



Phenological cues to breeding and the differential response of Pacific auks to variation in marine productivity

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ABSTRACT: Many bird species use features of the physical environment to cue breeding activity. We show that for 2 species of Pacific auks (zooplanktivorous Cassin's auklet *Ptychoramphus aleuticus* and generalist rhinoceros auklet *Cerorhinca monocerata*), spatio-temporal variation in marine production indicators surrounding a major breeding colony in the northeast Pacific Ocean can cue laying date. By utilizing a multi-year phenological time series and a spatio-temporal sliding-window analysis spanning November up until median lay dates in spring, chlorophyll *a* (chl *a*) concentrations in the surface ocean around the colony strongly predicted lay date. However, the response to this cue differed between species by over 2 mo, as each species was exposed to different, sequential water-masses. We show that for Cassin's auklets, chl *a* levels at Triangle Island, British Columbia (Canada) in February, nearly 2 mo prior to actual laying, strongly correlated with lay date in April (average $r = 0.83$). At this time, the ocean environment around Triangle Island is dominated by water-masses from the south-southeast. However, for sympatric rhinoceros auklets, chl *a* along broad shelf-break areas in April prior to lay dates in May strongly correlated with lay date (average $r = 0.76$). Occurring after the spring transition, these water-masses flow primarily from the northwest. Consistent with other bird species, both auks appear to respond to information about food production, but at different spatio-temporal scales. We suggest that these different responses to environmental cues reflect species-specific differences in female migration behaviour, and an attempt by Cassin's auklets to bet-hedge against phenological mismatches.

KEY WORDS: Lay date · Chlorophyll *a* · Breeding phenology · Egg-laying date · Seabirds · Time-series · *Ptychoramphus aleuticus* · *Cerorhinca monocerata*

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1. INTRODUCTION

The reproductive traits that contribute most to lifetime fitness in birds can be either directly or indirectly linked to a female's decision about when to breed (Perrins 1970). A predominate view is that the timing of breeding (i.e. breeding phenology, defined as when an individual initiates egg laying) is ultimately determined by the availability of food to support egg production and offspring growth (Lack 1968, Perrins 1970). For the majority of bird species,

breeding occurs each year within a limited, seasonal window of opportunity wherein environmental conditions are best suited to provide offspring with a readied supply of food resources. The literature concerning avian phenology is replete with examples illustrating how female birds rely on seasonally predictable environmental cues to synchronize laying activity so that offspring are given the best odds for survival (Perrins 1970, Williams 2012). For example, in passerines, the timing of egg laying has been linked to air temperature (Brommer et al. 2008, Por-

lier et al. 2012, Williams et al. 2015), to plant phenology (Bourgault et al. 2010), and to the emergence of insect prey species (Pearce-Higgins et al. 2010, Williams et al. 2015). When the interval between the perception of such cues and the breeding response is short (e.g. a lag-time of less than 1 mo), the risk of mismatching food availability to reproductive energy requirements is minimized (Padilla & Adolph 1996, Hipfner 2008, Lof et al. 2012). However, recent work, again with passerines, has shown that females can respond to environmental cues operating up to 3 mo before egg laying occurs (Husby et al. 2010, Williams et al. 2015). Such extreme lag times tend to occur in non-migratory passerines that are resident around breeding areas in winter, which exposes them to local environmental cues (Husby et al. 2010, Williams et al. 2015). Much less is known about the environmental variables that migratory birds use to cue laying activity, and where and when those cues best predict lay date.

For sedentary, non-migratory birds, i.e. those that remain resident near breeding colonies throughout the non-breeding period, local conditions can define an 'environment of selection' wherein physico-chemical cues of food availability and individuals' responsiveness to them result in selection for phenotypes that best predict an optimal time for breeding (e.g. lay date, Visser et al. 2010; although in seabirds age and experience can be important predictors of early laying propensity, Pyle et al. 2001). Studies examining such cues have found a consistent link between mid-winter indicators of food production and the initiation of laying months later. In European starlings *Sturnus vulgaris* a strong relationship between February temperatures at a local breeding area and breeding phenology months later has been observed, which predicts the temperature-dependent development and emergence of the starlings' primary insect prey in spring (Williams et al. 2015). A similar phenomenon has been identified in resident, non-migratory populations of seabirds. Even moderate upwelling in early to mid-winter can seed local areas with nutrients that enhance productivity and prey availability; such 'pre-conditioning' then leads to healthier populations and earlier starts to the breeding season, as demonstrated in resident (as opposed to migratory) populations of Cassin's auklets *Ptychoramphus aleuticus* and common murre *Uria aalge* at the Farallon Islands, California, USA (Schroeder et al. 2009, Black et al. 2010, Johns et al. 2020). Collectively, these studies suggest that mid-winter conditions and/or temperatures might set the trajectory of growth and final biomass of food resources, thus pro-

viding important local-area information about eventual breeding season prey availability and a cue for optimal breeding times in resident birds. However, migratory birds can be distributed thousands of kilometres away from breeding areas during the non-breeding period, far outside of their environment of selection. The environmental variables and cues that these birds experience prior to laying may thus be very different from those back at the local breeding area (Visser et al. 2004, Phillips et al. 2005, Shaffer et al. 2006). Although photoperiodic cues are used to initiate seasonally predictable movements towards breeding areas, and thus general times for breeding activity (Gwinner & Helm 2003), inter-annual variation in local environmental cues can be important for modifying or fine-tuning the precise dates on which laying begins.

In this study, we examined the relationship between pre-breeding indicators of food availability in the local 'environment of selection' and lay dates in 2 closely related, migratory Pacific seabirds, namely Cassin's auklets and rhinoceros auklets *Cerorhinca monocerata*, breeding in sympatry at an island colony in the north-east Pacific Ocean. Both species are known to migrate thousands of kilometres throughout the northern Pacific (although as noted, some populations of Cassin's auklets can be non-migratory; Schroeder et al. 2009, Black et al. 2010, Johns et al. 2020), spending the non-breeding period in winter from the Southern California Bight to northward areas in the Gulf of Alaska and the Aleutian Islands (Studholme et al. 2019, Ainley et al. 2020, Gaston & Dechesne 2020, Hipfner et al. 2020). Using a 10 yr phenological dataset for rhinoceros auklets and an 8 yr dataset for Cassin's auklets, we explored the hypothesis that indicators of marine food availability (chlorophyll *a*, chl *a*) and sea surface temperatures (SSTs) cue or predict lay date in both species. Although various seabird studies have revealed links between the timing of reproduction and covariates like upwelling strength, sea surface height, and other large-scale climatological phenomena like the El Niño–Southern Oscillation, the Pacific Decadal Oscillation, and the Southern Oscillation Index (Wolf et al. 2009), all of these tend to correlate with and influence levels of marine production. As our specific aim was to examine the links between food availability and lay dates, we decided to focus our analyses on the relevant food indicators that are easy to measure at local scales.

Recent tracking studies of Cassin's auklets (Studholme et al. 2019) and rhinoceros auklets (Hipfner et al. 2020) have revealed the great spatio-temporal ex-

tent of non-breeding migrations, and a degree of sexual dimorphism in the migratory behaviour of Cassin's auklets, where some females show a tendency to remain along the coast of British Columbia (Canada) relatively close to the breeding colony at Triangle Island year-round, while many females and most males migrate further afield towards southern California or the southern Alaskan coasts (Studholme et al. 2019). No matter which strategy is used, Cassin's auklets return to Triangle Island in early February, whereas rhinoceros auklets arrive in April (Studholme et al. 2019, Hipfner et al. 2020). We thus predict that mid-winter measures of local production at the 'environment of selection' around the colony (Visser et al. 2010, Williams et al. 2015) will predict the lay dates of female Cassin's auklets, due to their tendency to remain resident and/or return early in February. In contrast, for rhinoceros auklets which arrive later in April, springtime measures of local production may be more important for cueing the laying activity of females.

2. MATERIALS AND METHODS

2.1. Study location and field methods

This study was conducted at Triangle Island, British Columbia, Canada (50° 52' N, 129° 05' W). Triangle Island is the outermost island in the Scott Islands archipelago, within a productive transition zone between the California and Alaska Currents. The island harbours the largest seabird breeding colony along the Pacific coast of Canada, which includes the world's largest Cassin's auklet breeding colony with ~550 000 breeding pairs, and a large colony of ~42 000 pairs of rhinoceros auklets (Rodway 1991).

Our analysis of lay date consisted of 462 breeding events by female Cassin's auklets in 8 years, spanning a 17 yr period (1999, 2002–2007, and 2015), and 508 breeding events by female rhinoceros auklets in 10 years, spanning the same 17 yr period (1999–2007, 2015). At Triangle Island, sex was determined via bill depths (Knechtel 1998). For both species, all breeding events were for the first laying attempts only, and did not include any re-laying attempts or second broods (which do not occur at Triangle Island). In each year of study, we monitored >50 nest burrows, for both species, at 5 d intervals, from which we determined the median date of laying (Cassin's = 57.8 ± 16.2 SD nests yr⁻¹; rhinoceros = 50.8 ± 12.9 nests yr⁻¹). Nest monitoring began before initiation of laying for both species based on historical data. For Cassin's auklets,

laying begins in the spring, from late March to early April, while for rhinoceros auklets, laying generally begins in early May (Fig. 1). On each day of monitoring, the numbers of burrows containing eggs was recorded. Both species lay a single-egg clutch.

2.2. Oceanographic data and analysis

Both Cassin's auklets and rhinoceros auklets extensively use the Queen Charlotte Sound and shelf-break waters just prior to the breeding season (Studholme et al. 2019, Hipfner et al. 2020). We therefore defined a spatial grid around Triangle Island within which we explored correlations between the heterogeneous oceanography (Borstad et al. 2011) and lay date via a sliding window spatio-temporal analysis. The established grid encompasses the shelf-break waters near canyons and seamounts with sloping bathymetries where Cassin's auklets prefer to forage (Domalik et al. 2018), as well as the on- and off-shelf waters favoured by rhinoceros auklets. Details concerning the processing of the geolocation data and the calculation of utilization distribution contours can be found in Studholme et al. (2019) and Hipfner et al. (2020).

Daily satellite chlorophyll concentrations (chl *a*, mg m⁻³) with a 4 km resolution were retrieved from the Ocean Colour Climate Change Initiative project v.4.2 developed by the European Space Agency (<https://esa-oceancolour-cci.org/>), which merges global data from MERIS, Aqua-MODIS, SeaWiFS, and VIIRS. Daily SST (°C) with a 4 km resolution were retrieved from Pathfinder v.5.3 developed by NOAA (Saha et al. 2018). Only night data were used in the analysis, to avoid potential biological biases when averaging day and night temperature data (Wellington et al. 2001, Casey 2002, Wang & Tang 2010). Within the area of interest, the data were extracted in a series of contiguous bounding boxes, or 'cells', that each measured 0° 26' 27.6" by 0° 25' 58.8" (~49 km × 29 km or 1421 km²) for the N–S and E–W directions, respectively. A total of 17 cells were selected following the trend of the continental slope (Fig. 2). Collectively, all 17 cells cover an area of 24 157 km².

Daily average values of chl *a* and SST were calculated for each grid cell for the period from 1 November until the median lay date of each species in each year. Next, these daily chl *a* and SST values for each cell were averaged within a 10 d sliding temporal window, starting on 1 November and extending until 10 d before median lay date. Pearson's correlation coefficients between median lay date and the averages

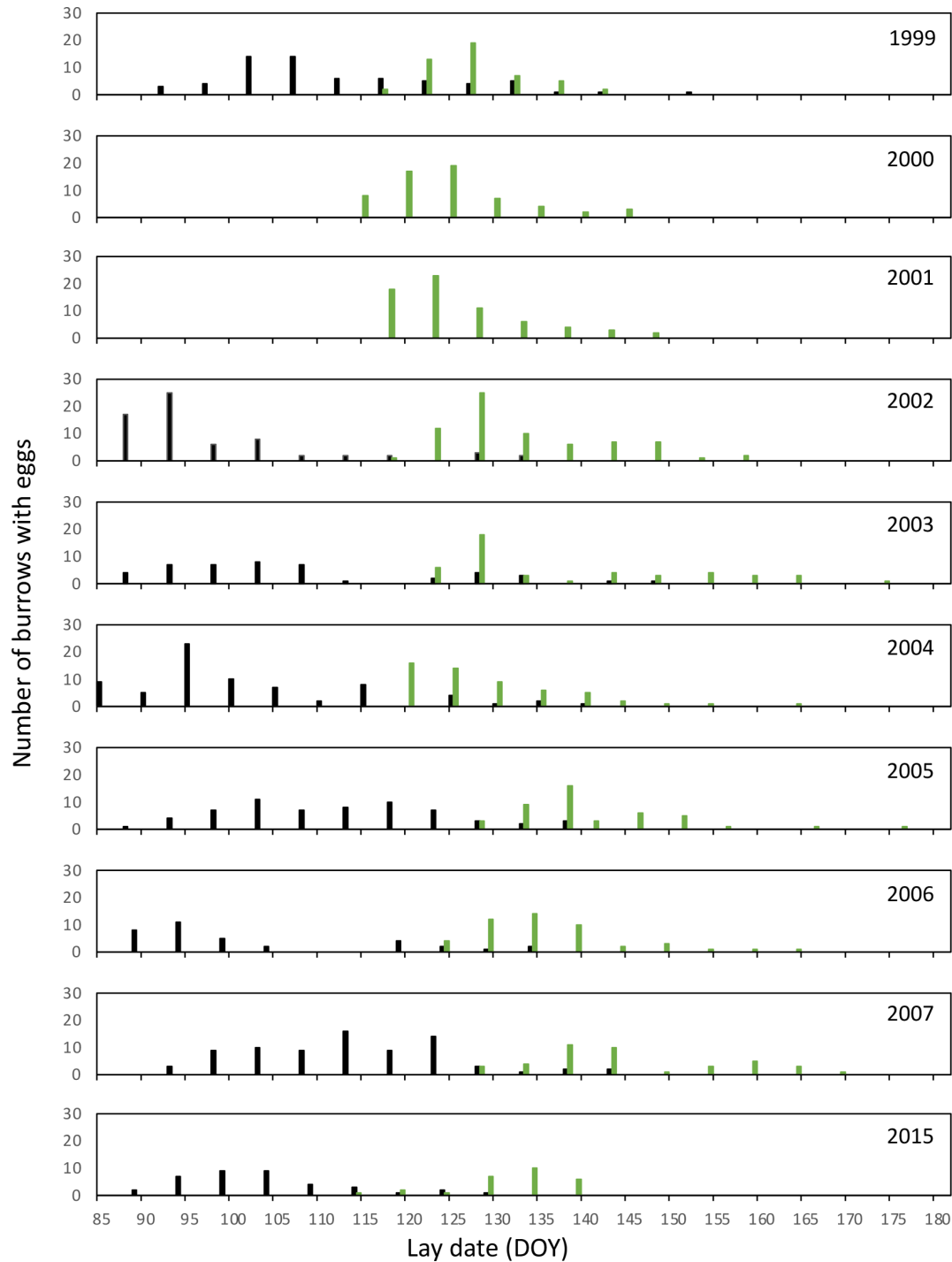


Fig. 1. Interannual distribution of Cassin's auklet (black bars) and rhinoceros auklet (green bars) laying activity at Triangle Island, British Columbia (Canada), in each year of study. Day of year (DOY) 91 = 1 April, DOY 121 = 1 May

of chl *a* and SST were calculated for all sliding temporal windows in all cells. Statistical significance was set at $\alpha = 0.05$. The Benjamini & Hochberg (B-H) correction, a Bonferroni-type test, was used to control for false discovery rate caused by multiple comparisons (Benjamini & Hochberg 1995, Cortés et al. 2020).

When phenological time series display a temporal trend, it is likely that spurious correlations will emerge when relating the phenological data to some other time series, like SST or chl *a*. It is thus important to screen for, and if present, account for temporal trends in median lay date (Noriega & Ventosa-

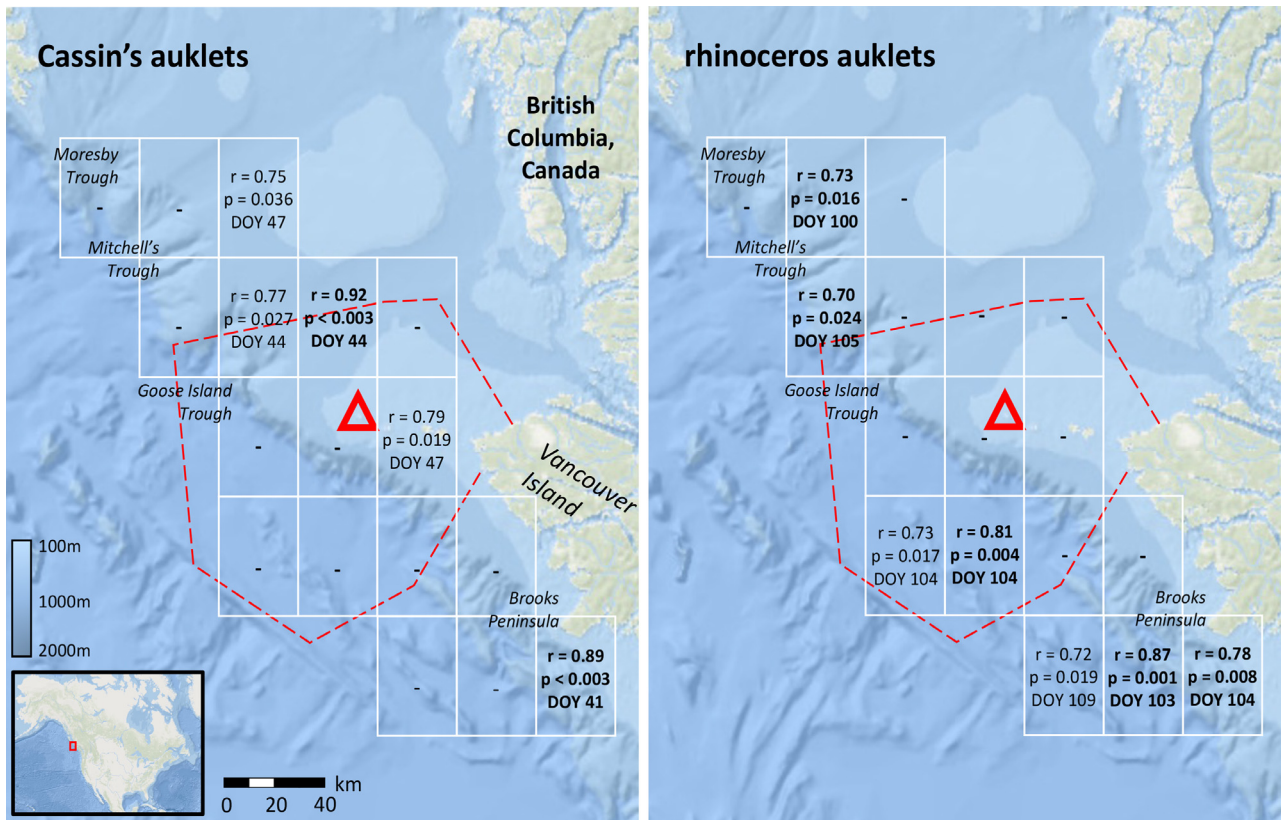


Fig. 2. Sliding spatio-temporal window analysis for female Cassin's auklets and rhinoceros auklets. The grid box represents the general distribution of female Cassin's auklets in mid-winter, as revealed by geolocation tracking (Studholme et al. 2019, Hipfner et al. 2020). This region was divided into a grid so that the sliding window analysis could calculate mean 10 d variation in oceanographic variables (chl *a*, sea surface temperature [SST]) across years and across a broad, spatially dynamic environment. Only correlations with chl *a* are presented here (no significant correlations between lay date and SST); those in **bold** indicate significance after multiple comparison testing (Benjamini-Hochberg corrections). Correlation coefficients between mean chl *a* and lay date and the associated p-values are presented in all cells where $r \geq 0.70$. The day of year (DOY) when a significant correlation occurred interannually is also presented. DOY 44 = 13 February and DOY 104 = 14 April. The breeding colony at Triangle Island, British Columbia, is indicated by the red triangle. The dashed line around the island represents the boundary of the Scott Islands Marine National Wildlife Area

Santaulària 2007, Haest et al. 2018). Following Haest et al. (2018), we examined whether linear, quadratic, or cubic trends were present in the time series.

From the sliding window analysis, chl *a* levels from the month that revealed the greatest number of high correlations between chl *a* and median lay date (February for Cassin's auklets, April for rhinoceros auklets) were plotted against the skew of lay dates. This was done to explore whether the shapes of the laying distributions were correlated with the most relevant local-area productivity indicator. This indicator value was calculated as the average monthly chl *a* value across all cells yielding significant correlations (i.e. all cells with $p < 0.05$, Fig. 2).

Lay date distributions, skew analyses, and Pearson's correlations between lay date and chl *a* were conducted using R version 4.0.2. Analysis of linear,

quadratic, and cubic trends in the phenological data were run using SPSS 27. Downloaded chl *a* and SST data were imported to Microsoft Excel version 16.54, wherein the correlational sliding window analysis was programmed.

3. RESULTS

The interannual distributions of lay dates at Triangle Island for both auk species are presented in Fig. 1. In general, the start of laying by Cassin's auklets varied by only 1 wk among years, and once initiated, most birds laid quickly while small numbers laid later as time advanced (e.g. laying is left-skewed with respect to date; Fig. 1). In contrast, the start of laying by rhinoceros auklets varied by up to 2 wk,

but once initiated, laying was distributed relatively normally without skew (Fig. 1).

We did not detect any statistically significant linear, quadratic, or cubic trends in phenological time series (all $p > 0.09$), indicating that the sliding spatio-temporal window analysis was not prone to spurious correlations due to trended phenological data (as per Noriega & Ventosa-Santaulària 2007, Haest et al. 2018). For Cassin's auklets: linear fit $R^2 = 0.017$, $F = 0.105$, $p = 0.757$; quadratic fit $R^2 = 0.046$, $F = 0.120$, $p = 0.890$; cubic fit $R^2 = 0.519$, $F = 1.435$, $p = 0.357$. For rhinoceros auklets: linear fit $R^2 = 0.142$, $F = 0.991$, $p = 0.358$; quadratic fit $R^2 = 0.369$, $F = 1.464$, $p = 0.313$; cubic fit $R^2 = 0.772$, $F = 4.514$, $p = 0.090$. We thus proceeded with interpretation of our spatio-temporal sliding-window correlation analysis.

For Cassin's auklets, variation in lay date and chl *a* revealed 5 cells within the study area that produced significant correlations: all were significant at the stated alpha level ($p < 0.05$), with 2 cells significant after at B-H correction to $p < 0.003$. The mean correlation across these 5 cells was $r = 0.83$, which occurred interannually on day of the year (DOY) 45,

or 14 February (Fig. 2). For rhinoceros auklets, 7 cells produced significant correlations, 3 of which were significant after B-H correction to $p < 0.008$. The mean correlation across these 7 cells was $r = 0.76$, which occurred on DOY 104 or 14 April (Fig. 2). As the sliding window component of the analysis ran at 10 d intervals, the midpoint date (i.e. DOY) when chl *a* levels in a given cell were significantly correlated with lay date is indicated at each cell (Fig. 2). Spatio-temporal variation in SST did not produce any significant correlations with lay date, and so we do not present these data in any figures.

For both species, the averaged chl *a* levels from cells where significant correlations were identified in the sliding window analysis (Fig. 2) were negatively correlated with median lay date (Fig. 3), indicating earlier laying when food production indicators were high (Cassin's auklets: $r = -0.956$, $p < 0.001$; rhinoceros auklets: $r = -0.756$, $p = 0.011$). The skew in Cassin's auklet lay date was positively correlated with February chl *a* levels (Pearson's correlation: $r = 0.747$, $p = 0.033$; Fig. 3). This suggests a greater synchrony (left skew) of laying when winter food indicators are high, and asynchrony when indicators are lower resulting in laying without a distinct peak and little skew. No significant correlations were observed between skewness and rhinoceros auklet lay dates ($p = 0.700$, Fig. 3).

4. DISCUSSION

Using multi-year phenological datasets, we have revealed significant population-level relationships between lay date and measures of local marine production in 2 species of Pacific auks breeding in sympatry at one of the largest breeding assemblies in the north Pacific, Triangle Island, British Columbia. The idea that breeding phenology is determined in part by the availability of food to support egg production and offspring growth dates back to Lack (1968), but what is most striking about our results is that the 2 species breeding in the same location in springtime differed markedly in their response to the timing of marine production measures. In 8 study years, April laying by Cassin's auklets was strongly correlated with

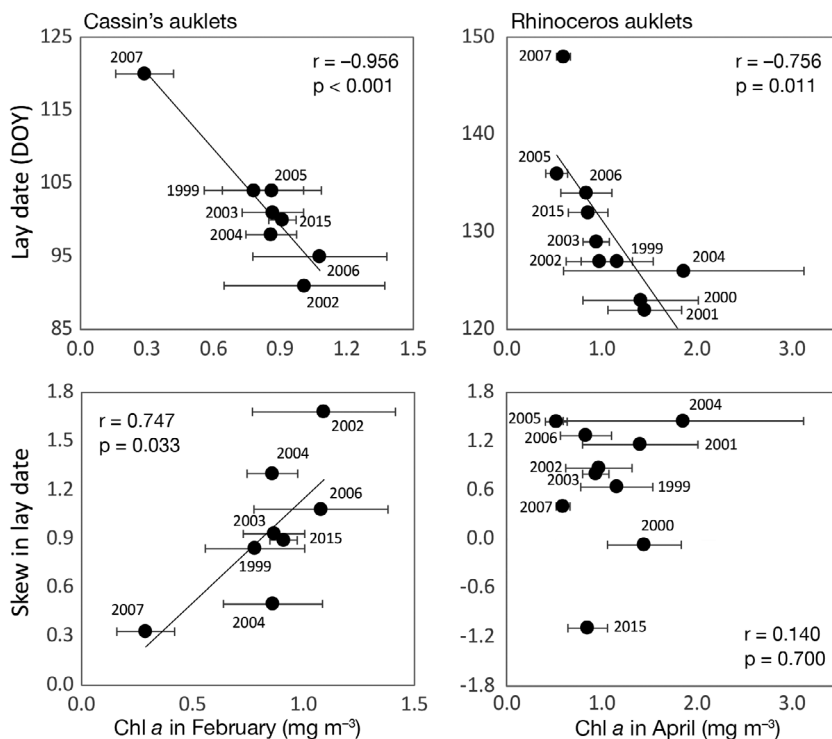


Fig. 3. Lay dates and skew in lay dates of Cassin's auklets and rhinoceros auklets relative to averaged chl *a* levels in February and April, respectively. Chl *a* values were averaged from all cells highlighted (with **bold** text) for Cassin's auklets and for rhinoceros auklets in Fig. 2. Solid lines indicate the direction of significant correlations. Interannually, all Cassin's auklets lay date DOYs fall within April, while for rhinoceros auklets DOYs fall within May

chl *a* concentrations in the shelf waters around Triangle Island up to 2 mo earlier, in mid-February. In contrast, 10 years of rhinoceros auklet data showed that May laying was correlated with chl *a* levels just a few weeks earlier in April, primarily along the shelf-break waters to the west, south, and south-east of Triangle Island (Fig. 2). These different spatial and temporal responses likely reflect exposure of females from each species to different seasonal water-mass movements along the British Columbia coast, facilitated by differences in migration behaviour and breeding schedule, and an attempt by Cassin's auklets to bet-hedge against phenological mismatches given their greater sensitivity (i.e. mortality) to poor ocean conditions in winter (Morrison et al. 2011). In contrast, rhinoceros auklets are much more resilient to poor ocean conditions in winter (Morrison et al. 2011).

4.1. Responses to the timing of chl *a* levels

Similar to many bird species, springtime measures of food production just weeks before laying predicted the inter-annual variation of rhinoceros auklet lay dates (Fig. 2). The link between April chlorophyll production and rhinoceros auklet laying was highly correlated, which corroborates the idea that early laying is facilitated by the arrival of high productivity water flowing southwards to Triangle Island during the spring transition in early April (Borstad et al. 2011). It is during this transitional state, when the northward flowing water-masses dominating the winter seascape are replaced by southward flowing waters, when female rhinoceros auklets begin arriving from wintering areas in the south (Hipfner et al. 2020). This transition is significant, as it determines the recruitment of young-of-the-year Pacific sandlance *Ammodytes hexapterus*, upon which female rhinoceros auklets depend to support a critical period of follicle recruitment and egg production (Hipfner et al. 2010a). Females consuming a diet composed principally of sandlance tend to develop yolks rich in lutein and zeaxanthin (Hipfner et al. 2010a), which are both linked to downstream fitness metrics like incubation success, chick growth, and fledging success (Hipfner et al. 2010b,d, Borstad et al. 2011). Pre-breeding food supply in April underlies the strong correlation between chl *a* and lay date for rhinoceros auklets (Fig. 3). Although some rhinoceros auklets can be found near the breeding colony in mid-winter (Hipfner et al. 2020), the proportion tends to be much smaller than that of Cassin's auklets (Studholme et al. 2019).

In contrast, the response of Cassin's auklets to marine production measures was timed very differently: chl *a* in early February, approximately 2 mo prior to laying, predicted median lay dates (Fig. 3). The areas showing the strongest correlations were to the north-west of Triangle Island, in the shallower waters of the continental shelf. In winter, the predominant influx of water to the region comes from the south-east along Vancouver Island, extending from the Davidson and California Currents further south. One might expect these 2 species, which are both highly migratory and show a high degree of distributional overlap in the north Pacific during the non-breeding period and lay sympatrically less than 1 mo apart (Studholme et al. 2019, Hipfner et al. 2020), to respond to similar local-area production cues in the waters surrounding Triangle Island, but this was not the case. Given that female Cassin's auklets are present around Triangle Island in mid-winter, i.e. earlier relative to rhinoceros auklets (Studholme et al. 2019), they may be choosing to remain close to, or return early to, the environment of selection (Visser et al. 2010), thus exposing themselves to local environmental conditions in mid-winter rather than those of known wintering areas such as the Southern California Bight or southern Alaska (Studholme et al. 2019). This partial migrancy or early return would thus explain the strong correlation between February chl *a* and lay date in Cassin's auklets, although this should be more rigorously tested with additional tracking work. However, even fully migratory females that migrate to the Southern California Bight or to southern Alaska will nevertheless return to Triangle Island in early February, as shown by Studholme et al. (2019). Thus, regardless of whether a Cassin's auklet shows partial or full migration, local distributions around Triangle Island in mid-winter are an important behavioural difference from rhinoceros auklets for 2 non-mutually exclusive reasons.

First, previous work experimentally testing the effects of date and intrinsic quality on Cassin's auklets showed a strong role of maternal quality during the early breeding stages of laying and incubation, presumably because those in good nutritional condition can maintain some constancy of incubation duties (Hipfner et al. 2010c). The ability of female Cassin's auklets to attain good pre-laying condition is largely determined by the degree of temporal matching with food supply, which is fundamentally linked to both lay date and to breeding success (Hipfner 2008, Hipfner et al. 2010b). This suggests a proximate mechanism wherein high chl *a* equates to good foraging opportunities and early laying. It may also be pos-

sible that some female Cassin's auklets remain locally distributed in winter, or at least return to the environment of selection early, to increase the probability that they will be present for the pre-breeding peak of *Neocalanus cristatus* production, a copepod species which strongly predicts Cassin's auklet breeding success when laying and production are temporally matched during the spring transition (Hipfner 2008).

Second, partial migration might also reflect the fact that female Cassin's auklets are far more susceptible to nutritional stress (Tate et al. 2021) and winter mortality than rhinoceros auklets, especially in years dominated by El Niño (Morrison et al. 2011) or other climate anomalies (e.g. 'The Blob'; Kintisch 2015, Jones et al. 2018, Tate et al. 2021). Winter mortality might select for a female-specific, partial migration strategy, or an early return of females, in an attempt to bet-hedge against years when marine production is poor. Although there could be thermoregulatory and energetic costs associated with local residency in mid-winter, there must be some overriding benefit conferred to females who are resident all winter long or who migrate from distant wintering areas to arrive at Triangle Island in early February (Studholme et al. 2019).

4.2. Hypotheses concerning the role of date and individual quality

In general, birds aim to lay as early as possible during a breeding season so as to avoid the seasonal decline in reproductive success that typically occurs (passerines, Verboven & Visser 1998; ducks, Dawson & Clark 2000; geese, Lepage et al. 2000; raptors, Daan et al. 1990; seabirds, Spear & Nur 1994), and there is some evidence of directional selection for early lay date (Sheldon et al. 2003), despite the potential costs of breeding too early (e.g. van Noordwijk et al. 1995). Two main hypotheses have been posed to explain this phenomenon. The 'date hypothesis' suggests that declining reproductive performance is driven by seasonally diminishing food supply or habitat quality, or a mismatch between laying date and peak environmental conditions, while the 'quality hypothesis' suggests that intrinsic differences between individual phenotypes permit higher-quality birds to lay earlier than lower-quality birds (Verhulst et al. 1995).

The median lay dates used as our indicator of variation in breeding phenology are driven by (1) the date of the start of laying by each species and (2) the distribution of laying that follows the first egg. In

Cassin's auklets, the date on which the first eggs are laid is mostly invariant, occurring annually at the very end of March and the first few days of April, over a span of ~7 d interannually (Fig. 1), but the laying distribution varies from synchronous in favourable years with high chl *a* levels (i.e. skewed towards early laying in 2002; Fig. 1) to asynchronous (prolonged and without a distinct peak) in unfavourable years with low production (as in 2007; Fig. 1). Viewed alternatively, there is a high degree of skew in the laying distribution of Cassin's auklets when local chl *a* levels are high in mid-winter (Fig. 3). In years when food availability/abundance is indeed good, this enables more females with inherently better quality (Johns et al. 2020) to lay earlier and accrue the energetic resources needed for egg production and early laying, while lower-quality individuals can also lay earlier. When conditions are poor, the laying distribution becomes less skewed and extends over a greater number of days. Consistent with many other bird species, early laying is the best strategy for Cassin's auklets, as indicated by experimental work showing that when the earliest laying females have their eggs removed, re-laying occurs after a 2 wk delay, and this delay causes those females to match the population-wide seasonal decline in breeding success common to many bird species (Hipfner et al. 2010d). This illustrates the risks associated with late laying in Cassin's auklets, and why some will still attempt to lay as early as possible irrespective of local area conditions. As we have shown here, the timing of spring chl *a* levels just prior to laying does not predict lay date, but rather, it is mid-winter chl *a* levels that matter. However, the mechanism linking mid-winter primary productivity to lay date is unknown, but presumably this involves nutritional conditioning and individual quality effects.

In contrast, rhinoceros auklets seem to have a greater flexibility to initiate and match laying activity to local area production after the spring transition. The date when first eggs are laid by female rhinoceros auklets varied by up to 2 wk interannually, but once initiated, the shape of the laying distribution remained fairly normal (unskewed) compared to Cassin's auklets (Fig. 1). This suggests that rhinoceros auklets are more flexible around the initiation of laying, with females more capable of tracking local breeding-area conditions upon their arrival from overwinter migration as a way to fine-tune actual lay dates (Hipfner et al. 2008). As such, the decision about when to begin laying does not conform to a simple rule of laying as early as possible, as seems the case for Cassin's auklets.

In conclusion, because both Cassin's auklets and rhinoceros auklets tend to exhibit predictable demographic and behavioural responses to environmental variation, they have been regarded as indicator species of conditions in marine ecosystems. Here, we show how intimately linked lay date is to marine conditions, but at different temporal scales, which suggests that there is a complex, species-specific relationship between the phenology of marine phytoplankton production, potential prey production, and the timing of breeding. The relationship between seabird life history and marine conditions is an important topic for study, especially because phenological responses to climate change can result in the destabilization of ecological processes, thereby threatening ecosystem function (Thackeray et al. 2016). A greater understanding of the proximate factors linking ocean conditions to seabird phenology is needed if we are to predict the effects of climate change and develop management plans. We note here that chl *a* levels in the shelf-break waters at Brooks Peninsula and to the northwest of Triangle Island (Fig. 2) provided important cues to laying in both species. Currently, these regions do not lie within the Scott Islands Marine National Wildlife Area, the boundaries of which were informed by auk foraging patterns observed during the summer breeding season alone.

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