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Winter pre-conditioning of seabird phenology in the California Current

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ABSTRACT: Climate change is predicted to affect the phasing and amplitude of upwelling in eastern boundary current marine ecosystems. Effects may be strongest during the spring or summer 'upwelling season,' but may also be influential during winter before the spring transition. We tested the hypothesis that wintertime environmental forcing 'pre-conditions' the ecosystem and affects the timing and success of breeding in 2 species of seabird, Cassin's auklet *Ptychoramphus aleuticus* and common murre *Uria aalge*, reproducing in the central California Current. Time series of the mean and variance of egg-laying dates were correlated with regional winds and sea surface temperature, which were used as proxies for the forcing and oceanic response of coastal upwelling, respectively. Winter proxies of upwelling were the most significant determinants of seabird reproductive phenology, with anomalously strong upwelling in January to March leading to earlier dates of egg-laying in both species. We hypothesized that anomalous (early) winter upwelling, even of weak magnitude or short duration, could seed the region with sufficient nutrients to enhance productivity and prey availability, leading to a healthier adult breeding population and an earlier start to the breeding season. The magnitude of the previous year's November winds were also positively correlated with the variance of egg-laying dates for the common murre, with upwelling-favorable winds leading to greater synchrony in egg-laying. We conclude that winter environmental conditions are important determinants of ecosystem dynamics in the California Current, and that seabird phenology is a particularly useful ecosystem indicator.

KEY WORDS: Cassin's auklet · Common murre · California current · Phenology · Upwelling · Winter · Ecosystem indicator

INTRODUCTION

Global climate change is expected to alter both the mean and variance of many meteorological and oceanographic parameters (Trenberth 2001, IPCC 2007), including the phasing and intensity of upwelling in eastern boundary current marine ecosystems. Changes in the phasing of upwelling may influence habitat suitability, primary productivity, and various mid-level ecological interactions (Stenseth et al. 2002, Parmesan 2006), with ascending effects to the upper trophic levels. The effects of changes in upwelling on ecosystem dynamics may be greatest during the spring-summer upwelling season, but may also be influential during winter before the spring transition.

As an apparent consequence of climate change, a variety of plant and animal parameters, including life history characteristics and demographic attributes, have shifted in a manner consistent with expectations under global climate warming. However, the vast majority (>90%) of changes documented to date come from terrestrial ecosystems and species (Richardson & Poloczanska 2008). Very few of these studies examined changes in biological time series, other than variability

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in the average parameter state, and whether mean values have shifted systematically through time. Phenology is defined as the timing of key events in plant or animal life histories, for example, the average dates of egg-laying in birds or bud burst in trees. Phenology is a very sensitive indicator of climate-driven ecosystem changes (Beebee 1995, Forchhammer et al. 1998, Stenseth & Mysterud 2002, Parmesan & Yohe 2003, Root et al. 2003, Parmesan 2006). In marine ecosystems, phenological changes have been related to climate variability and change for both lower (Mackas et al. 2001) and upper trophic level species (Abraham & Sydeman 2004).

A substantial component of the climate change literature for marine ecosystems concerns marine birds (Durant et al. 2004). Studies from the northern and southern hemispheres have related seabird phenology to oceanographic and atmospheric variability (Sydeman et al. 1991, 2006, Bertram et al. 2001, Abraham & Sydeman 2004, Frederiksen et al. 2004, Barbraud & Weimerskirch 2006, Reed et al. 2006, 2009, Byrd et al. 2008, Wolf et al. 2009), but none of these studies examined anything other than mean or median dates of reproduction, and most studies have looked at 'oceanographic climate' during the spring/summer breeding periods for the birds. Indeed, investigating within-season variability in winter, spring, and summer, and in relation to the distribution of dates of reproduction and reproductive success may be revealing. Moreover, few studies, with the exception of Abraham & Sydeman (2004), examined early oceanographic or climatic parameters that may 'pre-condition' ecosystems and influence the developing food webs upon which seabirds depend to obtain the resources for reproduction.

Seabirds have been proposed to be among the best environmental and ecological indicators for coastal marine ecosystems (Cairns 1987). Phenological attributes of seabirds are clearly relevant to evaluating the role of seabirds as indicators of marine ecosystem and food web dynamics. In particular, it has been argued that seabirds are reliable indicators because as top predators they 'integrate' and 'amplify' environmental variability to produce interpretable signals in their time series. This assumption has rarely been tested comprehensively (but see Wells et al. 2008).

In the present study, we evaluated the hypothesis that seabirds integrate environmental variability, and, as a result, demonstrate interpretable signals in their phenology that are significant in a climate change-ecosystem change context. We tested this hypothesis by correlating wind and sea surface temperature (SST) time series over a wide geographic area with egg-laying dates of 2 species of seabird in the California Current large marine ecosystem along the US west coast. Winds and SST were used as proxies for the forcing and oceanic response for coastal upwelling, respectively (Huyer 1983, Hickey 1998). We selected 2 species of birds, a planktivore (Cassin's auklet) and a piscivore (common murre), to examine differential responses to variation in the duration and phasing of upwelling. We investigated ecosystem pre-conditioning and how seabirds integrate environmental variation by considering how wind and SST influence phenology up to 6 to 8 mo before the initiation of reproduction each year.

MATERIALS AND METHODS

Egg laying data for Cassin's auklet *Ptychoramphus aleuticus* and common murre *Uria aalge*, herein referred to as auklet and murre, have been collected by biologists of the Point Reyes Bird Observatory (PRBO) under contract with the US Fish and Wildlife Service (USFWS) at Southeast Farallon Island (SEFI; 37° 41′ 53.88″ N, 123° 0′ 5.76″ W; Fig. 1) since the early 1970s. The Farallon National Wildlife Refuge, including SEFI and the North Farallon Islands, hosts one of the richest marine bird nesting colonies in the world, with at least 12 regularly breeding species (Sydeman et al. 2001). Auklets are planktivorous, feeding primarily on euphausiid crustaceans (Ainley et al. 1996, Abraham & Sydeman 2004, 2006) and have a foraging radius of ~60 km from the colony (Mills et al. 2007); they do not generally forage on inner shelf habitats (<50 m depth; Yen et al. 2005). In contrast, murres are omnivores and generally range within the 3000 m isobath, and ~100 km from the colony (Mills et al. 2007). Once murres finish molting they occupy nest sites on the Farallones in October and November (Ainley & Boekelheide 1990). Auklets inhabit the Farallones throughout the year, but in September and October they tend to molt at sea (Manuwal 1974). Each year, a variable number of birds is profiled, and the dates when eggs are laid and hatched are recorded and fledgling survival is observed (see Appendix 1 for summary statistics on reproductive timing). For both species, only the first egg-laying dates are considered in the calculation of the mean and variance time series. Thus, we have a 35 yr time series of the mean and variance of egg-laying dates for both auklets and murres. Hatching dates were not used, as the results were quantitatively similar to that of egg-laying dates, and we were most interested in the climate-oceanographic correlates of the initiation of breeding dates, which is best studied using egg-laying dates.

The environmental variables compared to the seabird phenology are based on satellite-derived SST and meridional wind data, available from the National Oceanic and Atmospheric Administration (NOAA)

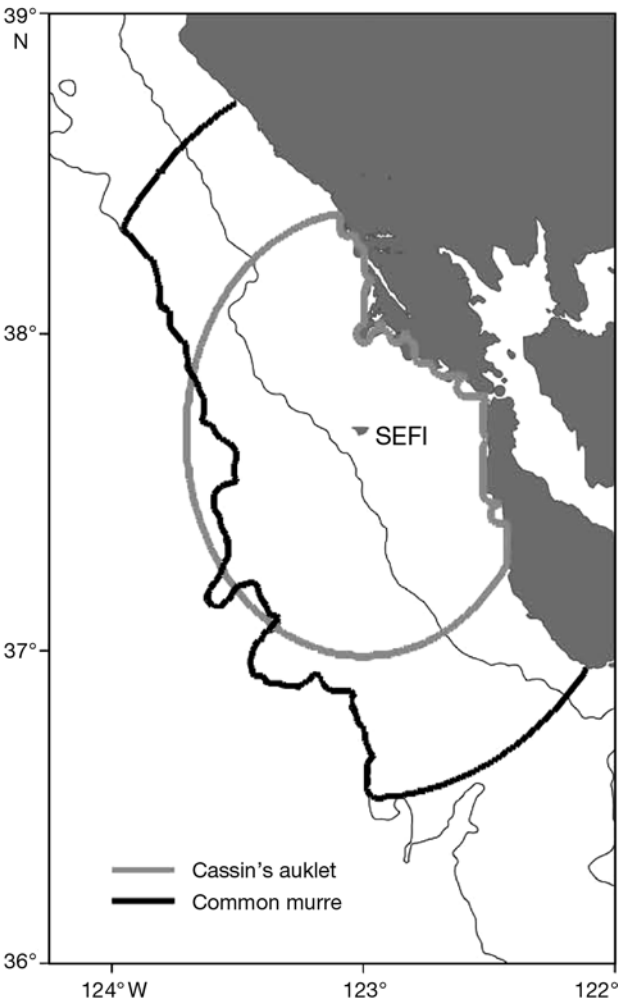

Fig. 1. Southeast Farallon Islands (SEFI), showing the estimated foraging ranges for common murre and Cassin's auklet. The 300 m and 3000 m isobath are contoured

Coastwatch Program (http://coastwatch.pfel.noaa.gov/data.html). The SST data come from Pathfinder version 5.0 day and night monthly composites, available from January 1985 to the present at a spatial resolution of 4.4 km (Kilpatrick et al. 2001). The wind data are from NOAA/NCDC blended monthly mean sea surface winds at 0.25° (~25 km) resolution (Zhang et al. 2006). The west coast of North America in the vicinity of the Farallon Islands is oriented in the north-south direction, thus the 'v' component of the wind is aligned along the north-south (meridional) direction and drives coastal upwelling. Southward winds (–v) are upwelling favorable, whereas northward winds (+v) cause downwelling.

Analyses have been performed over the time period common to the biological and physical time series (1988 to 2006). Gaps in the SST data were filled by a linear interpolation on the monthly mean time series at a particular grid location; for the months of January through March, only 8% of the total time series had >3 missing monthly values. Over 80% of the total time series had <5 missing months. Most gaps in the time series were only 1 mo in length, but some were up to 5 mo, especially in the coastal area around Point Conception, California (34.5° N, 121° W). There were no gaps in the meridional wind time series.

Statistical analyses. Spearman's rank correlation method (Kendall & Gibbons 1990) was used to relate the physical and biological series, as this technique does not assume normal distributions for the time series. The method calculates a correlation coefficient, C, and a probability, p, that the correlation is due to chance. The relationship between any 2 time series may be simultaneous (lag 0), or one may lead or lag the other. We derived spatial correlation maps between the monthly mean gridded satellite data for a particular month (winds and SST) and the annual mean and variance of egg-laying dates for each species. To examine the cumulative effect of upwelling, averages of consecutive months were also considered. Only spatial correlation maps with large areas of significant correlations were used in the final interpretation of the birds' response to the physical oceanic conditions. Given the large number of tests performed, correlations with $p < 0.01$ were assumed to be significant.

RESULTS

Variability in egg-laying dates

The mean and variance of egg-laying dates for both auklets and murres were related to annual reproductive success (number of chicks fledged per breeding pair). For both species, egg-laying dates were inversely related to breeding success ($C = -0.33$, $p < 0.06$ for auklets and $C = -0.39$, $p < 0.02$ for murres). That is, an early mean egg-laying date resulted in a larger number of viable fledglings per breeding pair. However, the 2 species show different relationships between egg-laying variances and reproductive success, especially since ~1990. Auklets were lower in trophic level, generally breeding earlier in the year, and having more variability in timing of egg-laying than murres. For auklets, variance in egg-laying corresponding to a longer breeding season, with younger birds typically breeding later in the season; this could result in a positive relationship with breeding success if the birds raise more than 1 clutch ('double-brood') in years of extended reproduction (Abraham & Sydeman 2004). In contrast, reproductive success of murres was enhanced when breeding synchrony was greatest (Birkhead 1977, Sydeman et al. 1991), with synchrony reflected by small variance in egg-laying dates ($C = -0.51$; $p < 0.01$).

The mean egg-laying dates for auklets and murres between 1972 and 2006 reveal substantial interannual variability (Fig. 2a). From 1972 to 2006, there was a positive trend in the auklet mean egg-laying dates (slope = 0.40 d yr^{-1}, $p = 0.14$) and a negative trend in the murre mean egg-laying dates (slope = −0.24 d yr^{-1}, $p = .07$). The planktivorous auklets initiated reproduction before murres in all years except 1992. In strong El Niño years (1983, 1992, 1998), the mean egg-laying dates for both species were significantly delayed; for auklets, the delay was upwards of 60 d, whereas for murres it was ~20 d. The mean egg-laying dates of the species were correlated ($C = 0.55$, $p < 0.01$). The variance in egg-laying dates (Fig. 2b) changed over the observation period. Until 1990, the variances of egg-laying dates for both species co-varied ($C = 0.46$, $p < 0.05$), but the correlation was negative ($C = -0.51$, $p < 0.05$) after 1990. During El Niño years, variance in egg-laying dates of auklets decreased, whereas for murres the variance increased. The mean and variance of egg-laying dates for auklets were inversely correlated ($C = -0.47$, $p < 0.01$) — when breeding early the population showed greater variability. For murres, there was no meaningful correlation between the mean and variance.

Correlation maps between meridional winds and egg-laying dates

Correlation maps constructed from correlations between meridional winds and mean egg-laying dates showed significant correlations only for the months of January, February, and January-February combined (other months are not shown). The correlations were positive and hold for both auklets (Fig. 3a) and murres (Fig. 3b), indicating that wintertime upwelling-favorable winds correspond to earlier mean egg-laying dates for both species. The January correlations for both species ranged between 0.58 and 0.76 for most of the region between 32°–44° N and 120°–128° W, encompassing almost the entire US West Coast. For auklets, the spatial correlations break down north of 41° N and in the area south of 36° N, shoreward of 123° W. For murres, the correlations break down primarily in the southern part of the domain. In February, the regions of high correlation for both auklets and murres lie south of the Farallon Islands, having values between 0.58 and 0.70.

The correlation map with the largest area of significant correlations was for the time series constructed by averaging the January and February meridional winds. The spatial extent of the correlation was similar for both auklets and murres, with high correla-

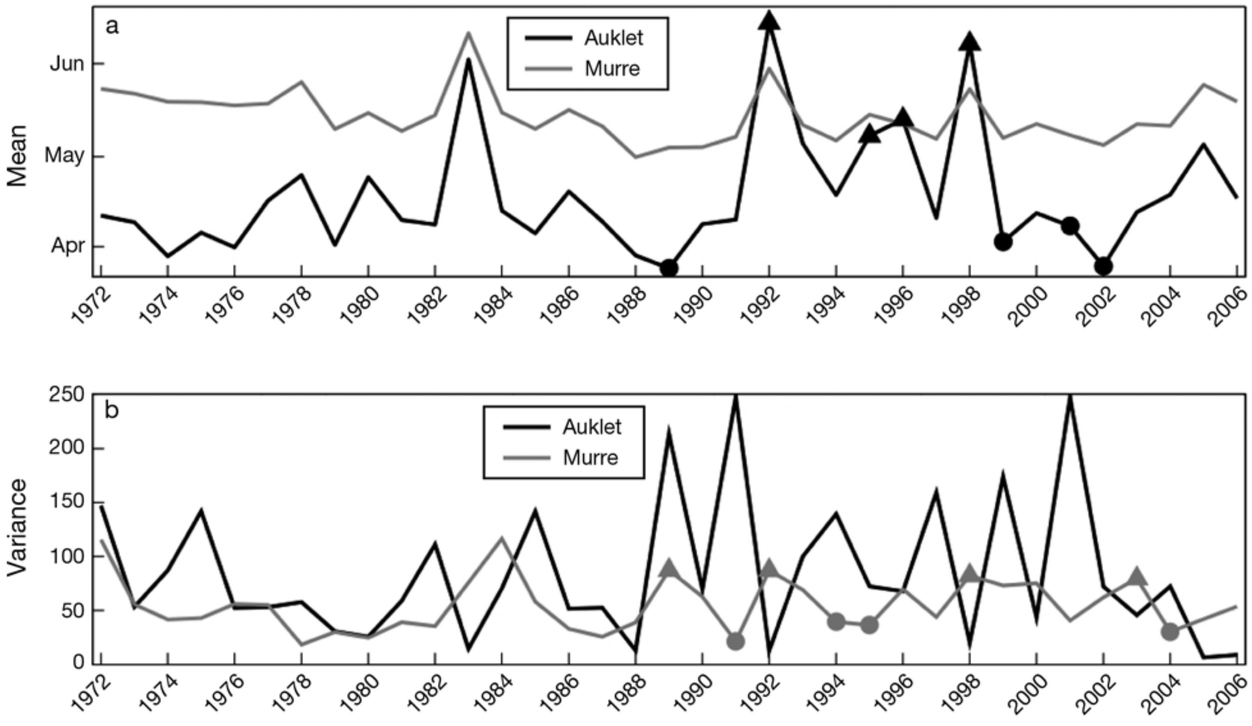

Fig. 2. *Ptychoramphus aleuticus* and *Uria aalge*. Time series of (a) mean of egg-laying dates and (b) variances of egg-laying dates. For the time period 1988 to 2006 (years of available wind and sea surface temperature (SST) data), the 4 years of the smallest (largest) values of auklet means and murre variances are marked with circles (triangles)

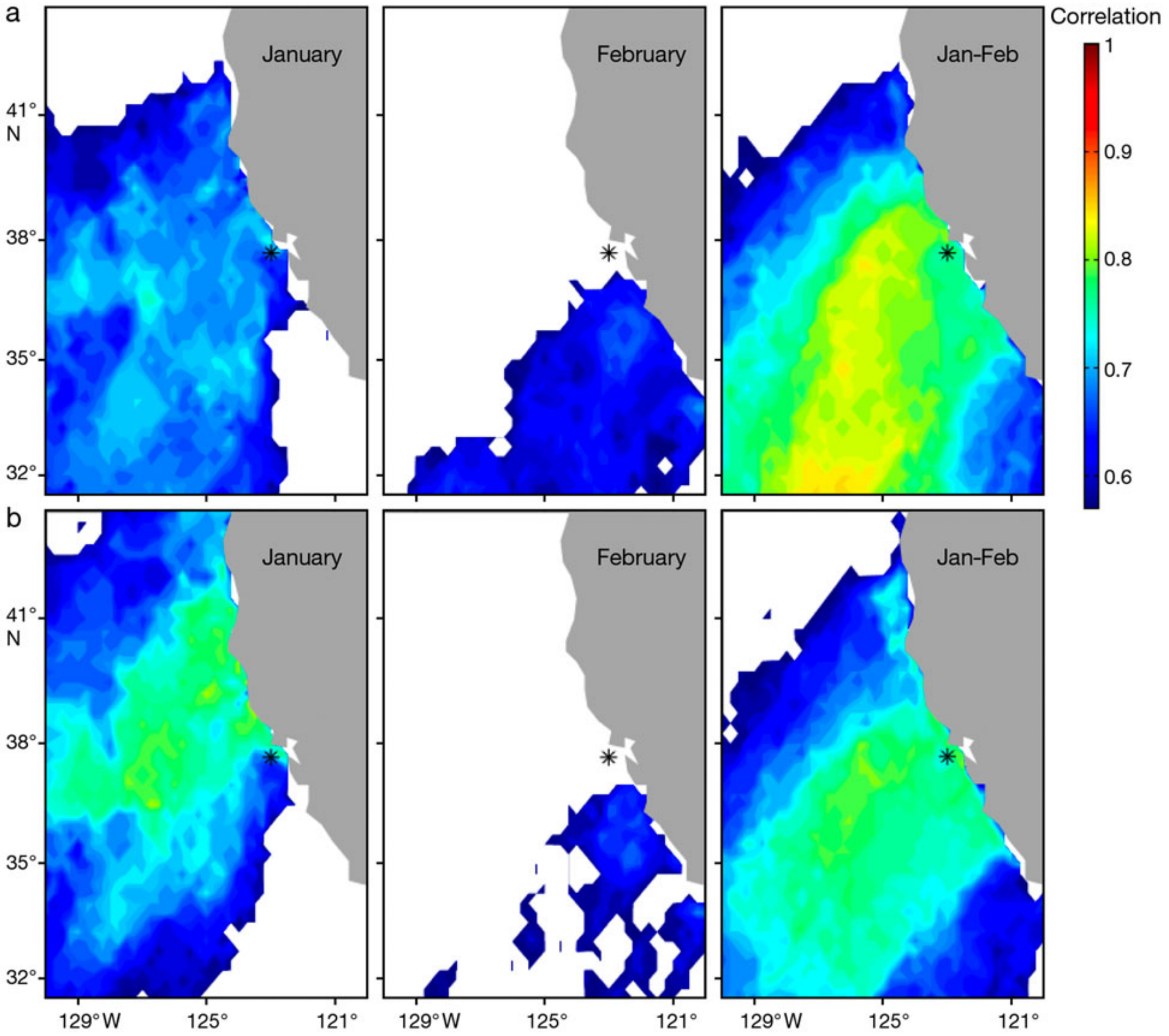

Fig. 3. *Ptychoramphus aleuticus* and *Uria aalge*. Correlations between meridional wind and mean egg-laying dates for (a) auklets and (b) murres. The spatial meridional wind data are the monthly means for January, February, and the average of January and February. For this and all subsequent correlation maps, a black asterisk marks the location of southeast Farallon Islands (SEFI). Only correlations with $p < 0.01$ are shown; areas in white are for non-significant correlations ($p > 0.01$)

tions throughout the domain, except for an increasing area of low or non-significant correlations north of approximately 40° N. It is interesting to note that while correlation values were highest for auklets in the composite of January-February winds, the January winds alone provided the highest correlations for murres. The relationships for both species are slightly non-linear; a quadratic regression of wintertime January-February winds explained 60.61% of the variance in mean egg-laying dates of auklets (Fig. 4a) and 44.87% of the variance in egg-laying dates of murres (Fig. 4b).

A strong positive relationship occured between meridional winds and variance of murre egg-laying dates (Fig. 5), but no such relationship existed for auklets. A positive correlation indicates that northward (downwelling favorable) winds are related to higher variance in murre egg-laying dates. Notably, the correlation was strongest in November of the previous year (e.g. the 1983 egg-laying variance was correlated to the November 1982 meridional winds), with a maximum correlation value of C = 0.94, centered at 42° N, 132° W, which decreases offshore to C = 0.59. This region of high positive correlation is located well to the northwest of the Farallon Islands, but corresponds to the center of the North Pacific (subtropical) High, which modulates coastal upwelling in the California Current (Schwing et al. 2002).

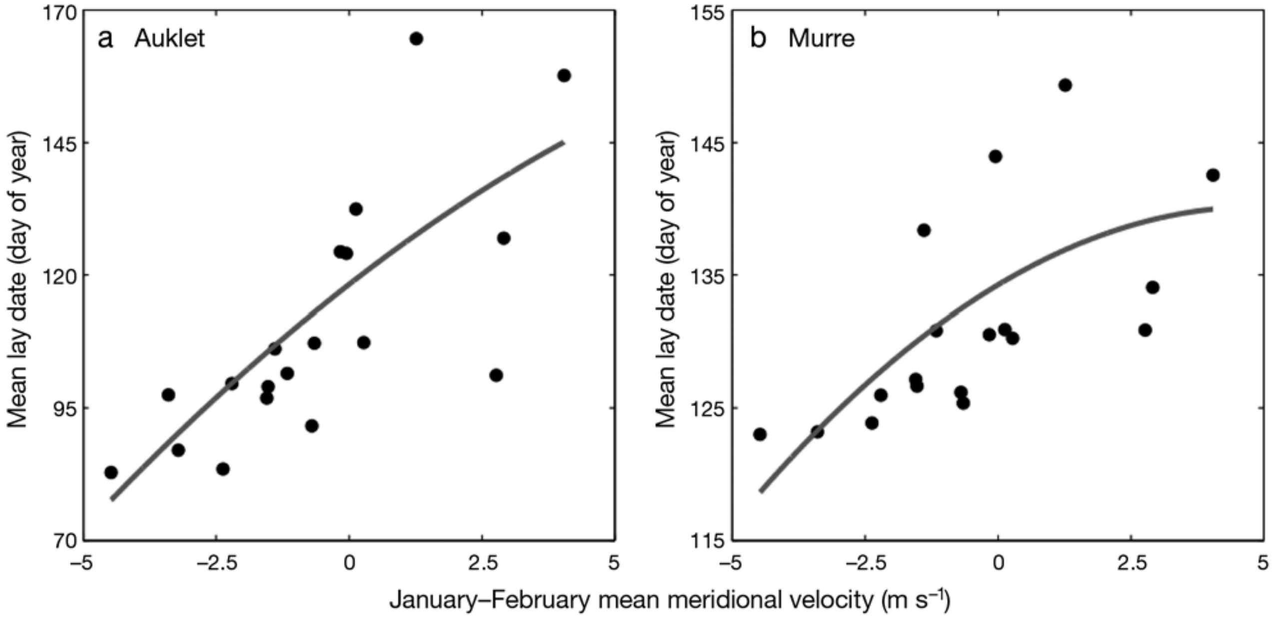

Fig. 4. *Ptychoramphus aleuticus* and *Uria aalge*. Bivariate plot between meridional wind and mean egg-laying dates for (a) auklet and (b) murre. Location of the January-February mean meridional wind data is 37.5° N, 125.5° W

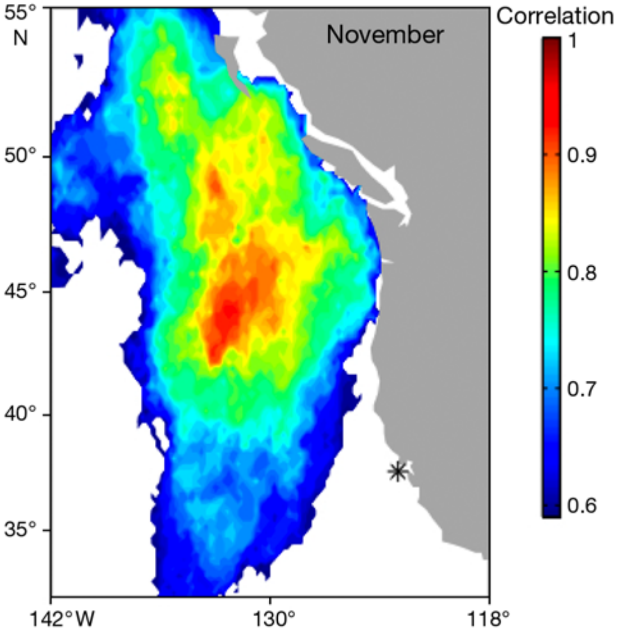

Fig. 5. *Uria aalge*. Correlations between meridional winds and variances of egg-laying dates for murres. Wind data are monthly means for November of the previous year

Correlation between SST and egg-laying dates

Correlation maps of SST and mean egg-laying dates for February, March, and February-March showed the greatest extent of significant positive correlations for both auklets (Fig. 6a) and murres (Fig. 6b). Positive correlations imply that both species lay their eggs earlier (later) when the regional SST is cool (warm). The correlation maps of SST have a much higher spatial resolution (4.4 km) than the wind correlation maps (approximately 25 km), and consequently appear grainier. Both auklets and murres had similar spatial correlation patterns, with higher correlations along the coast and decreasing correlations with increasing distance offshore. However, the offshore extent, as well as the magnitude, of the correlation coefficients was much higher for auklets than murres in all 3 temporal averages (February, March, and February-March).

In February, auklet correlation values were highest (C = 0.94) southward of the Farallon Islands, on the continental shelf. In March, the area of highest correlation (C = 0.97) was in the northern shelf area, around 42° N. The SST averaged over February and March had the highest spatial extent of significant correlation. The same spatial patterns were evident in the murre–SST correlation maps, though with generally lower correlations everywhere.

There were also significant correlations between SST and the variance of auklet egg-laying dates in February (Fig. 7). These correlations were negative, ranging from −0.79 to −0.58, implying that colder SSTs are associated with longer time spans of egg-laying periods. However, the spatial extent of the significant correlations was rather limited. No significant correlations were found between SST time series and variance of murre egg-laying dates.

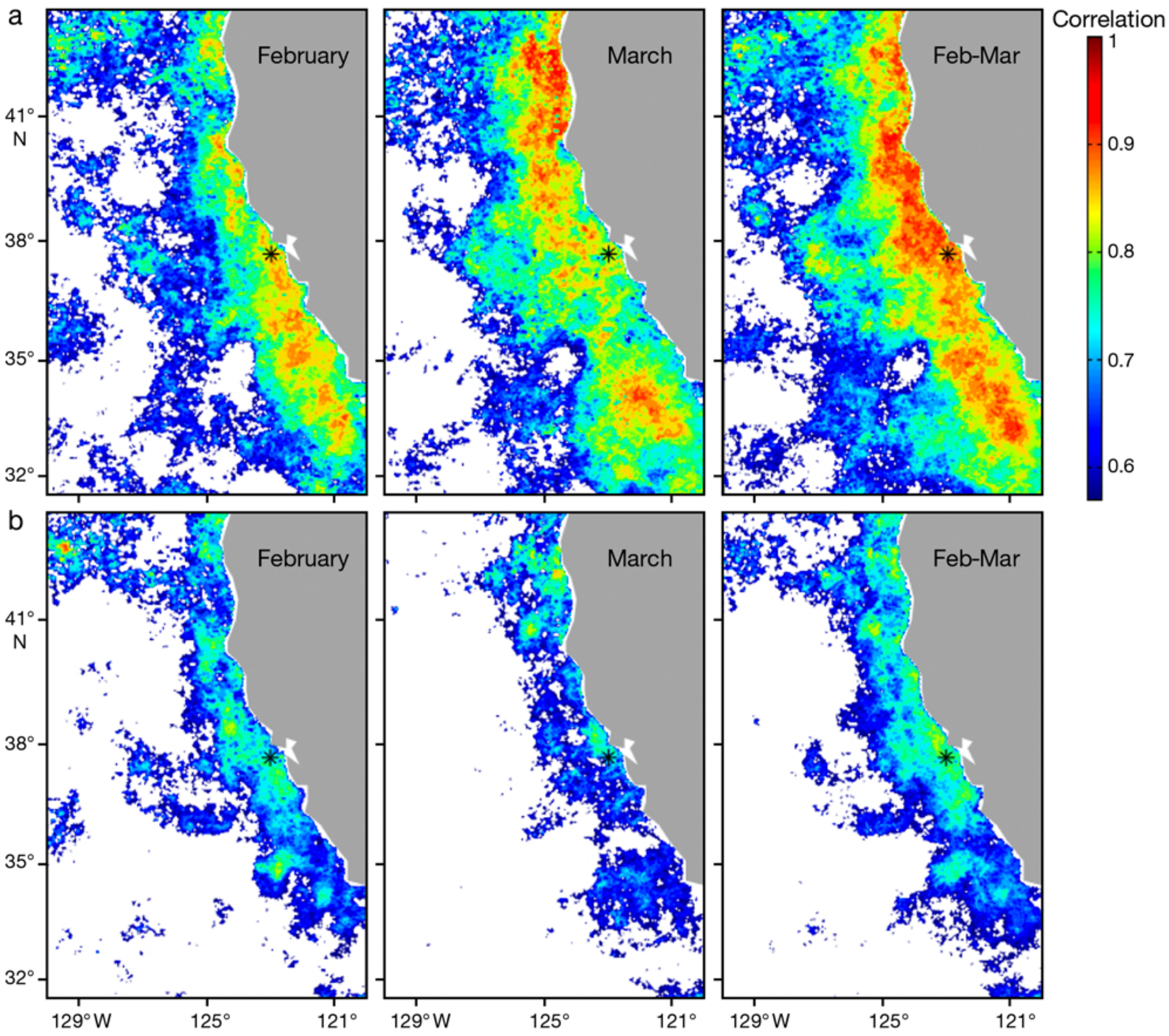

Fig. 6. *Ptychoramphus aleuticus* and *Uria aalge*. Correlations between sea surface temperature (SST) and mean egg-laying dates for (a) auklets and (b) murres. SST data are monthly means for February, March, and the average of February and March

DISCUSSION

We have evaluated the hypotheses that wintertime environmental forcing 'pre-conditions' the ecosystem and that seabirds 'integrate' environmental variability as demonstrated by interpretable signals in their timing of breeding (i.e. phenology). We tested these hypotheses by creating monthly estimates of winds and SSTs over the Northeast Pacific and producing spatial correlation maps to investigate the overall scales of integration. Upwelling in the central-northern California Current is most intense during the months of May to July each year (Bograd et al. 2009), but we found wintertime (November, January to March) proxies of upwelling to be the most significant determinants of seabird phenology. Upwelling in the California Current is the primary driver for primary and secondary productivity (Largier et al. 2006), so undoubtedly the relationships we have established are indirect, mediated by changes in prey resource availability. Herein, we compare the responses of these 2 species of seabird, an obligate planktivore (auklet) and an omnivore (murre), to winter environmental conditions, as indexed by surface winds (atmospheric forcing) and SSTs (oceanic response). We touch upon the specifics of prey resource availability later in this discussion. To our knowledge, this is one of the first attempts at a spatio-temporal integration of climate-oceanographic and

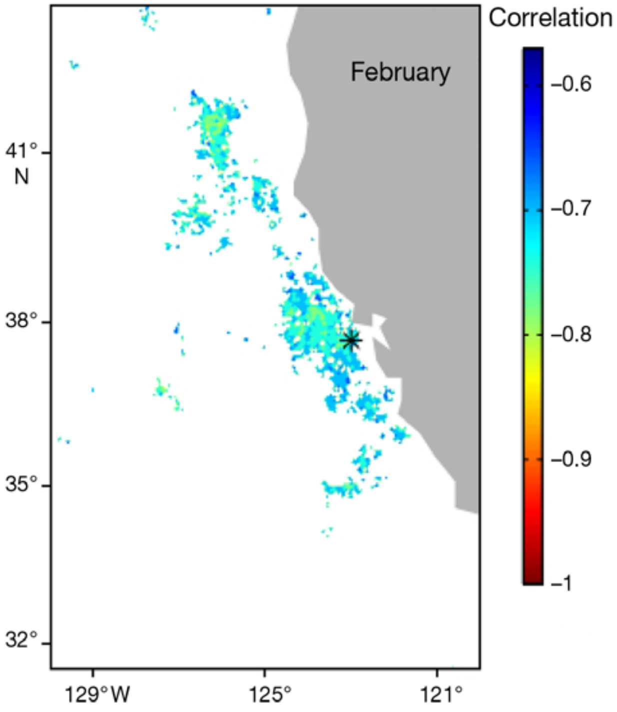

Fig. 7. *Ptychoramphus aleuticus*. Correlations between sea surface temperature (SST) and variances of egg-laying dates for auklets. SST data are monthly means for February

phenological variables. Clearly such information is critical to assessing the role of seabird phenology as an indicator of ecosystem dynamics, as has been recently proposed (Sydeman et al. 2008).

Ecosystem pre-conditioning

Previous studies have found relationships between wintertime oceanographic conditions and seabird ecology in the region (Abraham & Sydeman 2004, Miller & Sydeman 2004), but the temporal pattern of ecosystem 'pre-conditioning' revealed by the present study is considerably earlier than expected. The cumulative effect of meridional winds on the mean egg-laying dates for both species was strongest in winter (January and February). The spatial correlation maps revealed the strongest correlations to the north and southwest of the Farallones, presumably reflective of atmospheric forcing conducive to upwelling (Fig. 3). From an ornithological perspective, auklets and murres can produce eggs within ~10 to 15 d after fertilization (Astheimer 1986). The fast egg production and the spring timing of the average egg-laying (29 March to 7 May for auklets and 6 to 22 May for murres; Fig. 2a; Appendix 1) would suggest March/April environmen-

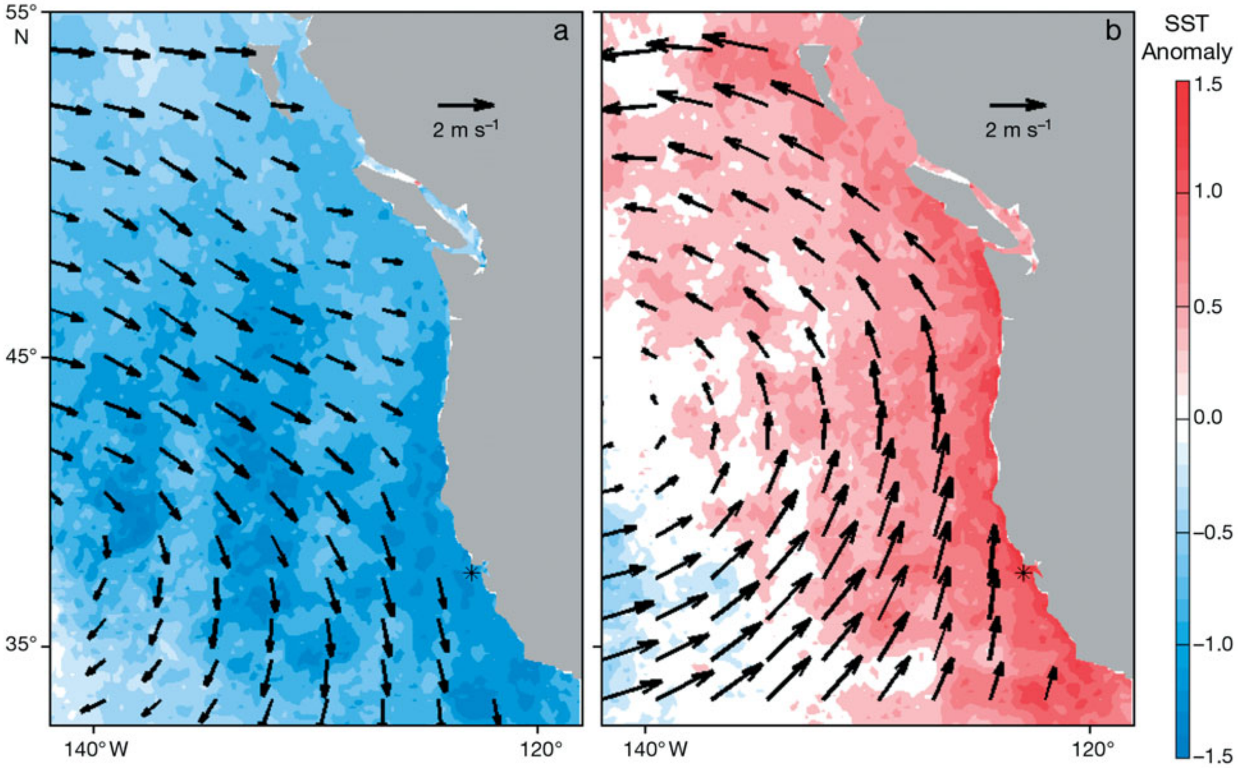

Fig. 8. *Ptychoramphus aleuticus*. Anomalies of January-February winds and February-March sea surface temperatures (SSTs) for (a) the 4 years of the earliest auklet egg-laying means and (b) mean of the 4 years of latest auklet egg-laying means. For clarity, arrows are plotted every 2.5°

tal signals being the most influential to the timing of breeding. However, from an ecosystem and food web development perspective, the winter relationships make sense. In the Point Arena region, upwelling is strongly intermittent in winter (Bograd et al. 2009). However, it is this intermittent upwelling that appears most significant to the timing of seabird egg-laying.

We hypothesize that intermittent upwelling in winter stimulates and fuels food web development, which ultimately affects seabird body condition and egg-laying dates. Estimates of the timing between upwelling and primary and secondary productivity are important in this regard. In the California Current system near Bodega Bay, upwelling followed by a relaxation of 3 to 7 d is most favorable for phytoplankton blooms (primary productivity; Wilkerson et al. 2006). For secondary production, the results are highly species dependent and also variable by year. Timing of seabird breeding is known to be influenced by the nutritional status of egg-laying females (Perrins 1970). Farallon auklets feed mostly on euphausiid crustaceans ('krill'). Coastal communities of *Euphausia pacifica* were comprised only of larval forms in January (Dorman et al. 2005). Our results show that upwelling during January and February is important to egg-laying of auklets and murres; therefore, it may be significant for the growth of krill as well. The prey of murres during the breeding season consists mainly of pacific hake, northern anchovy, and juvenile rockfish (Mills et al. 2007, Roth et al. 2008). Pacific hake spawn from January through March offshore of southern California, and juveniles and adults migrate northward to central California in the spring (Ressler et al. 2007, Agostini et al. 2008). Northern anchovy spawn year round, but late winter and early spring are peak spawning times (Parrish et al. 1986). Also, January through March is a very active period of fertilization/parturition for some species of rockfish in the California Current (Eschevarria & Lenarz 1984). Reed et al. (2009) used estimates of juvenile rockfish to show a relationship with murre phenology, although the forage fish data were obtained in May to June, after the egg-laying period of murres. Unfortunately, we lack data on the seasonal variation in food web components to estimate all the time lags involved. However, other studies on Farallon seabird phenology (Abraham & Sydeman 2004, Reed et al. 2009, Wolf et al. 2009) and seabird phenology elsewhere in the world (Frederiksen et al. 2004, Barbraud & Weimerskirch 2006, Reed et al. 2006, Byrd et al. 2008) have inferred, rather than demonstrated, that environmental relationships are due to variation in prey resources. In short, it seems that wintertime upwelling 'pre-conditions' the system and is important to the growth and development of many prey species that are likely related to the foraging success, body condition, and timing of breeding for these seabirds.

The seasonal cycle of water column structure in the California Current affects the biological utility of coastal upwelling. Surface stratification of the ocean off central-northern California is weakest in winter (Pennington & Chavez 2000, Palacios et al. 2004) and calculation of Brunt-Väisälä frequencies showed the lowest values in January-February at the M2 mooring located near Monterey Bay (data not shown). Thus the upwelling of nutrient-rich water in winter could occur with winds that are weaker or of shorter duration than the winds that would be required for significant nutrient-favorable upwelling later in the season. Thus anomalous (i.e. early) winter upwelling, even of weak magnitude or short duration, could seed the region with sufficient nutrients to enhance productivity and prey availability. This 'pre-conditioning' of the system would allow for a healthier adult breeding population, hence an earlier start to the breeding season.

To further illustrate these results, we have summarized wind patterns and SST for the 4 earliest (1989, 2002, 1999, 2001) and 4 latest (1995, 1996, 1998, 1992) years for auklet egg-laying (Fig. 2a). January-February meridional winds and February-March SSTs for these early/late years were averaged and then subtracted from the climatological means to form anomaly maps representing conditions that are favorable or unfavorable for early egg-laying. The anomalous wind patterns for the early egg-laying years correspond to an anomalously strong Subtropical High pressure system, resulting in anticyclonic wind anomalies and stronger coastal upwelling. The corresponding February-March SST anomalies over the region are cooler than the climatology by up to 1.5°C (Fig. 8a). In contrast, the January-February anomaly winds for the 4 latest years of auklet egg-laying show strongly downwelling favorable conditions along the entire coast, and February-March SST anomalies warmer by up to 1.5°C (Fig. 8b).

Within-season patterns: variance

Measures of central tendency (mean and/or median) and variance structures are often correlated as they are here (to some extent), but variance as a parameter provides a novel view of phenology. From a breeding success perspective, greater variance for auklets does not necessarily lead to better reproduction, but less variance for murres results in better reproductive output. We found that November winds of the previous year were related to murre variance in egg-laying dates, but we found no relationships for auklets. We do not understand why this difference exists between the species, although we assume November winds only have an effect on the prey of murres. Moreover, we found that murre and auklet variances were positively correlated before 1990 and negatively correlated thereafter. As noted in the 'Results', we surmise that greater variance for auklets and less variance for murres is a positive response to favorable environmental conditions, which means that it is the positive correlation between auklet and murre variance prior to 1990 that requires explanation. While we do not fully understand this relationship, before 1990 murre egg-laying dates advanced significantly (Sydeman 1999, Reed et al. 2009), and perhaps this change in overall breeding date was related to a change in the variance structure of the data. For auklets, the number of years with high variances (>150) only occurred after 1989, whereas there is no such shift to higher variances for the murres (Fig. 2b).

To illustrate the relationship between murre variance in egg-laying and environmental conditions, we applied the same process of looking at the average of the anomalous winds and SSTs for the 4 yr of smallest and largest variances. The 4 yr with the lowest variances are 1999, 2004, 1995, and 1994; the 4 yr with the highest variances are 2003, 1998, 1992, and 1989 (Fig. 2b). The wind and SST patterns associated with the largest/smallest variance years are very similar to those for the earliest/latest auklet egg-laying years (Fig. 8); because of the similarity the figure is not shown. Years with the smallest variances have anticyclonic November wind anomalies. The wind magnitudes are very large north of 45° N, with anomalies exceeding 4 m s^{-1} and directed from the northwest. The SST anomalies are cooler than the climatological mean over most of the region, with values between –0.5 to –1°C in the areas adjacent and to the north of the Farallones. The conditions for the highest variances are cyclonic wind anomalies; the SST anomalies over most of the region are warmer than the climatology. December SST anomalies of over 1.5°C are located just north of 45° N, with upwelling conditions around the Farallones with wind magnitudes ~1 m s^{-1} and SST anomalies of ~0.5°C.

Seabird phenology as an ecosystem indicator

Seabird phenology appears to be reflective of processes that determine ecosystem dynamics 3 to 5 mo prior to egg-laying for these species. Further refinements in understanding the mechanisms of the response are necessary, but we have a reasonable operational hypothesis, and have calibrated some of the functional relationships. Therefore, it seems appropriate to suggest seabird phenology as an indicator of wintertime ecosystem dynamics. Unlike for fish and other species in the system, the breeding timing of seabirds is relatively easy and inexpensive to measure. Indeed, it is hard to envision other taxa that could provide phenological indices of ecosystem dynamics early in each year. These indices could be extremely important in assessing ecosystem 'health' and resilience, and could be useful in a predictive context (Sydeman et al. 2008). Seabird phenology could provide a biological 'spring transition' index, which may be more meaningful to other biological organisms than a physically based index, such as changes in SST or sea level. Coupling both physical and biological indices of timing may be particularly useful for understanding ecosystem productivity.

CONCLUSIONS

Based on this investigation, we conclude that wintertime conditions are important determinants of ecosystem dynamics in the California Current and that future ecosystem studies should focus on physical forcing prior to the 'spring transition.' In some cases, the 'spring transition' may have been over-emphasized, when it is actually atmospheric–oceanographic interactions before the transition can be observed that are most significant to ecosystem productivity. The widespread correlations of winds and SST in January and February, and as early as November in the preceding year, support the notion that wintertime 'pre-conditioning' of the system is important. We have suggested that winds during periods of weak stratification may be mechanistically related to effectual upwelling in the system during winter, but this is certainly an area for future research.

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Appendix 1. *Ptychoramphus aleuticus* and *Uria aalge*. Summary statistics calculated and used for analysis of Cassin's auklet and common murre egg-laying dates

Year	Mean	Median	N	Max	Min	SD	Variance
Cassin's auklet							
1972	100.38	97.5	64	135	75	12.12	147.12
1973	98.13	96	62	124	90	7.29	53.22
1974	86.78	85	65	122	69	9.33	87.14
1975	94.69	91	70	131	77	11.91	141.89
1976	89.75	90	73	122	78	7.23	52.32
1977	105.35	105	71	133	93	7.28	53.11
1978	113.87	112	77	143	103	7.60	57.82
1979	90.59	90	75	112	78	5.53	30.62
1980	113.12	114	77	128	101	5.05	25.57
1981	98.94	99	80	120	88	7.67	58.86
1982	97.41	95	80	130	71	10.54	111.18
1983	152.35	155	37	162	148	3.81	14.56
1984	102.00	102	77	127	87	8.39	70.39
1985	94.46	91	78	146	81	11.90	141.75
1986	108.38	106	42	141	96	7.17	51.50
1987	98.43	96	39	121	86	7.24	52.46
1988	87.06	85	17	95	80	3.56	12.68
1989	82.83	81	41	131	66	14.60	213.44
1990	97.50	96	40	121	81	8.33	69.48
1991	99.03	96	40	146	81	15.73	247.56
1992	164.65	167	17	172	157	3.58	12.86
1993	124.38	121	37	161	116	10.00	100.07
1994	107.22	101	37	146	96	11.80	139.45
1995	126.97	126	31	161	121	8.50	72.36
1996	132.42	132	36	157	117	8.22	67.67
1997	99.59	96	39	146	86	12.61	159.14
1998	157.67	156	15	166	151	4.49	20.23
1999	91.63	86	32	121	71	13.18	173.79
2000	101.18	98	33	123	93	6.59	43.46

Appendix 1 (continued)

Year	Mean	Median	N	Max	Min	SD	Variance
2001	96.88	91	40	151	76	15.72	247.29
2002	83.50	81	36	106	71	8.49	72.14
2003	101.53	101	38	126	91	6.75	45.66
2004	107.36	104.5	42	142	97	8.51	72.43
2005	124.08	126	13	126	121	2.53	6.41
2006	106.16	106	32	111	101	2.97	8.84
Common murre							
1972	142.56	140	98	187	127	10.75	115.63
1973	141.00	139	130	161	130	7.45	55.59
1974	138.32	137	139	158	128	6.45	41.65
1975	138.17	136	137	162	130	6.55	42.99
1976	137.04	135	164	168	126	7.47	55.94
1977	137.69	137	108	160	126	7.42	55.07
1978	144.90	144	114	162	136	4.29	18.42
1979	129.20	130	135	161	116	5.47	29.99
1980	134.60	134	138	152	126	4.97	24.78
1981	128.55	128	135	160	117	6.25	39.17
1982	133.82	134	70	156	125	5.94	35.36
1983	161.08	162	45	181	143	8.70	75.76
1984	134.69	132	128	184	121	10.79	116.47
1985	129.27	128	110	166	118	7.62	58.14
1986	135.63	135	111	160	127	5.74	33.01
1987	130.17	130	114	156	118	5.06	25.66
1988	119.86	119	119	158	107	6.24	38.98
1989	123.01	121	126	162	107	9.35	87.42
1990	123.19	122	135	158	108	7.92	62.76
1991	126.65	126	125	146	110	4.60	21.22
1992	149.34	146	93	182	133	9.33	87.14
1993	130.53	128	112	169	119	8.31	69.09
1994	125.37	125	133	151	110	6.28	39.55
1995	134.04	134	142	162	123	6.03	36.47
1996	130.92	128	150	167	120	8.34	69.71
1997	125.96	125	143	157	115	6.62	43.83
1998	142.53	141	101	167	122	9.07	82.31
1999	126.17	125	102	164	114	8.54	73.07
2000	130.89	130	105	156	118	8.67	75.24
2001	127.16	127	130	157	113	6.37	40.64
2002	123.86	123	136	157	111	7.88	62.13
2003	130.84	128	147	164	116	8.92	79.65
2004	130.26	130	150	151	115	5.49	30.19
2005	143.94	144	168	177	131	6.48	42.01
2006	138.38	137	189	171	124	7.33	53.77

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