Gray shading indicates loadings $>|0.2|$.

a)		Eigenvalues and Proportions			
Component		Eigenvalue	Proportion	Cumulative	
1		4.305	0.308	0.308	
2		3.093	0.221	0.529	
3		1.770	0.126	0.655	
Species		Eigenvectors			
Species		Site	1	2	3
Common Murre	St. Paul	0.033	0.436	0.223	
	St. George	0.075	0.452	-0.184	
	Cape Peirce	0.242	0.302	0.009	
	Buldir	-0.066	0.121	-0.117	
Thick-billed Murre	St. Paul	-0.040	0.436	0.319	
	St. George	0.102	0.331	-0.364	
	Buldir	0.092	0.305	0.391	
Black-legged Kittiwake	St. Paul	0.419	-0.008	-0.116	
	St. George	0.423	-0.015	-0.139	
	Cape Peirce	0.312	0.072	0.103	
	Buldir	0.263	-0.237	0.435	
Red-legged Kittiwake	St. Paul	0.384	-0.129	-0.178	
	St. George	0.395	-0.023	-0.230	
	Buldir	0.292	-0.170	0.446	
b)		Eigenvalues and Proportions			
Component		Eigenvalue	Proportion	Cumulative	
1		5.409	0.361	0.361	
2		3.214	0.214	0.575	
3		1.746	0.116	0.691	
Species		Eigenvectors			
Species		Site	1	2	3
Common Murre	Bluff	0.033	0.365	0.128	
	St. Paul	0.164	-0.432	0.019	
	St. George	0.193	-0.230	0.514	
	Cape Peirce	0.208	0.340	0.225	
Thick-billed Murre	St. Paul	0.173	-0.443	0.048	
	St. George	0.276	-0.228	0.408	
	Buldir	0.193	0.157	-0.086	
Black-legged Kittiwake	Bluff	0.290	0.178	-0.189	
	St. Paul	0.387	0.069	0.017	
	St. George	0.282	0.039	0.016	
	Cape Peirce	0.285	0.278	0.303	
	Buldir	0.278	0.095	-0.382	
Red-legged Kittiwake	St. Paul	0.324	0.105	-0.060	
	St. George	0.322	-0.168	-0.209	
	Buldir	0.260	-0.176	-0.415	

Buldir loaded strongly on PC2_{allspecies}. To test the robustness of these results, we derived separate PC within each genus (Table S4). PC_{allspecies} and PC_{genus} for breeding success showed strong coherence (PC1_{allspecies} and PC1_{kittiwakes}: $\rho = 0.98$, $p < 0.001$, Fig. 2a; PC2_{allspecies} and PC1_{murre}: $\rho = 0.90$, $p < 0.001$, Fig. 2b). For phenology, PC1_{allspecies} explained 36% of the variance, while PC2_{allspecies} explained 21% of the variance (Table 2b). We found a similar pattern of loadings for phenology as we did for breeding success. As with breeding success, there was strong coherence between phenology PC_{allspecies} and PC_{genus} (PC1_{allspecies} and PC1_{kittiwakes}: $\rho = 0.95$, $p < 0.001$, Fig. 2c; PC2_{allspecies} and PC1_{murre}: $\rho = -0.82$, $p < 0.001$, Fig. 2d; Table S5).

3.4. BSAI environmental conditions

Monthly oceanographic environmental measurements (Fig. 3) showed few long-term trends (Table S2), but a relatively high degree of serial autocorrelation was evident for SST; serial autocorrelation was minimal for atmospheric variables (Fig. 4). Percent ice cover showed an annual cycle of autocorrelation with a rapid drop in autocorrelation due to the disappearance of the ice each summer. Annual ice cover was autocorrelated by lags and leads of

Table 3

Rank correlations between PCs for environmental conditions and PCs for seabird breeding success and phenology. Shown is Spearman rho (p -value). Gray shading indicates significance of $p < 0.01$.

	PC1 _{env}	PC2 _{env}	PC3 _{env}
Breeding Success PC1 _{allspecies}	-0.16 (0.45)	0.04 (0.86)	0.53 (<0.01)
Breeding Success PC2 _{allspecies}	-0.17 (0.43)	-0.55 (<0.01)	0.12 (0.56)
Phenology PC1 _{allspecies}	-0.20 (0.39)	0.22 (0.34)	-0.18 (0.44)
Phenology PC2 _{allspecies}	0.72 (<0.001)	-0.02 (0.95)	0.16 (0.50)

1 ($r = \sim 0.25$) and 2 ($r = \sim 0.35$) years, respectively. Monthly values of SST were autocorrelated for 12 ($r = \sim 0.4$) to 18 ($r = \sim 0.2$) months.

3.5. Multivariate environmental indicators

Results from PCA on the environmental parameters reveal components that accounted for 22%, 10%, and 9% of the variance (Fig. 5). We interpreted the first principal component (PC1_{env}) as representing SST at the annual time scales since loadings were consistently high across all months of the year. PC1_{env} was also related to ICE, particularly the presence or absence of ice in spring. We interpreted the second principal component (PC2_{env}) as representing the seasonal modes of variability in atmospheric-ocean coupling because loadings were high for winter-spring SLP and SST. Finally, we interpreted the third principal component (PC3_{env}) as representing fall SST, winter ICE (mainly February), and summer V winds because loadings were high for these parameters.

3.6. Relating seabird and environmental indicators

There were significant correlations between PC1_{env} and phenology PC2_{allspecies} ($\rho = 0.72$, $p < 0.001$), PC2_{env} and breeding success PC2_{allspecies} ($\rho = -0.55$, $p < 0.01$), and PC3_{env} and breeding success PC1_{allspecies} ($\rho = 0.53$, $p < 0.01$) (Table 3). These correlations indicate that 1) murre phenology is related to annual SST variability (later timing of breeding under warmer conditions), 2) murre breeding success relates to winter-spring SLP and SST (lower success under warmer conditions), and 3) kittiwake breeding success reflects variation in winter ice cover and summer winds (Figs. 6 and 7).

3.7. Seabird reproduction, pink salmon, and climate

There was a strong negative correlation between pink salmon abundance and PC1_{allspecies} breeding success ($\rho = -0.66$, $p = 0.001$), but not for PC2_{allspecies} breeding success ($\rho = 0.02$, $p = 0.94$). These relationships remained while integrating environmental indicators in regression models (Table 4). These results indicate that regional kittiwake breeding success is negatively related to pink salmon abundance while regional murre breeding success is unrelated to pink salmon abundance.

3.8. Path analysis

Zador et al. (2013) combined breeding success and phenology for Pribilof Island seabirds, including kittiwakes and murres, in a single multivariate analysis, using a shorter time series (1996 through 2011) than was used in our study (1989 through 2012). PC1 of Zador et al. was interpreted as "...an index to seabird hatch timing and reproductive success of diving seabird foragers" and PC2 "...primarily as a kittiwake reproductive success index" (Zador et al., 2013, p. 252). To compare these interpretations with our results where we separated phenology and breeding success indicators, we consider how our PC1 (kittiwake) and PC2 (murre) breeding success indicators relate to our PC1 (kittiwake) and PC2 (murre) phenology indicators. If the interpretation of Zador et al. (2013) is correct, we expected to see a relationship from ocean climate to

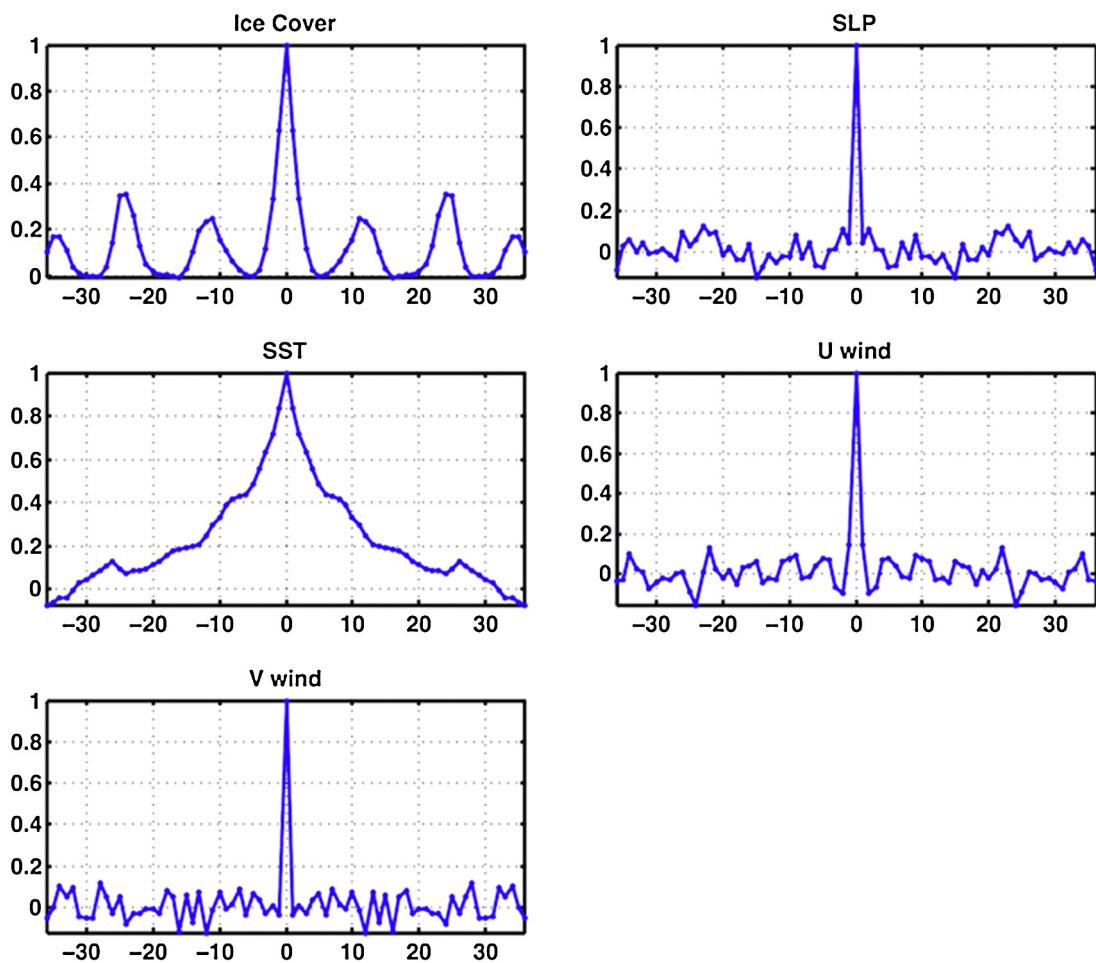


Fig. 4. Autocorrelation functions of monthly environmental parameters over 6-year periods. The x-axis indicates the monthly lag and leads of up to 36 months, and the y-axis shows the correlation coefficient between lag 0 and each month. Time 0 is mid-winter.

Table 4

Results of stepwise multiple regression on multivariate breeding success ($PC1_{\text{allspecies}}$ and $PC2_{\text{allspecies}}$) against $PC1-3_{\text{env}}$ and pink salmon abundance. Both forward and backward model selection resulted in the same end model.

	N	F	p > F	R ²	Predictor	Coefficient sign	t	p > t
PC1 (=kittiwakes)	24	23.06	<0.001	0.687	ln(Salmon)	−	−4.94	<0.001
PC2 (=murres)	24	6.87	0.016	0.238	$PC3_{\text{env}}$	+	3.50	0.002
					$PC2_{\text{env}}$	−	−2.62	0.016

phenology to breeding success for murres (i.e., an indirect pathway of response), but not for kittiwakes. Path analysis (see Thompson et al. (2012) for details of this method) suggests this is the case: the kittiwake breeding success indicator was best explained by a direct relationship with ocean climate ($PC3_{\text{env}}$), whereas the murre breeding success indicator was indirectly related to ocean climate ($PC2_{\text{env}}$) through phenology (Fig. 8). A possible explanation for this difference may be that murres have a foraging time buffer that can be adjusted to deal with fluctuations in prey abundance associated with ocean climate change, resulting in much lower variability in breeding success than kittiwakes, which have no such buffer (Zador and Piatt, 1999; Frederiksen et al., 2007b; Piatt and Harding, 2007; Piatt et al., 2007; Shultz et al., 2009). However, phenology in both genera was strongly influenced by ocean climate, and breeding success was strongly influenced by timing of breeding in murres (Shultz et al., 2009), just as our analysis here suggests.

4. Discussion

Modes of variability in marine ecosystems may be better revealed using multivariate approaches if individual time series are noisy (Frederiksen et al., 2007a), as was the case for our study (Figs. S1 and S2), and if there is reasonably strong covariance between individual time series. Strong coherence was evident for kittiwake breeding success phenology time series (within sites, breeding success and phenology were almost always negatively related, Table S3; see also Byrd et al. (2008)), but murre breeding success and phenology time series covariance was weak (see Spatial Variability below). Given these relationships, it would have been appropriate to combine kittiwake phenology and breeding success parameters in multivariate space as has been done for the Pribilof Islands (Zador et al., 2013), but at the ecosystem-scale of this study, combining murre and kittiwake data was not appropriate. Indeed, the modes

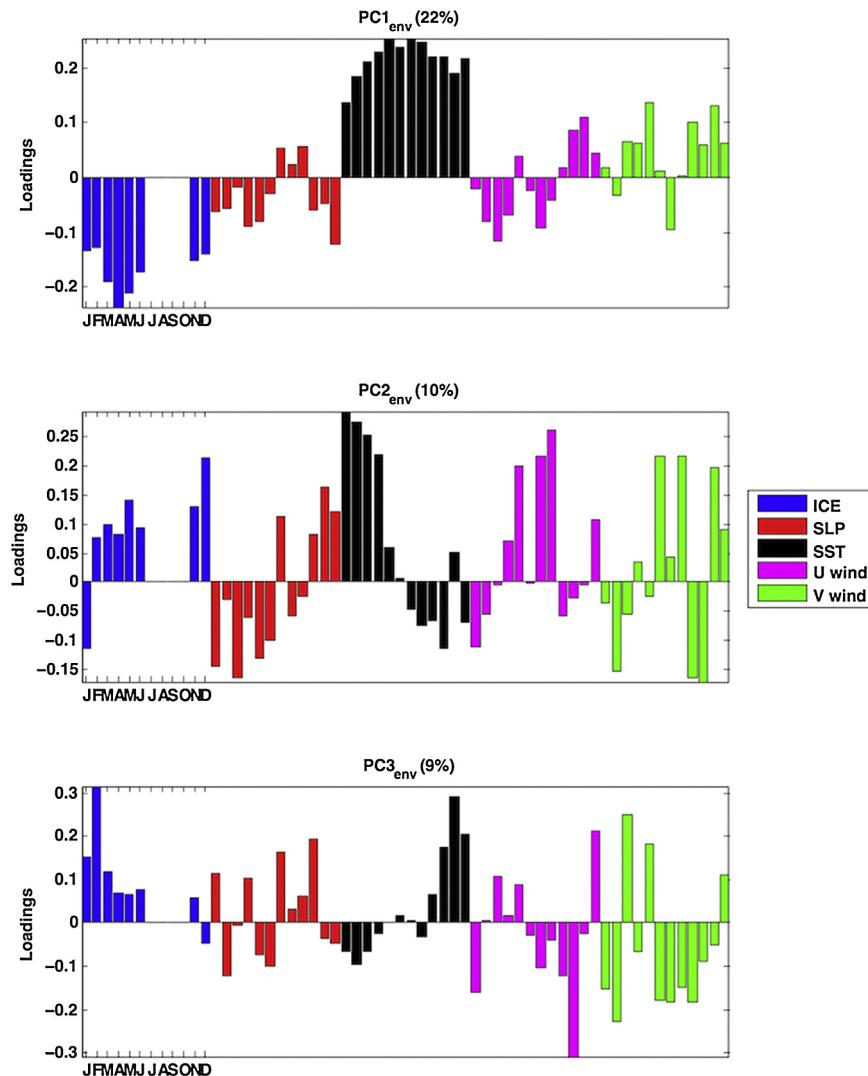


Fig. 5. Loadings of PC1–3_{env}. Color represents each environmental parameter, and each bar represents the loadings for each month of the year. These principal components explain 22%, 10%, and 9% of the total variance of the environmental parameters. We interpret PC1 as an indicator of ice cover and temperature at the interannual scale as all months loaded similarly on the eigenvalue. We interpret PC2 as an indicator of seasonal modes of variability, particularly with SLP and SST in the early part of each year. We interpret PC3 as an indicator of SST and ice cover in the late fall/winter (November–June) and V wind in the summer.

of variability shown by each of these species-parameters were very different.

The BSAI kittiwake breeding success indicator exhibited quasi-biennial variability, a pattern first described by Zador et al. (2013). The BSAI murre breeding success indicator showed less overall variability, but was interspersed with strong interannual (negative) anomalies. While the kittiwake indicator oscillated between positive and negative values almost every year, only the years 1998 and 2005 stood out for the murre indicator. The strong negative deviations in 1998 may reflect the exceptionally strong El Niño conditions experienced in that year (McPhaden, 1999), while the moderate negative deviations in the 2000s may reflect a series of moderate (2002–2003, 2009–2010) El Niño events in that decade. The BSAI kittiwake phenology indicators showed serial autocorrelation (i.e., multiple “early” or “late” years in sequence), but murres exhibited only weak interannual variability and a trend toward *earlier* breeding through time. Given the shortness of this time series (1989–2008) as well as spatial variability in murre timing, we do not know if this trend is robust, but it does match trends in timing presented by Byrd et al. (2008), with a few extra years of data. In summary, PCA-derived indicators capture different modes of temporal variability shown by these seabirds. Murres and kittiwakes

differ in their life history strategies, foraging behavior, and diet (Sinclair et al., 2008; Renner et al., 2012; Harding et al., 2013), so it is possible these varying modes of variability reflect fundamental ecological differences in these species. At the ecosystem scale, differences between genera were larger than the spatial differences within each genus, which demonstrates that seabirds of different genera should not be combined to produce large-scale multivariate seabird indicators.

4.1. Spatial variability

There was remarkable coherence between colonies for kittiwake breeding success and phenology (Table 2), with all sites loading strongly and positively. Indeed, for phenology every site-by-site correlation was positive and significant at $p < 0.1$, except one (Table 1b). Buldir, the most distant site compared to the others, showed the lowest loadings on PCs, but nonetheless showed similarity in modes of variability with the eastern Bering Sea sites. There was coherence between the murre colonies, though it was considerably weaker. Murre breeding success was fairly coherent (all sites loaded positively >0.2 , with the exception of common murres at Buldir), but there was lack of coherence for murre phenology,

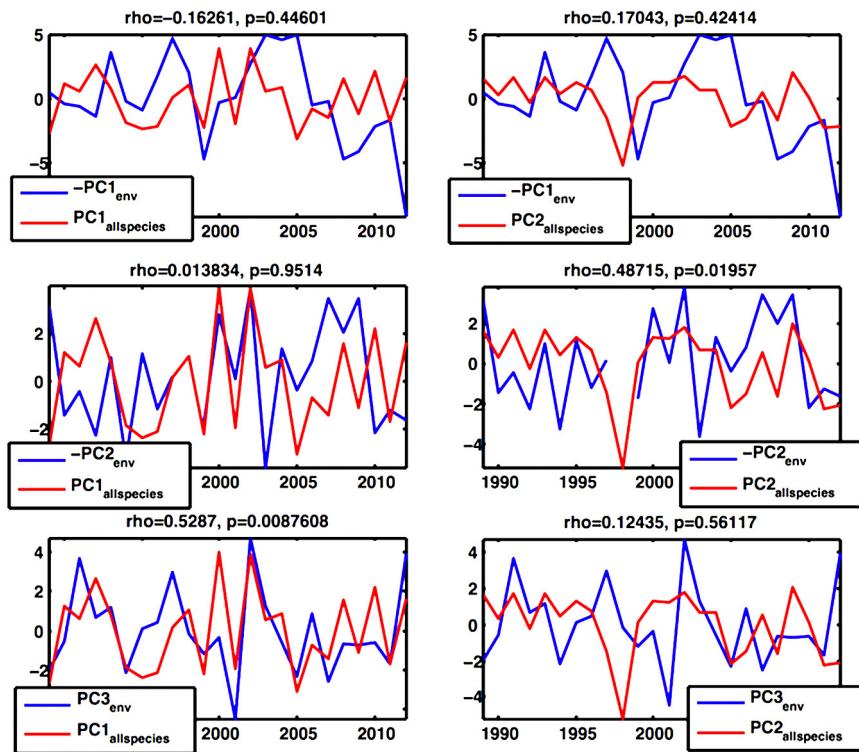


Fig. 6. PC scores of environmental parameters (blue) and seabird breeding success (red). a) PC₁_{env} (inverted) and PC₁_{allspecies}, b) PC₁_{env} (inverted) and PC₂_{allspecies}, c), PC₂_{env} (inverted) and PC₁_{allspecies}, d) PC₂_{env} (inverted) and PC₂_{allspecies}, e) PC₃_{env} and PC₁_{allspecies}, and f) PC₃_{env} and PC₂_{allspecies}. Spearman rank correlation rho and p-value are shown at the top of each plot.

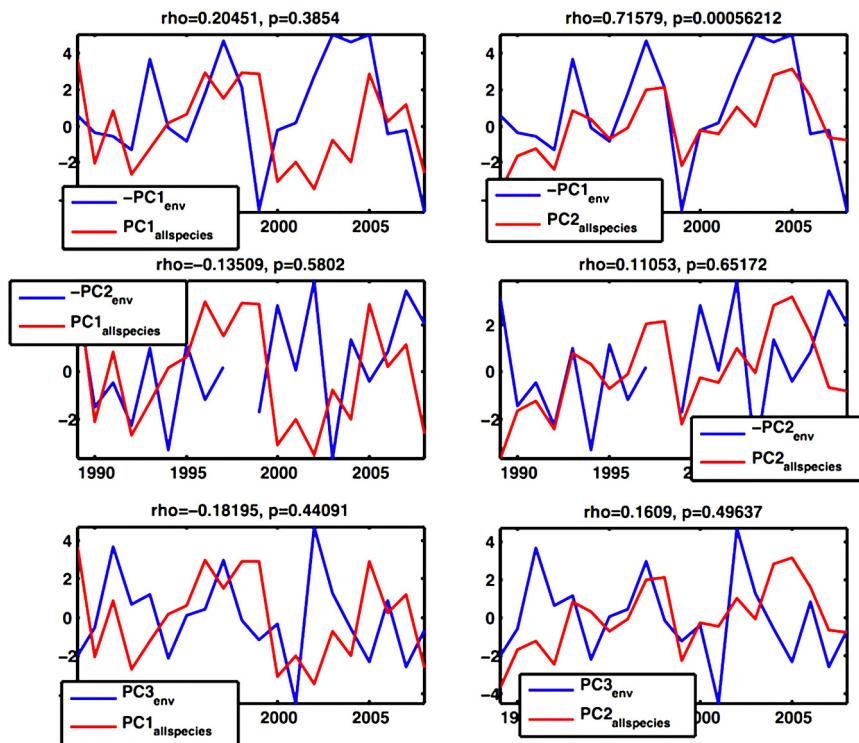


Fig. 7. PC scores of environmental parameters (blue) and seabird phenology (red). a) PC₁_{env} (inverted) and PC₁_{allspecies}, b) PC₁_{env} (inverted) and PC₂_{allspecies}, c), PC₂_{env} (inverted) and PC₁_{allspecies}, d) PC₂_{env} (inverted) and PC₂_{allspecies}, e) PC₃_{env} and PC₁_{allspecies}, and f) PC₃_{env} and PC₂_{allspecies}. Spearman rank correlation rho and p-value for each pair of PCs are shown at the top of each plot.

with Buldir, Bluff, and Cape Peirce loading positively while the Pribilof colonies (St. Paul and St. George) loaded negatively (Table 2). We interpret this difference as reflective of spatial variability in

trends in murre phenology, with the timing of breeding at Bluff and Cape Peirce becoming earlier through time, while that of Pribilof murres becoming later, at least for the study period examined

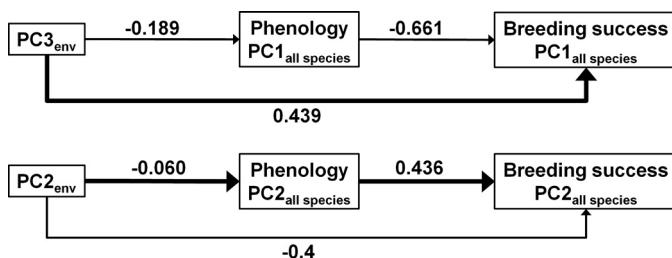


Fig. 8. Path analysis results showing: the dominant direct effect of PC3_{env} on kittiwake breeding success (represented by PC1_{all species}; top); and the indirect effect of PC2_{env} on murre breeding success (represented by PC2_{all species}) via phenology (bottom). Numbers along paths indicate standardized coefficients.

(Fig. S2). We do not know the causes of these different trends in phenology between sites, though we suspect that differences in food availability – perhaps mediated by seasonal changes in water temperature – are involved (Shultz et al., 2009). Bluff and Cape Peirce are coastal sites, thus patterns in sea ice break-up there are very different from the patterns of sea ice break-up that affect the Pribilofs. Also, we note that Buldir, in the western Aleutians, is not directly affected by sea ice, as the eastern Bering Sea sites are. Bluff and Cape Peirce also are influenced by warmer, more stratified coastal currents flowing north along the inner Eastern Bering Sea shelf (Stabeno et al., 1999). Last, murres have much greater foraging flexibility than kittiwakes and are ‘buffered’ against changes in food supply (Zador and Piatt, 1999; Piatt et al., 2007; Piatt and Harding, 2007). Thus, there are robust oceanographic and life history explanations for why Bluff and Cape Peirce appear to be distinct from the Pribilofs and Buldir when combining phenological data for murres in multivariate space.

4.2. What do the indicators indicate?

As noted above, multivariate indicators can be used to identify commonalities, hence ‘modes of variability’, in multiple parameters, and they can also show differences. Multivariate indicators also may be used to examine shared sensitivities to forcing functions (e.g., Frederiksen et al., 2007a,b; Zador et al., 2013; Black et al., 2014). To determine what our derived indicators indicate, we related them to an array of physical factors in the BSAI ecosystem (ice cover, SLP, SST, and meridional and zonal winds), environmental conditions known to affect pelagic food webs in this region (Hunt et al., 2002, 2011; Coyle et al., 2011; Stabeno et al., 2012; Hermann et al., 2013). Our regression model of the kittiwake breeding success indicator explained nearly 70% of the variation and suggested, based on our PC3_{env}, that breeding success was positively related to colder SST/greater ice cover during the winter preceding each breeding season and negatively related to pink salmon abundance. While we did not derive indices of winter conditions per se, the second principal component from our PCA of environmental conditions (PC2_{env}) reflects conditions early in the year, before the breeding season for these seabirds. These results thereby corroborate recent studies (Byrd et al., 2008; Springer and van Vliet, 2014), although these studies did not examine effects of climatic and biological interactions simultaneously, and suggest that food availability is the mechanism involved in these relationships. Our results differ somewhat from Zador et al. (2013), who found relationships between kittiwake breeding success and ice concentrations two years before the year of breeding. Zador et al. examined SST at an annual scale only, whereas we created seasonal indices. We also included sites other than the Pribilof Islands, as well as pink salmon abundance in our models, which may have helped to reveal physical covariates of kittiwake breeding success in the months before the kittiwake breeding season. Kittiwakes

winter well outside the BSAI ecosystem (Sydeman et al., 2010; Orben et al., 2015), so relationships between kittiwake breeding success and fall/winter conditions in the BSAI must be related to factors that influence the food webs in proximity to the colonies during the breeding season. These correlations suggest that local food web developments during the non-breeding season influence foraging opportunities for kittiwakes during the breeding season. We do not know how this mechanism works exactly, but perhaps colder, icier conditions in fall and winter facilitate the over-winter survival of forage fish or production of zooplankton, possibly euphausiids, that the kittiwakes consume in spring (Mueter et al., 2011; Hunt et al., 2011; Heintz et al., 2013). Another possibility is that colder winter conditions stimulate early blooms of sea ice-dependent phytoplankton which lengthens the growing season, to the benefit of kittiwakes (Hunt et al., 2011).

Our regression model for the murre breeding success indicator was much weaker than the kittiwake model, explained 25% of the variation, and showed a relationship to PC2_{env} (i.e., breeding success was negatively related to high pressure and warm SST during the winter/spring preceding each breeding season), but not pink salmon abundance. Similarly, Springer and van Vliet (2014) also did not find any effects of pink salmon on murre breeding biology. We found a strong correlation between murre phenology and PC1_{env} (Table 3; phenology was later when annual SST increased), an effect that was probably mediated by effects of SST on food availability (Shultz et al., 2009). Zador et al. (2013) found similar patterns related to water column properties: seabird hatching was delayed and murre productivity lower when bottom and SST were higher in the previous 1–2 years, when spring (May) wind mixing was stronger in the year of and year before breeding, and when late summer (August) stratification was higher the year before.

5. Conclusions

We interpret our findings on the relevance of fall/winter (early spring) SLP (lower pressure), SST (colder), and ice cover (more) as evidence for environmental preconditioning for greater lower trophic level productivity, particularly lipid-rich large copepods and euphausiids (Coyle et al., 2011; Hunt et al., 2011), which then has a positive effect on the kittiwake and murre prey base (i.e., age-0 and age-1 pollock), and hence improved seabird breeding success. Our results concerning the importance of “early season” conditions may be relevant across marine ecosystems. For example, early season conditions lagged at the scale of months is critical to seabird phenology and breeding success in the Antarctic (Inchausti et al., 2003; Olivier et al., 2005), Gulf of Alaska (Shultz et al., 2009), and California Current (Black et al., 2011; García-Reyes et al., 2013). Our results showing positive relationships for ice cover and negative relationships for SLP and SST 4–8 months prior to each breeding season provide another example of how early season environmental conditions that affect local food webs are important to seabirds. In this case, environmental conditions in fall/winter support earlier timing for breeding and higher seabird breeding success, modified for the kittiwakes by the abundance of pink salmon each year. Future modeling of wintering conditions on the Bering Sea ecosystem, salmon, and seabirds is warranted.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2017.03.013>.

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