

# Oceanographic drivers of winter habitat use in Cassin's Auklets

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**Abstract.** Reduced prey abundance and severe weather can lead to a greater risk of mortality for seabirds during the non-breeding winter months. Resource patterns in some regions are shifting and becoming more variable in relation to past conditions, potentially further impacting survival and carryover to the breeding season. As animal tracking technologies and methods to analyze movement data have advanced, it has become increasingly feasible to draw fine-scale inference about how environmental variation affects foraging behavior and habitat use of seabirds during this critical period. Here, we used archival light-sensing tags to evaluate how interannual variation in oceanography affected the winter distribution of Cassin's Auklets from Southeast Farallon Island, California. Thirty-five out of 93 geolocators deployed from 2015 to 2017 were recovered and successfully recorded light-level data, from which geographic positions were estimated. Step-selection functions were applied to identify environmental covariates that best explained winter movement decisions and habitat use, revealing Cassin's Auklets dispersed farther from the colony during a winter with warm SST anomalies, but remained more centralized near the breeding colony during two average winters. Movement patterns were driven by avoidance of areas with higher sea surface temperatures and possible limits of dispersal from the breeding colony, and selection for areas with well-defined mesoscale fronts and cooler surface waters. Through multiple years of tagging and the application of step-selection functions, a robust and widely applied approach for analyzing animal movement in terrestrial species, we show how interannual differences in the movement patterns of a small seabird are driven by oceanographic variability across years. Understanding the winter habitat use of seabirds can help inform changes in population structure and measures of reproductive success, aiding managers in determining potential causes of breeding failures.

*Key words:* geocator; habitat use; marine predator; movement ecology; seabird; step-selection function.

## INTRODUCTION

Released from the obligation of incubation and care of dependent young, many seabirds disperse widely from colonies during the non-breeding winter period to access more favorable foraging locations. Conditions experienced during the winter can strongly impact the probability of survival to, and success during, the subsequent summer breeding season (Frederiksen et al. 2004, Pineda and Lobo 2009, Sydeman and Bograd 2009, Harding et al. 2011). Departures from climatological norms can result in reduced primary production and more severe storms during the winter, leading to a higher risk of mortality for seabirds through starvation and injury (Barbraud and Weimerskirch 2003, Harris et al. 2005, Genovart et al. 2013). Despite this, the ways in which interannual variation in oceanographic conditions affect winter space use is not well understood for most seabirds.

Important foraging habitat for marine megafauna described by telemetry data has been linked with remotely collected environmental covariates, particularly sea surface temperature (SST), chlorophyll *a* concentration, and upwelling strength. These and other oceanographic variables are strong drivers of primary production and are treated as indirect measures of prey abundance and distribution. Mesoscale features such as oceanographic fronts, eddies, and filaments can amplify prey abundance through physical processes that concentrate plankton or enhance primary production (Space et al. 1998). Tracking studies on a wide range of taxa show marine predators such as seabirds regularly visit predictable mesoscale fronts (Bost et al. 2009), large features that partially control the at-sea distribution and foraging success of many seabird groups (Russell et al. 1999, Tew et al. 2009). Environmental perturbations, such as abnormally warm surface waters, have been linked to a reduction or absence of traditionally reliable fronts and foraging "hotspots" (Kahru et al. 2018), leading to changes in the dispersal and distribution patterns of megafauna. Thus, multi-year tracking studies of marine

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predators can inform managers on the expected effects of interannual variation and directional climate change on the movements and behavior of marine megafauna.

The breeding success and survival of smaller obligate planktivores, in particular Auklets, are highly sensitive to environmental variability during the summer season (Kitaysky and Golubova 2000, Veit and Manne 2015). The Cassin's Auklet (*Ptychoramphus aleuticus*), for example, has experienced major population declines following the 1998 and 2004 El Niños and other localized sea surface temperature anomalies (Nur et al. 2011). The longest running time series of life history and reproductive data on Cassin's Auklets comes from a colony on Southeast Farallon Island (SEFI), California, where a sample of known-aged individuals have been studied since 1983. A strong connection between summer oceanographic conditions and breeding success has been established for this study population (Lee et al. 2007, Wolf et al. 2010, Johns et al. 2017). Given that little is understood about the effects of winter oceanography on Cassin's Auklets, coupling the 36-yr time series with measurements of non-breeding movement and habitat use across multiple years would lead to a better understanding of how this and similar species adjust to interannual variation in oceanography. Information on how winter foraging conditions may carry over to the following breeding season and impact overall population dynamics is particularly important given expected future warmer climate scenarios.

The limited information on the winter habitat use of Cassin's Auklets comes from extensive ship-based and aerial surveys along the California coast in the early 1980s. Those surveys found Auklets dispersed from their major colony at SEFI to west of the Southern California Bight and throughout the central California coast following the breeding season (Briggs et al. 1987). Aerial surveys during the same period also revealed a shift to deeper water west of the shelf break in the winter months (Briggs et al. 1987). In more recent work using radio telemetry, Adams et al. (2004) demonstrated that some individuals from colonies in the Channel Islands moved north to productive upwelling regions post-breeding. Currently, the most cost-effective devices used to track small seabirds over long periods are miniature archival light-sensing tags, hereafter "geolocators." Recent geocator tagging work on Cassin's Auklets at several colonies in British Columbia show post-breeding dispersal events into central and southern California during the winter (Studholme et al. 2019). These studies, however, did not directly statistically connect winter movements of individuals to oceanographic conditions, and no such studies have been conducted on populations of Cassin's Auklets breeding in the southern portion of their range.

We used movement data derived from geolocators to describe how interannual variation in oceanographic conditions impacted the movement decisions and space-use patterns of a small planktivorous seabird over multiple years of tagging. Specifically, our objectives were to

(1) characterize the winter movement behavior of Cassin's Auklets from SEFI, (2) estimate how spatial patterns in oceanographic conditions affect habitat use and movement decisions using a step-selection function analysis, and (3) interpret interannual changes in habitat use in the context of variation in parameters that drive the abundance and distribution of zooplankton on which this sentinel species depends. Finally, habitat selection and movement results were compared to 36 yr of demographic data from the same colony to infer links between winter movement behavior, oceanography and climate, and population dynamics.

## METHODS

### *Tag deployment*

The study colony on Southeast Farallon Island is located approximately 43 km west of San Francisco in California (37°42' N, 123°00' W). Ninety-three Migrate Technology Intigeo-C65 geocator tags were deployed in mid-June during the summer chick provisioning periods of 2015–2017 (Table 1). Uniquely marked Auklets from established pairs breeding in artificial wooden nest boxes were selected for tag deployment to increase the odds of tag recovery. Geolocators were mounted to plastic Darvic overlapping leg bands using UV-stable cable ties and glue, and secured to the bird's left tarsus. Birds not previously banded received a numeric stainless steel band on the right tarsus. Total mass of each tag did not exceed 1 g and were expected to have no effect on flight, foraging, or reproduction (Carey 2011, Kim et al. 2014). Recovery of tags occurred the following season during the egg-laying period in late March and early April. Pre- and post-deployment calibration periods were conducted on the island for 7 d each, to establish the relationship between observed and predicted light intensity for each tag, and to account for changes in tag opacity over time.

Although there was no expectation of adverse tag effects, to be cautious we compared the reproductive output of tagged and untagged pairs. As part of a long-term continuous monitoring program, hatching success (HS) and fledging success (FS) of active pairs within a sample of ~446 nest boxes were recorded (Pyle 2001), providing detailed reproductive information on tagged and untagged individuals. To test whether carrying a tag had an effect on breeding success the following year, generalized linear mixed models (GLMM, binomial with logit link) were fit with the R package lme4 (Bates et al. 2015) with HS and FS as response variables, tag as a fixed factor, and year as a random intercept term.

### *Data processing*

Twilight events corresponding to sunrise and sunset were annotated and validated from raw light-level data with the package GeoLight (Lisovski and Hahn 2012). Unrealistic erroneous twilight events from

TABLE 1. Summary of the number of geolocator tags deployed and retrieved on Cassin's Auklets from Southeast Farallon Island over the course of three tagging winters, along with number of tags with recoverable data.

Winter	No. deployed	No. retrieved	Success rate	Data recovered	Sex		
					M	F	UNK
2015–2016	26	17	65%	13†	4	8	1
2016–2017	34	26	76%	9	5	4	0
2017–2018	33	24	73%	13†	6	6	1
Combined	93	67	72%	35	15	18	2

† Eight tags were removed (four from 2015–2016 and four from 2017–2018) to eliminate repeated measures of individuals tagged during multiple seasons and independence issues for individuals tagged from the same pair.

weather-related or behavioral shading were visually identified and excluded. An extension of the template fitting method (Ekstrom 2007) in the package FlightR (Rakhimberdiev et al. 2017) was used to estimate twice daily positions from raw light-level data, with longitude derived from the timing of local noon and midnight and latitude from day length. Error in the estimation of latitude using light-level data has been shown to range from 70 to 300 km depending on the degree of shading during twilight events (Phillips et al. 2004, Shaffer et al. 2005). The amount of error is reduced when using the template fitting observational model approach in FlightR, improving the error in latitude estimates to roughly 30–40 km (Rakhimberdiev et al. 2015). A hidden Markov model implemented using a particle filter in FlightR provided mean positions every 12 h, following the workflow outlined in Rakhimberdiev et al. (2015). Particles were constrained within a spatial box of 20° N × 50° N and 110° W × 135° W to reduce processing time, a robust dispersal area for Cassin's Auklets based on preliminary model runs on a subset of tags. This generated the most probable track of each Auklet, based on a set of priors for an assumed conservative max flight speed of 70 km/h (Spear and Ainley 1997), and a mask to exclude movements over land. Only movements during winter months (November through January) were analyzed here.

#### *Modeling habitat selection*

To determine how winter conditions influenced the distribution and movement patterns of Cassin's Auklets, step-selection functions (SSFs) were used to estimate selection coefficients for a set of biologically relevant environmental covariates (Fortin et al. 2005, Thurfjell et al. 2014). Unlike resource selection functions, SSFs couple observed “used” locations with a set of conditionally available “unused” locations at each step along the movement path. For each observed location, 20 matched available locations were generated by drawing a random step length from a gamma distribution and random turn angle from a Von Mises distribution (Avgar et al. 2016), both fitted with maximum likelihood to empirical step length and turn angle distributions from the tracking data (Appendix S1: Fig. S1). This assumed the available

locations were selected from a correlated random walk (CRW) on the same temporal and spatial scale as the animals' movements, and that only locations within one movement step of the current location were available for the conditional comparison. Aspects of the underlying movement model used in FlightR and possible stationary behavior of Auklets caused step lengths to be highly skewed toward 0, resulting in matched available locations that were spatially identical to observed locations. This caused many of the available steps to be environmentally identical to the observed step, and the invariance between the available and observed step did not permit estimation of sensible selection coefficients. To avoid this issue, step lengths less than 60 km, a conservative approximate error around each estimated geolocation (temporal resolution of each step = 12 h), were excluded before fitting the gamma distribution to empirical step lengths.

#### *Oceanographic covariates*

Spatially and temporally explicit environmental covariates known or hypothesized to be relevant to the movement ecology of Cassin's Auklets (Adams et al. 2010, Manugian et al. 2015) were extracted for all observed and available locations. Static covariates included bathymetry (depth), distance to the 200-m isobath (dis2shelf), and natural log of the distance to Southeast Farallon Island (dist2isl). Bathymetry and distance to shelf break were chosen to test whether Auklets favored the nearshore or offshore habitats, and distance to island to explain potential limits to dispersal from the breeding colony. Remotely gathered dynamic covariates included sea surface temperature (SST), an index for SST frontal features (front), and natural log of chlorophyll *a* concentration (chl *a*). Sea surface temperature can influence processes that drive primary production (Whitney 2015), which can be directly measured by the concentration of chlorophyll *a*, thus both variables are potential indicators of favorable foraging habitat. Temporal consistency of sea surface temperature and frontal features can change on time scales of weeks or less, through interactions with physical forces such as wind-stress and bathymetric features (Castelao et al. 2006), generally longer than the 12-h resolution of time-steps

within bird tracks used. Three-day interpolations of SST provided the highest temporal resolution while avoiding loss of data from cloud cover associated with winter storms. The frontal probability index applies an edge detection algorithm to identify pixels with gradients greater than  $0.375^{\circ}\text{C}$  (Breaker et al. 2005). A temporal resolution of 1 month was used to describe persistent large-scale frontal features that aggregate biological productivity, which were hypothesized to be important for lower trophic level predators like Cassin's Auklets (Bakun 2006, Bost et al. 2009, Tew et al. 2009). Covariates were extracted from the National Oceanographic and Atmospheric Administration ERDDAP data server using the R packages `extractomatic` (Mendelssohn 2018) and `rerddap` (Chamberlain 2017). Information on the source, resolution, and units of covariates are provided in Table 2.

#### Step-selection functions

Step-selection functions were fitted using conditional logistic regression, which parameterizes an exponential function to estimate the relative likelihood of Auklets selecting specific habitat characteristics during their next step (Avagar et al. 2017). The movement-independent habitat weighting function took the general form

$$\hat{w}(X) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 \dots \beta_p x_p)$$

with  $X$  a vector of matched observed and available locations, and  $\beta_i$  (for  $i = 1, 2, \dots, p$ ) the estimated selection coefficients for environmental covariates  $x_i$  (for  $i = 1, 2, \dots, p$ ). Greater positive values of  $\beta_i$  indicated a higher likelihood of Auklets choosing a set of environmental conditions, while more negative values indicated a higher likelihood of avoiding those conditions. Environmental covariates were standardized to enable direct comparison of the strength of regression coefficients. A standardized squared term for SST was also included to address the hypothesis that Auklets may avoid both extreme warm- and cold-water masses in favor of intermediate SSTs.

Rather than using a mixed-modeling framework to account for inter-individual variation in habitat selection

among Auklets, which can be computationally challenging for conditional logistic regression models (Duchesne et al. 2010), random-coefficients were estimated with a two-step approach. This involved applying the `Ts.estim()` function in the package `TwoStepCLogit` to first estimate coefficients for each individual and then combining those estimates using restricted maximum likelihood to achieve population-level coefficients (Craiu et al. 2011). This provided a pragmatic, robust method for dealing with individual variation when estimating selection parameters (Murtaugh 2007). Model selection was performed using Akaike's information criterion (Burnham and Anderson 2002) by fitting a biologically motivated candidate model set containing all possible combinations of covariates of interest with the `clogit()` function in the R package `Survival` (Therneau 2015). The `clogit()` function allows for computation of AIC, providing a measure of the most parsimonious model for each year.

Predictive performance of SSFs for each year was assessed with  $k$ -fold cross validation (Fortin et al. 2009). This was accomplished by first fitting the AIC-selected SSF to a training data set of 80% of the strata (selected randomly), and using this SSF to rank the estimated  $\hat{w}(X)$  for observed against available locations with the remaining 20% of data (Fortin et al. 2009). Ranks of observed locations were then tallied into 21 potential bins (lowest  $\hat{w}(X)$  = rank 1, highest  $\hat{w}(X)$  = rank 21), and Spearman's rank correlation ( $r_s$ ) applied between the bin's rank and frequency. The process was repeated 100 times to achieve a distribution of  $r_s$  assuming a non-random pattern of habitat selection. This procedure was also performed by ranking a randomly selected available location against the 19 other available locations (1–20) for each stratum and repeating 100 times to achieve a distribution of  $\bar{r}_s$  assuming a random pattern of habitat selection. Years where  $\bar{r}_s$  of observed locations was highly positive and different from  $\bar{r}_s$  of random available locations indicated the SSF model was predicting habitat selection in response to environmental covariates beyond random chance.

In addition to the new movement data collected, long-term data on lay date of the first clutch, annual estimates of the number of breeding individuals, and mean annual productivity (average number of chicks fledged per pair)

TABLE 2. List of covariates used to infer Auklet habitat selection, including the units, data set name on ERDDAP server, spatial (degrees) and temporal resolution, and a brief description.

Covariate	Units	Data set	Resolution		Description
			Spatial (degrees)	Temporal	
Depth	m	etopo180	0.01	NA	bathymetry
dis2shelf	m	NA	0.01	NA	distance to 200-m isobath
dist2isl	m	NA	0.01	NA	distance to southeast Farallon Island
SST	$^{\circ}\text{C}$	jplMURSSST41SST	0.01	3-d	sea surface temperature
Front	index	erdGAtfntmday	0.05	month	SST front probability index
Chl <i>a</i>	$\text{mg}/\text{m}^3$	erdMWchl3day	0.01	3-d	chlorophyll <i>a</i> concentration

Notes: NA, not applicable.



were used to place observed behavioral patterns in the context of population dynamics to understand potential carryover effects of winter movement patterns on summer productivity (Johns and Warzybok 2018). All statistical analyses were carried out in R version 3.5.1 (R Core Team 2018).

## RESULTS

### *Tag recovery and effects*

Overall tag recovery rate across all three winters was 72%, with 65% for the winter of 2015–2016, 76% for the winter of 2016–2017, and 73% for the winter of 2017–2018 (Table 1). Despite a high success rate in 2016–2017, a manufacturer defect in some of the housings of tags deployed during this period allowed water intrusion and tag failure, resulting in recoverable data from only nine of the 26 tags retrieved. The defect did not impact data quality of successful tags. Given limitations in the number of birds available for tagging, some Auklets were tagged from the same pair and during multiple seasons. To avoid violating assumptions of repeated measures and independence, data from four tags were excluded from the winter of 2015–2016 and four from 2017–2018, leaving a total of 35 tags in our sample. The mean  $\pm$  standard deviation of hatching success (HS) for tagged and untagged Cassin's Auklets was  $0.90 \pm 0.3$  ( $n = 42$ ) and  $0.86 \pm 0.34$  ( $n = 707$ ), respectively. Mean fledging success (FS) for tagged and untagged Auklets was  $0.92 \pm 0.27$  ( $n = 38$ ) and  $0.91 \pm 0.29$  ( $n = 610$ ), respectively. The proportion of variance ( $\pm$  standard deviation) explained by the random term *year* was  $0.05 \pm 0.23$  for HS and  $0.04 \pm 0.19$  for FS. There was no significant difference in mean HS ( $\chi^2(1) = 0.63$ ,  $P = 0.43$ ) or FS ( $\chi^2(1) = 0.11$ ,  $P = 0.74$ ) between untagged and tagged Auklets, indicating handling, attachment method, and mass of tags had no discernable effect on reproductive performance.

### *Winter distribution*

Position estimates showed core winter use by Cassin's Auklets from SEFI was bounded by Cape Mendocino ( $40.4^\circ$  N) in Northern California and Point Conception in Southern California ( $34.4^\circ$  N; Fig. 1). Although most of the tagged Auklets remained off the central California coast, some individuals moved to the shelf break off northern Baja California, Mexico for much of the winter period (Fig. 1). Of the three winter periods examined (1 November–31 January), sea surface temperatures across latitudes used by Cassin's Auklets were abnormally warmer than the long-term average during the winter of 2015–2016, and closer to the long-term average during the winters of 2016–2017 and 2017–2018 (Thompson et al. 2018). Following this trend, SST fronts throughout the California Current System and chlorophyll *a* concentrations during the spring transition were also lower

than average during the period of 2015–2016 compared to the other two tagging periods in this study (Thompson et al. 2018). Auklets traveled further south ( $34.6^\circ \pm 1.8^\circ$  N; mean  $\pm$  SD) and dispersed to greater distances from SEFI ( $359 \pm 192$  km) during the winter of 2015–2016, compared to a more limited distribution off central California and smaller dispersal distances during in the winters of 2016–2017 ( $36.6^\circ \pm 1.0^\circ$  N,  $135 \pm 100$  km) and 2017–2018 ( $36.5^\circ \pm 1.9^\circ$  N,  $172 \pm 236$  km; Figs. 1, 2). Auklets were more centralized around the Farallon Islands particularly during the month of December in 2017 ( $105 \pm 38$  km; Fig. 2), with little movement north or offshore of the breeding colony (Fig. 1). There was also a high occurrence of stationary behavior near SEFI during the months of December and January, particularly during the winters of 2016–2017 and 2017–2018 (Fig. 2).

### *Habitat selection*

All covariates were tested for collinearity, and terms with a Spearman's rank correlation ( $r_s$ ) values  $>0.9$  were excluded. Prior to performing model selection, the predictor *dis2shelf* was excluded due to strong collinearity

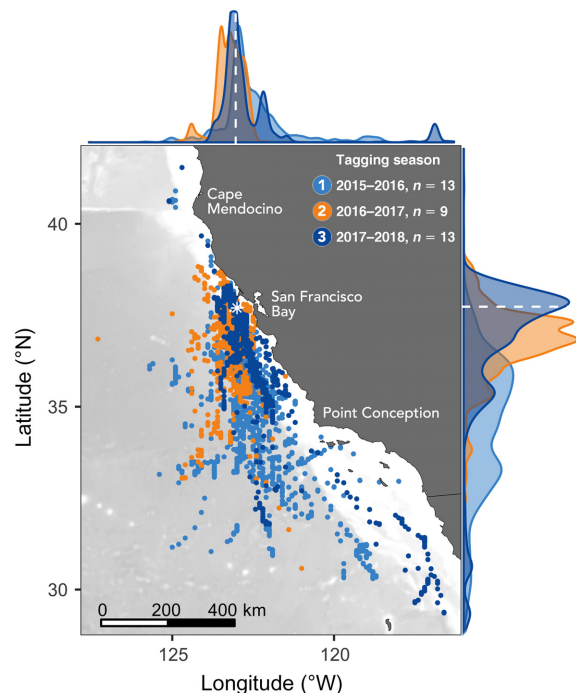


FIG. 1. Estimated positions of Cassin's Auklets from Southeast Farallon Island (white asterisk, dashed lines on density plots) during the months of November, December, and January. Locations are colored by tagging years: light blue, winter of 2015–2016; orange, winter of 2016–2017; dark blue, winter of 2017–2018. Number of tags recovered and successfully downloaded shown as  $n$ . Density plots along the axes highlight core usage areas during each winter period. Map is oriented north up. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

with depth ( $r_s = 0.95$ ), and moderate collinearity with chl  $a$  ( $r_s = 0.67$ ). The full conditional logistic regression model using linear predictors depth, dist2isl, chl  $a$ , front, and a quadratic term for SST (Fig. 4a–e) had the lowest AIC score for the winter of 2017–2018, and was within 2  $\Delta$ AIC of best competing models for winters 2015–2016 and 2016–2017 (Appendix S1: Table S1). Thus, habitat selection coefficients were estimated by fitting the full model to data from each of the three winters examined. K-fold cross validation confirmed a high degree of predictive ability of SSFs for all three winters, with positive  $\bar{r}_s$  values for observed locations greater than expected by chance alone (Appendix S1: Fig. S2).

Interannual differences in movement patterns translated to variability in habitat selection among the three tagging winters, especially for the winter of 2015–2016. Auklets were consistently more likely to avoid greater distances from SEFI, with strongly negative  $\beta$  (SE) estimates for dist2isl for the winters of 2015–2016,  $-0.91$  (0.23); 2016–2017,  $-0.99$  (0.22); and 2017–2018,  $-0.95$  (0.40; Table 3). Distance from SEFI generally had the largest effect on habitat selection over all other covariates examined (Fig. 3). Auklets also consistently avoided areas of increasing SST values, with negative estimates for the winters of 2015–2016,  $-0.19$  (0.09); 2016–2017,  $-0.29$  (0.11); and 2017–2018,  $-1.07$  (0.45) (Table 3), a pattern that was most pronounced in 2017–2018

(Fig. 3). The presence of SST fronts showed a variable effect across all years (Fig. 3). Auklets were more likely to move into areas with higher frontal probability index values during the winters of 2016–2017, 0.17 (0.07) and 2017–2018, 0.10 (0.08), but were more likely to avoid such areas during the winter of 2015–2016,  $-0.20$  (0.13) (Table 3). The winter of 2015–2016 had the only reliable population-level estimate for the effect of depth, 0.99 (0.17) (Table 3), which showed Auklets were more likely to select for deeper water during that period (Fig. 3). Coefficient estimates for depth for winters 2016–2017 and 2017–2018 and chl  $a$  for all three winters had 95% confidence intervals that overlapped with 0 (Fig. 3), likely reflecting high variability in the response among individuals to these conditions. Thus, chl  $a$  and depth were considered weak predictors of habitat selection at the population level. There was a large amount of intraspecific variability in selection coefficients among individuals during the winter of 2017–2018, particularly with respect to SST and fronts (Fig. 3). Sex did not appear to influence habitat selection (Fig. 3). The probability of space use for a single representative day is visualized in Fig. 4f, which combines the likelihood surface based on selection weights ( $\hat{w}(X)$ ) from all relevant environmental covariates to a movement kernel of available locations derived from the fitted SSF.

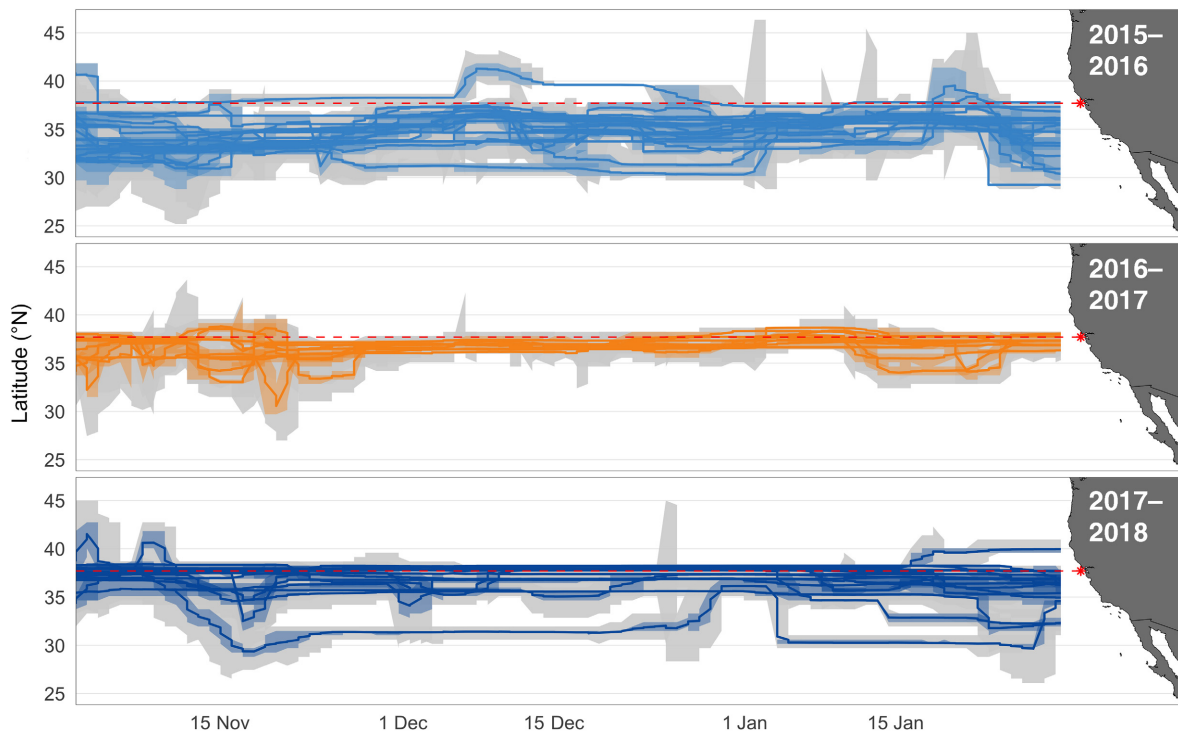


FIG. 2. Mean estimated latitude from light-level data for each tagged Auklet during the winters of 2015–2016, 2016–2017, and 2017–2018 in relation to the California coast. Shaded areas represent the probability of occurrence within the first and third quartiles (color) and within the 95% credible interval (light gray) of the model runs. Red asterisk and dashed line show latitude of South-east Farallon Island. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

TABLE 3. Estimates of population-level beta coefficients ( $\beta$ ) with associated standard errors in parentheses and variance in individual-level coefficient estimates (var) for each environmental covariate tested.

Covariate	2015–2016		2016–2017		2017–2018	
	$\beta$	var	$\beta$	var	$\beta$	var
Depth	<b>0.99 (0.17)</b>	0.32	0.04 (0.13)	0.11	–0.32 (0.23)	0.58
log(dist2isl)	<b>–0.91 (0.23)</b>	0.54	<b>–0.99 (0.22)</b>	0.40	<b>–0.95 (0.40)</b>	2.12
SST	0.15 (0.22)	0.34	0.17 (0.27)	0.48	–0.23 (0.53)	2.99
SST <sup>2</sup>	<b>–0.19 (0.09)</b>	0.05	<b>–0.29 (0.11)</b>	0.08	<b>–1.07 (0.45)</b>	2.29
Front	–0.20 (0.13)	0.20	<b>0.17 (0.07)</b>	0.03	<b>0.10 (0.08)</b>	0.07
log(chl <i>a</i> )	0.09 (0.20)	0.42	–0.33 (0.17)	0.24	0.06 (0.23)	0.60

Notes: Results are shown for the three winters. Boldface type indicates 95% confidence intervals of estimates did not overlap 0.

## DISCUSSION

Unlike many terrestrial bird species that depart summer breeding locations to well-defined wintering grounds, Cassin's Auklets from the Farallon Islands demonstrate a non-migratory space-use pattern during the winter period. The core area of non-breeding habitat use of tagged Auklets was focused around the same latitude as the breeding colony. Auklets did, however, exhibit considerable interannual differences in their offshore and southern movements that were directly relatable to oceanographic variation. In this respect, Cassin's Auklets are typical of most seabirds, responding to a set of dynamic environmental conditions driven by climatic forces that vary on both short- and long-term scales instead of relying on fixed overwintering areas. Mesoscale atmospheric and oceanographic features, such as upwelling-favorable winds and sea surface temperature fronts, play key roles in strengthening primary production and prey aggregation, which in turn, drives the distribution of marine predators (Tew et al. 2009, Scales et al. 2018). When warming surface waters or shifts in climate norms diminish these features, prey availability may become locally sparse, altering reliable foraging areas and forcing marine predators like Auklets to search more broadly for food.

During the three winters analyzed, Cassin's Auklets avoided the warmest waters and generally remained in locations where SST values ranged between 12°C and 15°C, aligning with previous studies that have identified SST as one of the most important habitat variables for Cassin's Auklet distribution (Oedekoven et al. 2001, Studholme et al. 2019). The combination of a strong El Niño during the winter of 2015–2016, and a lingering marine heat wave until the summer of 2016, resulted in warmer than average temperatures (Harvey et al. 2018) and lower than normal measures of SST fronts (Kahru et al. 2018) off the California coast. These anomalously warm conditions and reduced frontal regions are very likely responsible for the much wider distribution of Auklets during the winter of 2015–2016. Similar to our findings, Auklets from colonies in British Columbia tagged with geolocators also travelled more broadly and further south

during this period (Studholme et al. 2019), suggesting a possible range-wide behavioral response to abnormally warm surface waters and a subsequent lack of prey. Conversely, upwelling-favorable winds during the winter of 2016–2017 and a weak La Niña in the winter of 2017–2018 resulted in average to cooler temperatures in those years (Harvey et al. 2018). Lingering biological effects from the warm SST anomaly in the California Current System, in the form of reproductive failures and low at-sea counts for some seabird species, were still observed during the summer of 2017 (Thompson et al. 2018). This indicates only the relatively constrained movements during the winter of 2017–18 are most representative of non-breeding habitat use under climatologically normal conditions.

The negative association between SST fronts and habitat selection during the warm 2015–16 winter season and weak association with chlorophyll *a* concentrations across all years were unexpected findings (Table 3). Auklets are assumed to cue in on mesoscale frontal features, as these structures tend to aggregate higher densities of zooplankton. Kahru et al. (2018) described a significant reduction in the frequency of SST fronts in the California Current System during the marine heat wave of 2015–2016. Rather than actively avoiding SST fronts as the model coefficients we report suggest, a general absence of fronts within the wintering region used by Cassin's Auklets may have resulted in a negative association with such features. Alternatively, there is a fitness benefit for marine predators to remember reliable foraging habitats as a means to efficiently relocate areas of high productivity (Weimerskirch 2007, Fagan et al. 2013). Although it is unclear whether Cassin's Auklets possess this ability, the work of Studholme et al. (2019) suggests fixed migratory tactics for Cassin's Auklets in British Columbia, and the negative association with SST fronts we report during 2015–2016 may reflect individuals traveling to reliably productive areas that lacked strong frontal features during an abnormally warm winter. While retained as an important predictor for all years, a temporal lag in the response of zooplankton to phytoplankton blooms (Franks 1992) likely explains the weak relationship between Auklet habitat selection and chlorophyll *a* concentration.

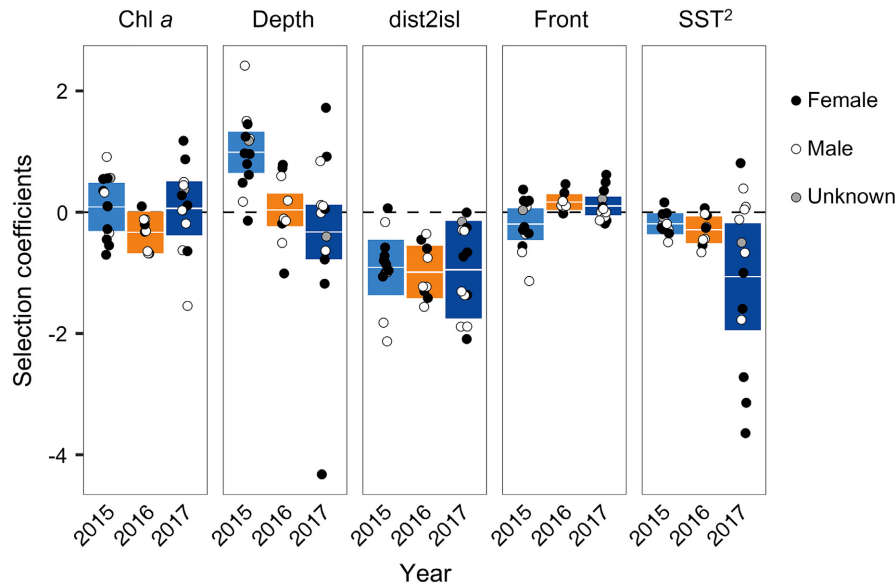


FIG. 3. Population-level coefficient estimates (white line) and associated 95% confidence intervals (bars) of the selection preferences for covariates chlorophyll *a* concentration (Chl *a*; mg/m<sup>3</sup>), ocean depth (depth; m), distance to Southeast Farallon Island (dist2isl; km), and squared sea surface temperature (SST<sup>2</sup>; °C), and SST front index (front). Positive values indicate a selection for and negative values an avoidance of that covariate. Bars are colored by years: light blue, winter of 2015–2016; orange, winter of 2016–2017; dark blue, winter of 2017–2018. Individual parameter estimates are represented by circles, with black for females, white for males, and gray for undetermined sex. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Despite the coarse resolution of position estimates from light-level data, which may also partially explain the weak relationship between some habitat features and selection in our analysis, distribution models can still be applied to geolocator data of marine predators to arrive at more informed conclusions of habitat use (Quillfeldt et al. 2017). Traditional statistical approaches used in hypothesis testing to explain space-use and population-level movement patterns of seabirds have included generalized linear mixed models (GLMM), generalized additive models (GAM), state-space models (SSM), and kernel density utilization distributions (Wakefield et al. 2009), to name a few. Here we applied SSFs, a powerful and easily implemented method for analyzing movement behavior, developed and largely used by terrestrial ecologists to explain these same patterns (Fortin et al. 2005, Thurfjell et al. 2014). Unlike commonly used GAMs and GLMMs, SSFs estimate more robust and interpretable coefficients when modeling resource selection, relating movement to environmental covariates by accounting for spatial and temporal constraints of the movement process (Craiu et al. 2011). Step-selection functions have become more prevalent in movement studies of terrestrial vertebrates (Thurfjell et al. 2014), but to our knowledge, this is the first example of using SSFs to describe habitat preferences of a marine bird. Step-selection functions should be considered a viable option for modeling the habitat use of marine predators, even with inherently noisy movement data.

#### *Implications of movement on population dynamics*

Longitudinal data on the behavior and movement of seabirds are essential for linking oceanographic parameters to reproductive success and survival. For Cassin's Auklets, variability in local oceanography during the breeding season directly impact the timing of egg laying (Wolf et al. 2009), amount of reproductive investment (Johns et al. 2017), productivity (Wolf et al. 2010), and survival (Lee et al. 2007). Since the highly specialized foraging ecology of lower trophic level consumers, like Auklets, links their at-sea movements to areas of high marine productivity (Boyd et al. 2008, Adams et al. 2010), movement data of the type we analyzed can be used to connect specific foraging behaviors with oceanographic variability and reproductive success; although not without its limitations.

The habitat preferences of Cassin's Auklets we report here, in the context of intense surface warming experienced in the eastern North Pacific over the past several decades, may have important effects on movement behavior that could impact population dynamics and viability over the long term. The steady increase in average SST over time has periodically been exacerbated by shorter-term interannual phenomena, most notably El Niño Southern Oscillation (ENSO). The frequency and magnitude of strong ENSO events are predicted to increase and intensify in the future, potentially impacting the spatial patterns and community structure of a wide range of taxa (Mcgowan et al. 1998, Harley et al.



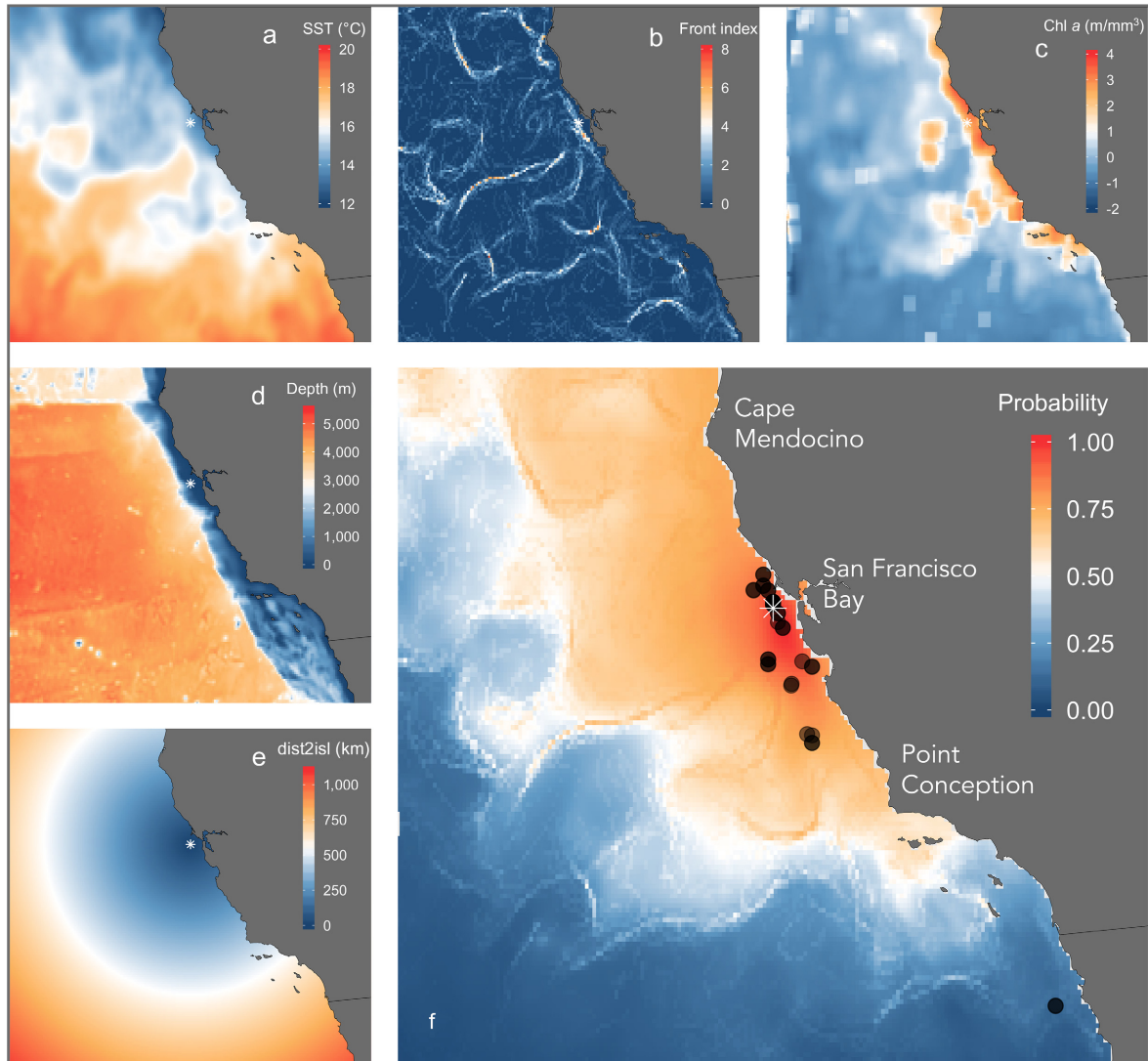


FIG. 4. Environmental covariates that define the winter habitat of Cassin's Auklets; (a) sea surface temperature (SST), (b) sea surface temperature frontal index (front), (c) chlorophyll *a* concentration (chl *a*), (d) depth to seafloor (depth), (e) distance from Southeast Farallon Island (dist2isl). See Table 2 for details of covariates. A single day (12 December 2017) is depicted for dynamic covariates. (f) Example of the probability of selection for a single day by combining estimated habitat preference for covariates a–e and space-use availability. Warm colors represent a higher likelihood of use, cooler colors a higher likelihood of avoidance. Black dots show estimated locations of tagged Auklets on 12 December 2017. Location of Southeast Farallon Island denoted as a white asterisk. Maps are oriented north up. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

2006). Most recently during the winter of 2013–2014, a large area of the Eastern North Pacific experienced a marine heat wave with surface water anomalies exceeding 2.5°C (Bond et al. 2015). This “blob” of anomalously warm surface water persisted into the spring of 2015, and a similar phenomenon appears to be developing in the current winter (2019–2020) based on remote sensing data from the National Oceanic and Atmospheric Administration. Such events cause greater stratification that limits the advection of deep, nutrient-rich water to the surface (Di Lorenzo et al. 2005), resulting in a decrease in primary production.

A steady warming of the central California coast is concerning given this region is regularly visited by overwintering Cassin's Auklets from both northern and southern colonies (Briggs et al. 1988, Adams et al. 2010, Studholme et al. 2019), suggesting the waters around SEFI are an important source of planktivorous prey targeted by this species. The diet of Cassin's Auklets is somewhat plastic and changes in response to local prey abundance, predominantly switching between the euphausiids *Thysanoessa spinifera* and *Euphausia pacifica*. Auklets tend to diversify their diet when the larger *T. spinifera* are more limited, targeting the smaller *E.*

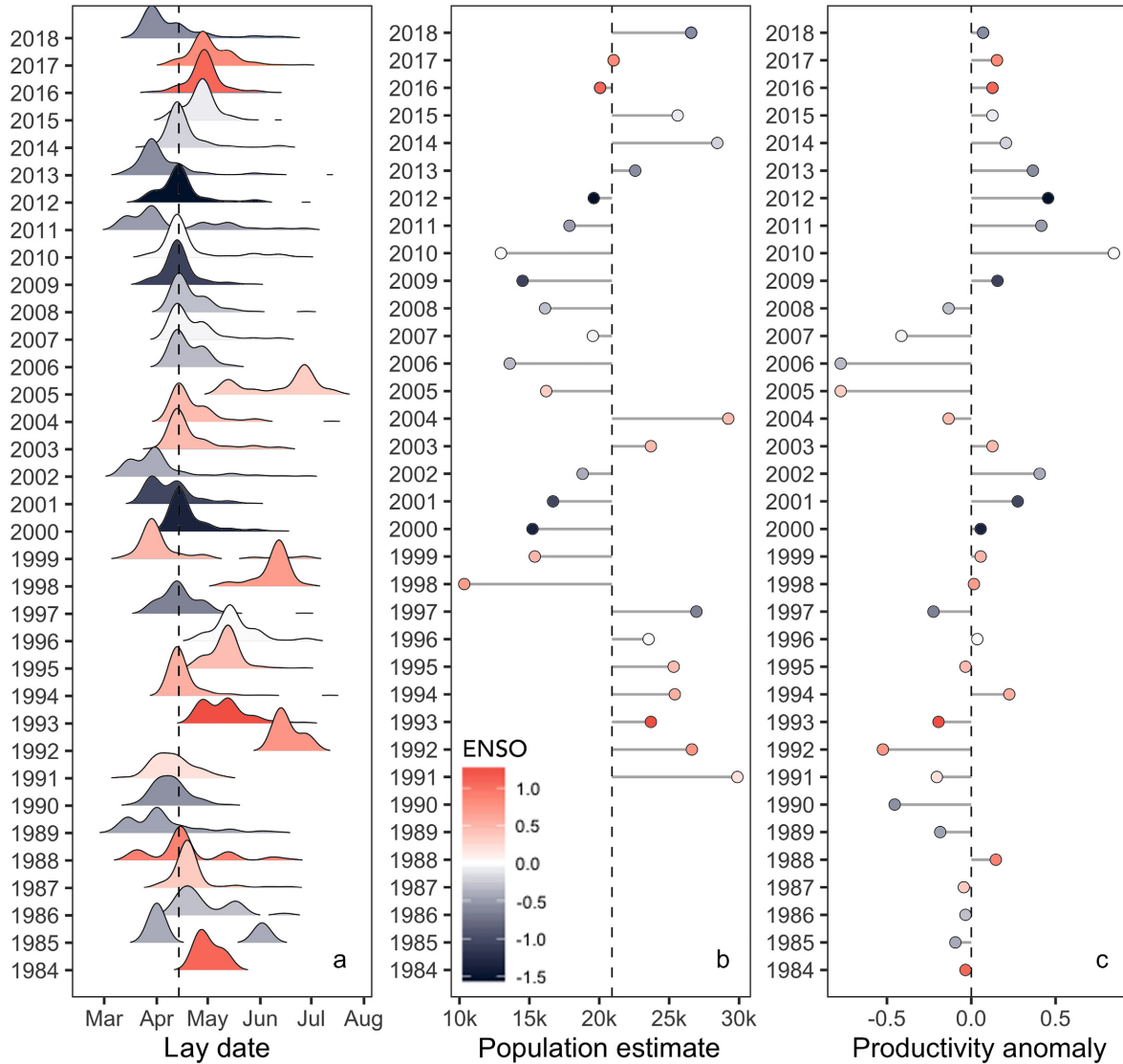


FIG. 5. Long-term population parameters (a) lay date of the first clutch, (b) estimate of the number of birds in attendance at the breeding colony (no estimates were made prior to 1991), and (c) average productivity anomaly for Cassin's Auklets on Southeast Farallon Island. Colors represent mean winter (November–January) El Niño Southern Oscillation (ENSO) index during the previous year for the latitude of SEFI, as a visual metric for environmental conditions during the winter leading up to the breeding season. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

*pacifica* when available, along with mysids, amphipods, copepods, larval fish, and squid (Ainley et al. 1996, Manugian et al. 2015). Anomalous northern advection along the California coast is understood to delay the onset of upwelling and reduce euphausiid abundance during extreme warm-water events (Dorman et al. 2011). Similar advection and subsequent decline in primary production led up to the winter of 2015–2016 (Whitney 2015), likely resulting in a destabilization of a predictable supply of prey, including *E. pacifica*; forcing Auklets to travel longer distances and over deeper, more offshore waters to find profitable zooplankton abundances. For Cassin's Auklets, the marine heat wave in

the Eastern North Pacific during 2014–2015 led to one of the largest die-offs ever recorded for this species on the U.S. west coast (Jones et al. 2018). Along with an increased risk of mortality, poor conditions and lack of adequate prey during the winter may force birds to skip reproduction the following year (Genovart et al. 2013).

The majority of studies on seabird survival and breeding success in relation to warm-water anomalies and environmental variability have focused on indirect changes in food web structures and prey availability during the spring and summer months (Sydeman et al. 2012). Leveraging the 36-yr mark–recapture and breeding data from the SEFI population, we can begin to

draw inference about the how winter oceanography, which we show here strongly affect movement and foraging of Auklets, impacts breeding behavior and population dynamics. Estimates of the number of Cassin's Auklets in attendance at the SEFI breeding colony fell substantially below those of previous years during the summers of 2016 and 2017, and strongly rebounded above the long-term average for the summer of 2018 following the much cooler winter of 2017–2018 (Fig. 5b). This trend may reflect poorer marine conditions during the 2015 and 2016, given suspected difficult foraging inferred by broader movement patterns from tracking results. Of the three winters in this study, lay dates following the winter of 2017–2018 were earlier than average compared to the previous two winters (Fig. 5a). Early lay dates with Cassin's Auklets are associated with improved marine productivity during the pre-breeding period (Black et al. 2011) and greater reproductive investment and success (Johns et al. 2017), providing further evidence that conditions in 2017–2018 had rebounded from the marine heat wave of 2015–2017. Average annual productivity for Auklets remained relatively consistent following the three winters examined (Fig. 5c), suggesting reproductive success depends more on summer marine conditions and less on winter constraints. Instead, the impacts of poor winter conditions are on adult survival and/or degree of reproductive skipping, rather than subsequent breeding success of the individuals who attended the breeding colony the following year. It may also be that a higher proportion of lower quality birds initiated a breeding attempt during normal to above average years, resulting in a higher estimate for the number of birds in attendance at the colony while reducing the overall productivity for the population. Given our estimates of resource selection are derived from individuals that survived the winter and were able to initiate a reproductive attempt the following year, the high variability in selection coefficients during the winter of 2017–2018 may reflect a greater diversity of experience and quality among individuals that returned to the colony. Conversely, the coefficients we estimated for the winter of 2015–2016 may be biased to represent only high-quality individuals relative to the overall population.

While we have suggested possible links to movement patterns and carry-over effects to the breeding season, analyses targeting individual-level patterns of this nature would require a much larger sample size of uniquely marked birds across a greater time series. This study is the first to demonstrate winter movement patterns and quantify habitat selection parameters of Cassin's Auklets from this population, but continued tagging of individuals with known breeding histories will be necessary to accurately model how individual winter movement decisions impact future reproductive success.

#### CONCLUSIONS

There is now compelling evidence that oceans are warming at an accelerated rate (Cheng et al. 2019). Much

of this change is occurring at higher latitudes and toward the poles. In regions such as the west coast of Greenland, SST anomalies have reached values  $>4^{\circ}\text{C}$  above modern averages (Timmermans and Proshutinsky 2015). Shifts in the non-breeding distribution of seabird species that occupy regions affected by anomalously warm water have been well documented, particularly in traditionally productive upwelling regions (Grémillet and Boulinier 2009). Advances in lightweight tagging technologies have allowed long-duration tracking of a wide range of seabirds, allowing quantitative inference on the connections between the spatial ecology of seabirds and warming seascapes. We suggest a dynamic foraging strategy for Cassin's Auklets during the non-breeding period, where birds adjust their movement decisions in response to environmental cues. Continued inquiry of the at-sea foraging decisions of seabirds that exploit temporally and spatially variable environments, through the application of robust animal movement models, will shed light on the behavioral response of seabirds to climate-related changes in prey availability. If collected over long time scales, such data sets will provide a nuanced understanding of how marine predators like seabirds will adapt or be harmed by expected warmer climates. Baseline information of this nature would be of particular value to managers tasked with monitoring and protecting sensitive populations of seabirds in the face of changing climatic norms (Grémillet and Boulinier 2009).

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2068/full>

DATA AVAILABILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.m0cfxpnzv>