LAYING SEQUENCE AND OCEANOGRAPHIC FACTORS AFFECT EGG SIZE IN SCRIPPS'S MURRELETS *SYNTHLIBORAMPHUS SCRIPPSI* AT SANTA BARBARA ISLAND

MARCELA I. TODD ZARAGOZA[1], AMELIA J. DuVALL[2], JIM A. HOWARD[3], DAVID M. MAZURKIEWICZ[4] & SARAH J. CONVERSE[5]

[1]School of Environmental and Forest Sciences, University of Washington, Seattle, Washington 98195, USA (marcelat99@outlook.com)
[2]Washington Cooperative Fish and Wildlife Research Unit, School of Aquatic and Fishery Sciences,
University of Washington, Seattle, Washington 98195, USA
[3]California Institute of Environmental Studies, Davis, California 95617, USA
[4]Channel Islands National Park, Ventura, California 93001, USA
[5]U.S. Geological Survey, Washington Cooperative Fish and Wildlife Research Unit, School of Environmental and
Forest Sciences & School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington 98195, USA

ABSTRACT

TODD ZARAGOZA, M.I., DuVALL, A.J., HOWARD, J.A., MAZURKIEWICZ, D.M. & CONVERSE, S.J. 2023. Laying sequence and oceanographic factors affect egg size in Scripps's Murrelets *Synthliboramphus scrippsi* at Santa Barbara Island. *Marine Ornithology* 51: 1–9.

Egg size is an important avian life history parameter, with larger eggs indicating greater investment of resources in the chick. Prey availability can affect such investment. We investigated the effects of oceanographic conditions and laying sequence on Scripps's Murrelet *Synthliboramphus scrippsi* egg size at Santa Barbara Island, California during 2009–2017. We evaluated oceanographic covariates characterizing marine productivity for their effect on egg size, including large-scale oceanographic indices such as the Pacific Decadal Oscillation (PDO) index, Oceanic Niño Index (ONI), and North Pacific Gyre Oscillation (NPGO) index. We also evaluated a larval anchovy catch-per-unit-effort (ANCHL) index and the Biologically Effective Upwelling Transport Index (BEUTI) as region-wide indices, and sea surface temperature (SST) as a local index. We evaluated oceanographic conditions over the entire year and during the breeding season only. We also considered the contribution of lagged effects to oceanographic conditions. Our results generally ran counter to our hypothesis that increased ocean productivity should increase egg size. Based on Akaike's Information Criterion, the four top-ranked models provided support for an association between larger eggs and conditions indicative of lower oceanographic productivity, including lower values of BEUTI and NPGO, and higher values of ONI, PDO, and SST. The only result that supported our hypothesis was a positive relationship between ANCHL and egg size, although the 95% confidence interval for the effect included 0. The strongest relationship detected was between laying sequence and egg size, as second eggs were considerably larger than first eggs. Our results indicate substantial complexity in the relationship between ocean productivity and seabird demography. A better understanding of how ocean productivity affects seabird breeding outcomes through multiple mechanisms will help improve predictions of how seabirds will respond to changing ocean conditions.

Key words: Alcidae, egg size, laying sequence, index, ocean productivity, monitoring

INTRODUCTION

Fluctuating marine conditions that affect prey availability have direct impacts on seabirds. For example, Cassin's Auklets *Ptychoramphus aleuticus* at Triangle Island (British Columbia, Canada) and the Farallon Islands (California, USA) exhibit reduced offspring survival and fledgling mass due to limited prey availability in years with warm sea surface temperature (SST; Ainley *et al.* 1990, 1995; Hipfner 2008). Changes in marine conditions have also been linked to declines in growth rate and fledging success of Tufted Puffins *Fratercula cirrhata* off the coast of British Columbia (Gjerdrum 2003) and changes in clutch size of Scripps's Murrelets *Synthliboramphus scrippsi* off the coast of California (Roth *et al.* 2005).

In general, egg size varies with the amount of energy invested in egg production, and the energy available to invest can vary with environmental conditions (Williams 2005). In Norway, Atlantic Puffin *Fratercula arctica* populations at two separate colonies (investigated during 1980–2011) showed parallel declines in population size and egg volume (Barrett *et al*. 2012). Investigators found relationships between egg volume and various prey population indices (both positive and negative effects), the North Atlantic Oscillation (positive effects), and SST (negative effects), and they concluded that low food availability led to lower egg size. In contrast, Hipfner (2012) found that egg size increased with SST for Glaucous-winged Gulls *Larus glaucescens* at Triangle Island, but the effect was small and limited to one and three-egg clutches.

The Scripps's Murrelet (hereafter "murrelet") is a small seabird in the Alcidae family that breeds on islands in the southern California Current, from southern California, USA, to central and Baja California, Mexico. Little is known about the relationship between marine or other oceanographic conditions and murrelet breeding success. Research has indicated that higher ocean productivity leads to earlier clutch initiation and larger clutch sizes (Roth *et al.* 2005). Also, Thomsen & Green (2017) found a negative correlation between murrelet nest success and drought severity at Santa Barbara Island, USA, due to drought-induced predation on eggs by deer mice *Peromyscus maniculatus* introduced to the island by Indigenous peoples. However, there has not been any analysis of

the relationship between oceanographic conditions and egg size. Murrelet eggs represent, on average, 24% of the female body mass, making them one of the largest eggs relative to body mass in the Alcidae family (Sealy 1975). Moreover, females typically lay two eggs (range one to two), with the second egg laid ~8 d after the first (Murray *et al*. 1983). Murrelet chicks are precocial, departing the nest ~1–2 d after hatching. This precociality requires large eggs, and females must forage for several days before laying each egg to obtain the necessary nutrients (Murray *et al*. 1983).

The largest USA-based breeding colony of murrelets occurs at Santa Barbara Island (SBI), Channel Islands National Park, California, USA (Carter *et al*. 1992; Fig. 1). SBI is in the southern California Current System (CCS), a dynamic marine ecosystem with pronounced inter-annual fluctuations in productivity (Checkley & Barth 2009). The southern CCS is resilient, and like other eastern boundary currents, it can quickly recover from negative perturbations to maintain generally high productivity (Bograd & Lynn 2001, Bakun *et al*. 2015, Brady *et al*. 2017). However, climate change models suggest that future upwelling patterns in the CCS system are imminent (Brady *et al*. 2017). Furthermore, simulations predict changes in stratification (Bakun *et al*. 2015), hypoxia, and acidification, all of which can affect pelagic seabirds (Pozo Buil *et al*. 2021). Under a high-emissions climate scenario,

Brady *et al*. (2017) found that internal variability will remain the dominant factor in determining trends in the CCS. Thus, it will not be possible to discern between anthropogenic forcing and natural variability in this system until the second half of the 21st century. Uncertainty regarding the extent to which climate change will impact oceanographic processes suggests that a better understanding of the mechanisms by which murrelets are responding to their environment will prove valuable by improving our ability to predict how this species, and other seabirds, will respond to climate change. SBI provides an opportunity to investigate how marine productivity may influence murrelet egg size.

Consistent with results for Atlantic Puffins by Barrett *et al*. (2012), we hypothesized that greater marine productivity would lead to larger eggs. Therefore, we predicted a positive relationship between egg size and oceanographic indices associated with higher ocean productivity at multiple spatial scales. We hypothesized that oceanographic conditions during the pre-laying season may impact individual fitness, and thus egg size, so we tested the inclusion of oceanographic covariates at two temporal scales: (i) during the breeding season only and (ii) during the breeding and non-breeding season (i.e., entire year). In addition, we hypothesized that the impact of oceanographic conditions on individual fitness may not manifest immediately, so we tested the inclusion of a lag effect
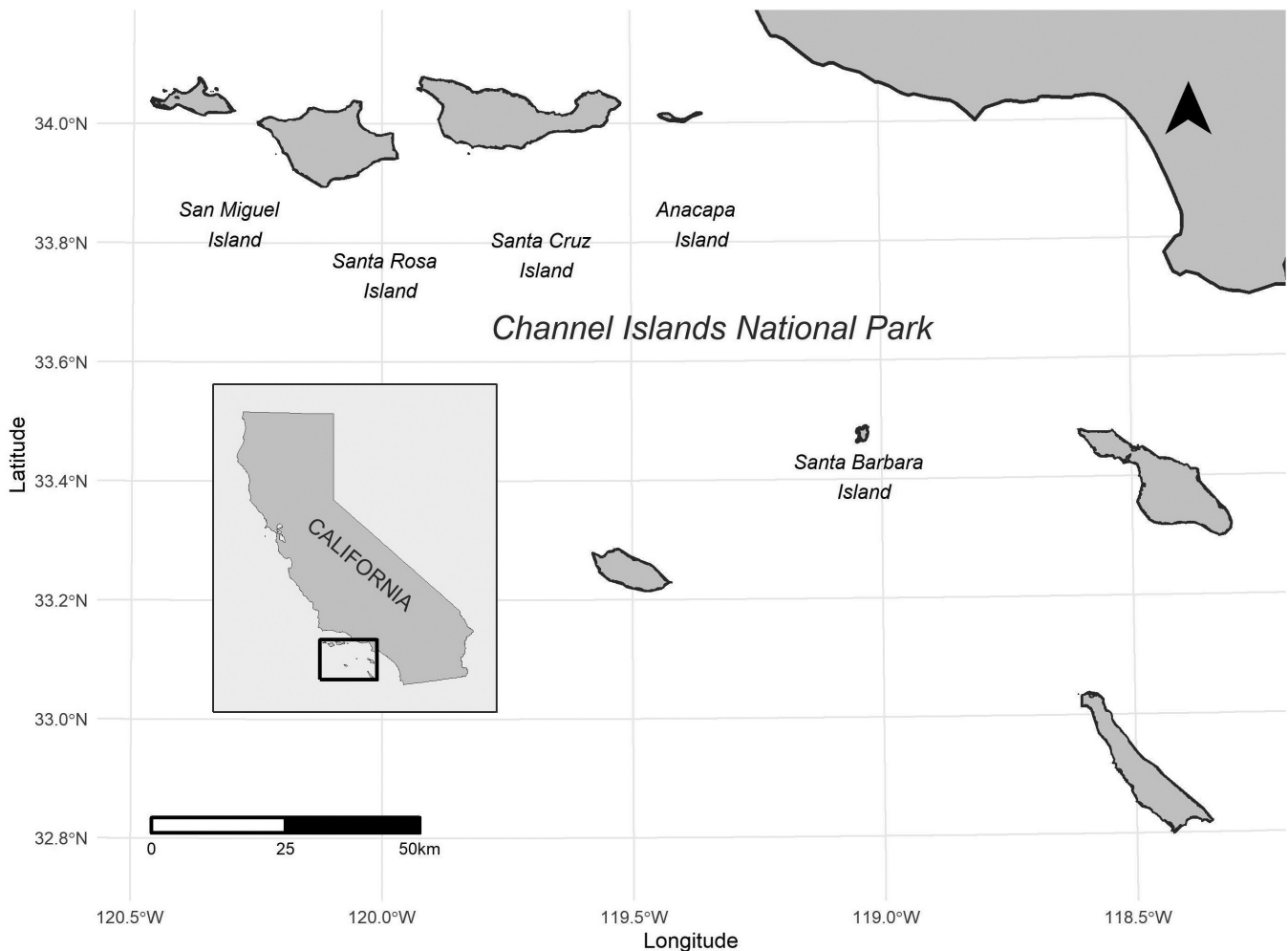

Fig. 1. The eight Channel Islands in the Southern California Bight, USA. The five labeled islands comprise Channel Islands National Park wholly or in part.

on covariates. We also hypothesized that there would be inherent differences between the size of the first and second eggs laid in each clutch based on the findings of Murray *et al.* (1983).

METHODS

Study site and data collection

Santa Barbara Island (33.4756°N, 119.0373°W) is the smallest (2.6 km^2) of the eight main California Channel Islands. Data were collected from 2009 to 2017 during the breeding season, which lasts from approximately March to June (Murray *et al.* 1983). To obtain egg measurements, we removed accessible eggs from the nest and measured maximum width and length (± 0.1 mm) using Vernier calipers. Eggs were considered accessible if they were within safe reach and no adult bird was present at the nest. After measurement, we returned the egg to its original position and orientation. We only measured eggs once at each nest. If both eggs were present upon first encounter, we could not determine laying sequence, but if the nest was encountered between the laying of the first and second

eggs, eggs were labeled with a marker to indicate laying sequence. We only included eggs in this analysis for which laying sequence was known. Egg size data were obtained from eight monitoring plots on SBI for this analysis: Arch Point North Cliffs, Bunkhouse, Boxthorn, Cat Canyon, Dock, Elephant Seal Cove, Landing Cove, and West Cliffs (Fig. 2).

Oceanographic covariates

We obtained oceanographic data from the California Current Integrated Ecosystem Assessment Program, part of the National Oceanic and Atmospheric Administration (NOAA) interdisciplinary research along the US West Coast (NOAA n.d.). At the largest spatial scale, we considered the Oceanic Niño Index (ONI), the North Pacific Gyre Oscillation (NPGO), and the Pacific Decadal Oscillation (PDO). ONI is a measure of air pressure fluctuations and SST anomalies in the El Niño 3.4 region (lower values indicate higher productivity; Climate Prediction Center Internet Team n.d.). NPGO is the second dominant mode of sea surface height anomalies in the North Pacific (higher values indicate
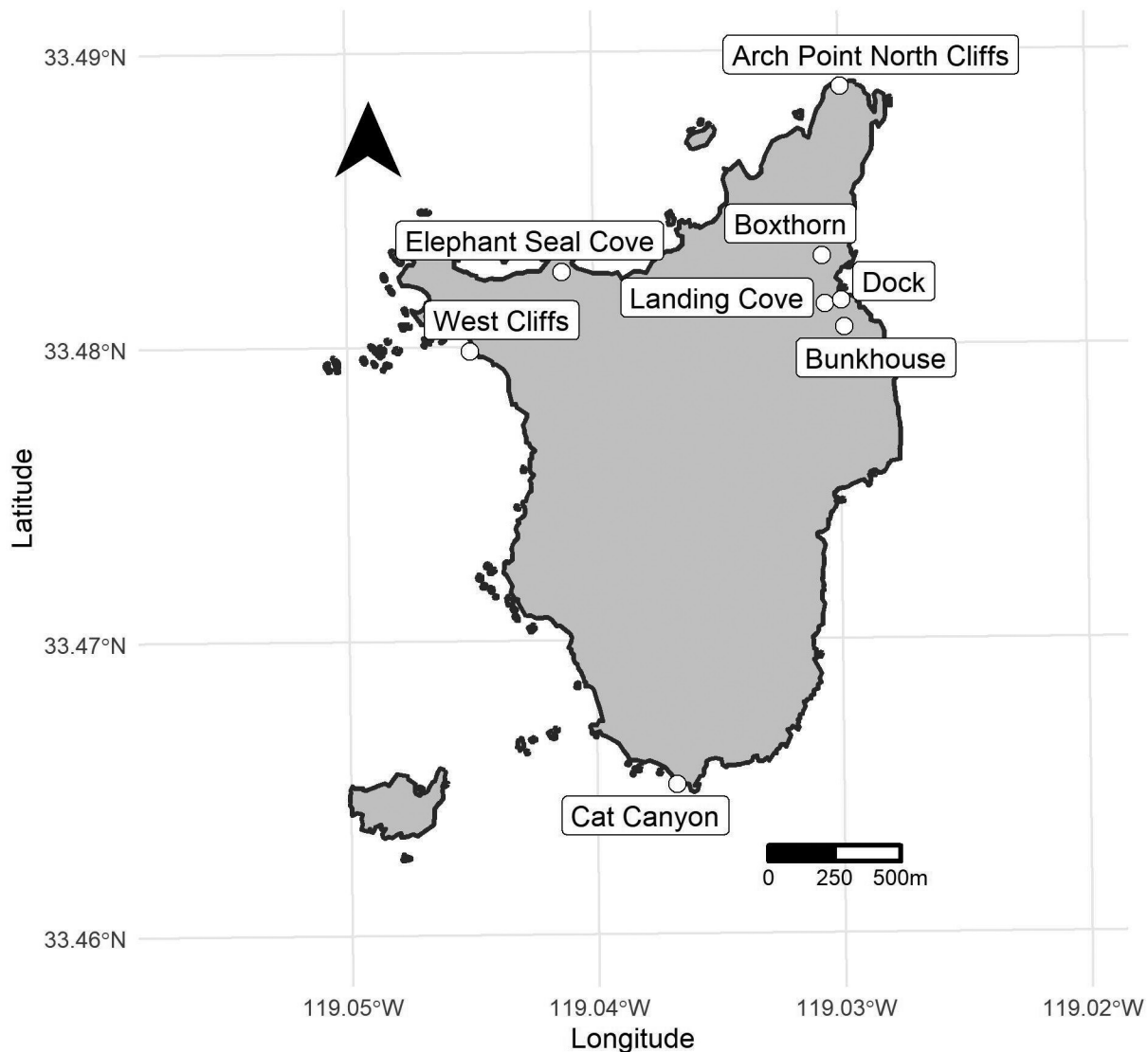

Fig. 2. Map of the monitoring plots at Santa Barbara Island, California, USA, where data were collected on Scripps's Murrelet *Synthliboramphus scrippsi* egg size during 2009–2017.

higher productivity; Chenillat *et al.* 2012). Upwelling variability is strongly correlated with NPGO along the eastern North Pacific coast south of 38°N (Lorenzo *et al.* 2008). The PDO is the dominant mode of SST anomalies in the North Pacific, indicating shifts in ocean temperatures (lower values indicate higher productivity; Chenillat *et al.* 2012). At the regional scale, we considered the Biologically Effective Upwelling Transport Index (BEUTI) and larval anchovy *Engraulis mordax* catch-per-unit-effort (ANCHL). BEUTI provides an estimate of vertical nitrate flux, which is the amount of nitrate upwelled/downwelled near the US West Coast at a latitude of 39°N (higher values indicate higher productivity; Jacox *et al.* 2018). Larval anchovy data were collected in the spring by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) lines 76.7–93.3, stations 28.0–120.0, and represent catch-per-unit sampling effort (higher values are directly indicative of greater resource availability). Finally, at the local scale, we considered SST: SST data were collected by the National Oceanic and Atmospheric Administration's buoy station 46025 (33.758°N, 119.044°W), approximately 31 km north of SBI (lower values indicate higher productivity; Ainley *et al.* 1995).

We averaged covariate data that were reported at a monthly scale to create input covariates at two temporal scales (except for ANCHL, for which only an annual index, collected in spring, was available). We created a 12-mo covariate (covariate values averaged from July in year *t*-1 to June in year *t* to model egg size observed in year *t*) and a 6-mo covariate ("breeding season," from January in year *t* to June in year *t*). We included values through June to encompass the murrelet breeding season. Clutch initiation commences in March and peaks in April, but it extends for several months into the summer (Murray *et al.* 1983). We used the ANCHL covariate collected in spring of year *t* to model egg size observed in year *t*. We also considered analogous covariates with a 1-year lag, where values from either July in year *t*-2 (12-mo lagged covariate) or January of year *t*-1 (6-month lagged covariate) through June in year *t*-1 were used to model egg size in year *t*. An ANCHL lagged covariate was considered as well, i.e., ANCHL collected in spring of year *t*-1 used to model eggs observed in year *t*. All covariates were Z-scored before modeling.

Model formulation and selection

We developed a set of models to investigate the relationship between oceanographic covariates and egg size, calculated as egg size = egg length × egg width. Egg size was modeled using a linear mixed model with normal errors and random processes. Initially, we considered two random effects: (1) plot random effect, which was included to account for potential variability in egg size by plot that could arise due to the unique characteristics of each plot (e.g., different microclimates) and the birds using the plots (e.g., different feeding areas); (2) observer random effect, which was included to account for potential differences in how different observers measured eggs. Our general model was:

$$y_i = \beta_0 + \beta_k x_k + \alpha_p + \alpha_o + \varepsilon_i$$
$$\alpha_p \sim N(0, \sigma^2_{\alpha_p})$$
$$\alpha_o \sim N(0, \sigma^2_{\alpha_o})$$
$$\epsilon_i \sim N(0, \sigma^2)$$

where y_i is the size of egg *i*, β_0 is an intercept, *k* is the number of predictors in a given model, β_k are model coefficients for covariates x_k (including laying sequence), α_p is a random effect of plot *p* with

variance $\sigma^2_{\alpha_p}$, α_o is a random effect of observer *o* with variance $\sigma^2_{\alpha_o}$, and ϵ_i and is the residual error for egg *i* with model variance σ^2.

We began by evaluating the appropriate temporal scale for each covariate. We built four single-variable models without random effects (using the *lm* function in R; R Core Team 2021), i.e., 6-mo, 12-mo, 6-mo lagged, and 12-mo lagged for all covariates except ANCHL, for which we built two single-variable models (unlagged and lagged). The single-variable models for each covariate were compared using Akaike's Information Criterion (AIC) = $-2ln(L)+2k$, where *L* is the maximum value of the likelihood function for the model and *k* is the number of fixed effect parameters in the model. We used the form of the covariate that appeared in the top-ranked model in all subsequent analyses.

Next, we evaluated support for the inclusion of random effects of plot and observer. We performed bootstrapped likelihood ratio tests (*exactLRT* and *exactRLRT* functions in the "RLRsim" package; Scheipl 2008) in R (R Core Team 2021). When performing these tests, we used the "global" form for the fixed effects portion of the model. Because of correlations between covariates (see below), the number of fixed effect covariates in our global model was five (three oceanographic covariates, laying sequence, and intercept) rather than eight.

Once we identified the form of the input covariates and the random effects structure, we considered all possible combinations of covariates in a series of models, except that covariates with a correlation coefficient that had an absolute value ≥ 0.65 were not included in the same model. These correlated covariate pairs included ANCHL/NPGO, ANCHL/ONI, ANCHL/PDO, BEUTI/ONI, BEUTI/PDO, NPGO/PDO, NPGO/SST, and ONI/PDO. We also included laying sequence to determine whether and how egg size differed between the first and second eggs laid in a clutch. Models were fit using the function *lmer* in the "lme4" package (Bates 2015) in R (R Core Team 2021) and compared using AIC. We performed model diagnostics on the five-parameter model (including the random effects retained based on the likelihood ratio tests) to determine whether model assumptions were reasonably met. Diagnostics included Q-Q plots to evaluate the normality of residuals and residual plots along with Levene's test to evaluate whether residuals had equal variance.

All data and analysis code can be found at https://github.com/Quantitative-Conservation-Lab/Todd-Zaragoza_etal.

Ethics statement

This research was conducted in collaboration and with approval from Channel Islands National Park. Data were collected by Channel Islands National Park staff as well as National Park Service cooperators and permittees, in compliance with contemporaneous inventory and monitoring protocols.

RESULTS

For the 2009–2017 records in which laying sequence was known, there were 695 values for the first egg and 177 values for the second egg in the clutch (*n* = 872 total samples; Table 1). There were eight different plots with egg measurements, with the number of eggs per plot varying between one and 275. There were 27 different observers who measured eggs, with the number of eggs per observer varying

TABLE 1
The number of Scripps's Murrelet *Synthliboramphus scrippsi* egg records from monitoring plots at Santa Barbara Island, California, USA from 2009–2017

Year	Total records[a]	Egg 1	Egg 2
2009	7	3	4
2010	135	109	26
2011	90	75	15
2012	123	97	26
2013	92	71	21
2014	101	84	17
2015	121	96	25
2016	133	104	29
2017	70	56	14
Total	872	695	177

[a] Records indicate measurements for which laying sequence was known, including the total number of records for the first and second egg laid in a clutch.

between one and 192. Model diagnostics were acceptable but did alert us to two outliers for which egg size was notably small (> 6 standard deviations [SD] smaller than the mean egg size calculated with those two eggs excluded). These eggs (removed from analyses) were in the same nest but were measured by different observers on different dates, indicating that both eggs in the clutch were physiologically abnormal rather than incorrectly measured.

Temporal forms of the covariates, identified in the first model selection step, included the 12-mo lagged covariate form for BEUTI; 6-mo lagged covariate form for ONI and PDO; 6-mo unlagged covariate form for NPGO and SST; and unlagged covariate form for ANCHL (Table 2). Only these forms of the covariates were used in subsequent modeling.

Based on likelihood ratio test results, we elected to retain the plot random effect ($p = 0.0598$) but not the observer random effect ($p = 0.1836$). Thus, all mixed models included only plot as a random effect. The plot random effect had a variance of 161.8, while the residual variance was 10701.0.

Using combinations of the seven potential fixed effects (six oceanographic covariates and laying sequence) without large correlations between predictors, and the plot random effect, we fit 30 models. The four top-ranked models accounted for 98% of the total model weight and had an Akaike weight > 0.05, where Akaike weight represents the relative likelihood that the model is the best model in the set (Table 3). Each of the covariates we considered appeared in one or more of these four top-ranked models.

Top-ranked models did not indicate a positive relationship between oceanographic indices associated with presumed higher ocean productivity and egg size. Instead, the relationships we found in the four top-ranked models between the oceanographic covariates and egg size were generally opposite to what we had predicted (Table 4). We found negative relationships between NPGO and egg size (first- and second-ranked models) and BEUTI and egg size (first- and third-ranked models). We found positive relationships between ONI and egg size (second-ranked model), PDO and egg size (fourth-ranked model), and SST and egg size (third- and fourth-ranked models). The only result that supported our initial prediction was the positive relationship between ANCHL and egg size (third-ranked model), though the 95% confidence interval for this effect included 0. Lastly, we found that laying sequence had a much bigger effect on egg size than any of the oceanographic covariates, with the second egg laid being substantially larger than the first. Laying sequence appeared in all of the top-ranked models.

TABLE 3
Fixed effects and Akaike Information Criterion (AIC) values for the four top-ranked models fitted to Scripps's Murrelet *Synthliboramphus scrippsi* egg size at Santa Barbara, California, USA

Fixed effects[a]	AIC	ΔAIC	AIC$_w$
SEQ, BEUTI, NPGO	10 558.27	0.00	0.58
SEQ, NPGO, ONI	10 559.64	1.37	0.29
SEQ, ANCHL, BEUTI, SST	10 562.81	4.54	0.06
SEQ, PDO, SST	10 563.05	4.78	0.05

[a] ANCHL = Larval anchovy catch-per-unit effort; BEUTI = Biologically Effective Upwelling Transport Index; NPGO = North Pacific Oscillation; ONI = Ocean Niño Index; PDO = Pacific Decadal Oscillation; SEQ = laying sequence; SST = sea surface temperature.

TABLE 2
The form of six oceanographic covariates selected for modeling Scripps's Murrelet *Synthliboramphus scrippsi* egg size at Santa Barbara Island, California, USA

Spatial dimension	Covariate[a]	Covariate form	Monthly values averaged to model eggs observed in year *t*
Large-scale	Pacific Decadal Oscillation (PDO) Index	6-mo lagged	January through June, year *t*-1
Large-scale	Oceanic Niño Index (ONI)	6-mo lagged	January through June, year *t*-1
Large-scale	North Pacific Gyre Oscillation (NPGO) Index	6-mo unlagged	January through June, year *t*
Regional	Larval anchovy catch-per-unit-effort (ANCHL)	Unlagged	Spring metric, year *t*
Regional	Biologically Effective Upwelling Transport Index (BEUTI)	12-mo lagged	July year *t*-2 through June, year *t*-1
Local	Sea surface temperature (SST)	6-mo unlagged	January through June, year *t*

[a] For each covariate except ANCHL, four covariate forms were considered: 12-mo lagged, 6-mo lagged, 12-mo unlagged, and 6-mo unlagged. For ANCHL, which was a single value each year collected in spring, only lagged and unlagged forms were considered.

TABLE 4

Parameter estimates, standard errors, and 95% confidence intervals for parameters in the four top-ranked models fit to Scripps's Murrelet *Synthliboramphus scrippsi* egg size at Santa Barbara Island, California, USA

Model[a]	Parameter[a]	Estimate	Standard error	95% confidence interval
SEQ, NPGO, BEUTI	SEQ	36.18	8.71	(19.20, 53.35)
	NPGO	-15.61	3.52	(-22.91, -4.32)
	BEUTI	-13.34	4.71	(-22.67, -8.86)
SEQ, NPGO, ONI	SEQ	36.54	8.72	(19.57, 53.76)
	NPGO	-13.43	3.85	(-21.09, -6.04)
	ONI	12.40	4.86	(3.15, 22.32)
SEQ, ANCHL, BEUTI, SST	SEQ	36.18	8.74	(19.20, 53.50)
	ANCHL	4.81	5.46	(-5.64, 15.76)
	BEUTI	-14.31	5.46	(-25.59, -4.01)
	SST	8.98	4.21	(0.76, 17.27)
SEQ, PDO, SST	SEQ	36.22	8.74	(19.21, 53.45)
	PDO	19.28	4.53	(10.74, 28.76)
	SST	2.89	4.03	(-5.13, 10.66)

[a] ANCHL = Larval anchovy catch-per-unit effort; BEUTI = Biologically Effective Upwelling Transport Index; NPGO = North Pacific Oscillation; ONI = Oceanic Niño Index; PDO = Pacific Decadal Oscillation; SEQ = laying sequence; SST = sea surface temperature.

DISCUSSION

Our analysis revealed that laying sequence, as well as large-scale and region-wide oceanographic processes, drive egg size differences in murrelets. However, the relationships that we found between egg size and oceanographic conditions were generally opposite to what we had predicted, based on our hypothesis that presumed greater ocean productivity should lead to larger murrelet eggs.

We found a negative relationship between NPGO and egg size and between BEUTI and egg size. Thomsen & Green (2019) previously found a positive relationship between NPGO and murrelet nest success, suggesting that a better understanding of the relationship between egg size and nest success is needed. Greater NPGO values were also linked to greater reproductive success for Laysan *Phoebastria immutabilis* and Black-footed *Ph. nigripes* albatrosses breeding in the Northwest Hawaiian Islands (Thorne *et al*. 2015). When NPGO is positive, changes in wind forces create upwelling-favorable conditions in the CCS (Lorenzo *et al*. 2008), creating a particularly productive planktonic ecosystem throughout the spring and summer (Chenillat *et al*. 2012). Similarly, BEUTI aims to capture the bottom-up dynamics of productivity, with a positive value indicating the drawing of nutrient-rich water toward the surface and a negative value indicating the movement of nutrient-rich water in the opposite direction (Jacox *et al*. 2016).

We found a positive relationship between ONI and egg size, PDO and egg size, and SST and egg size (Table 4). Positive ONI values indicate warmer waters, which presumably are not ideal conditions for murrelet prey, particularly northern anchovy (larvae and juveniles). During positive ONI phases, juvenile and adult anchovy abundances have been shown to decline off Southern California (Fiedler *et al*. 1986). PDO captures SST variations in the North Pacific, where a positive phase is associated with higher SST, resulting in reduced biological productivity (Wen *et al*. 2004).

Barrett *et al*. (2012) suggested that decreased thermoregulatory costs counteracting the metabolic cost of producing an egg may result in a link between higher water temperature and larger eggs. Similarly, Hipfner (2012) proposed that during warm-water years, female Glaucous-winged Gulls expend less energy on self-maintenance and invest more energy into producing larger eggs. The specific mechanisms by which PDO and SST influence murrelet egg size remain unclear.

The one covariate effect that supported our hypothesis was the relationship between ANCHL and egg size, which was positive, though the 95% confidence interval included 0. ANCHL is the only one of our covariates that directly captures the mechanism by which we expect ocean productivity, related to and a proxy for prey availability, to affect the murrelet food web and thus impact murrelet demography. Diet information for murrelets is limited but the species appears to be a generalist feeder that preys on subadult and adult northern anchovy as well as other small pelagic fish and euphausiids (Hamilton *et al*. 2004). The central stock of northern anchovy is found in the southern California Current, ranging from San Francisco Bay to central Baja California. It is the most abundant small pelagic fish in the region (Sydeman *et al*. 2020) and is an important forage fish for many seabirds in the region, including California Brown Pelicans *Pelecanus occidentalis californicus* (Anderson *et al*. 1980) and Elegant Terns *Thalasseus elegans* (Schaffner 1986). Anchovy are known for highly variable population dynamics that have been previously linked to the PDO (e.g., Chavez *et al*. 2003) and upwelling (e.g., Checkley *et al*. 2017) among other factors. Recent research using a long time series (1957–2015) did not find a relationship between anchovy biomass and PDO, local temperature, or the Multivariate El Niño Southern Oscillation index, but it did find that biomass was positively related to springtime upwelling intensity with a 2-yr lag (Sydeman *et al*. 2020). Anchovy biomass was also weakly negatively related to Pacific sardine *Sardinops sagax* biomass

(Sydeman *et al*. 2020). These two species of forage fish have long been believed to be asynchronous, but recent findings by Siple *et al*. (2020) suggest that evidence of this relationship has likely been misrepresented by the use of landings data and short time series that do not adequately characterize the underlying ecological processes. However, scales found in sediments in the Santa Barbara Basin have demonstrated periods where anchovy and sardine deposition rates are complementary and periods where they are opposite (Checkley *et al*. 2017). Further research with a time series that is more than twice the length of the period of fluctuation is required to understand the mechanisms behind these fluctuations (Siple *et al*. 2020). While we found a weak relationship between egg size and ANCHL, our results are further complicated because our study period (2009–2017) occurred during a decline in anchovy abundance from 2009 to 2015 (MacCall *et al*. 2016, Sydeman *et al*. 2020). Thus, while our results support a mechanism between ocean productivity and murrelet demography, they also reveal an incomplete understanding of how ocean productivity may be driving food resources for murrelets.

Our support for a plot random effect indicates the possibility that birds nesting in different areas may also feed in different areas. We lack contemporary fine-scale foraging information for murrelets during the breeding season, but tracking data from the 1990s and early 2000s show that murrelets can fly long distances in short periods of time to forage (Whitworth *et al.* 1995). Individuals forage within the Southern California Bight during the breeding season, with breeders foraging at greater distances than non-breeders, likely due to energy needs for incubation (Hamilton *et al.* 2011). At-sea surveys indicate that during the non-breeding season, murrelets disperse as far north as Vancouver Island, Canada, with the highest densities between central Baja California and central Oregon (Karnovsky *et al.* 2005). Individual quality of females may also influence foraging ability and thus egg size (e.g., Sorensen *et al*. 2009), but we were unable to uniquely identify individuals in this study. More information on murrelet foraging, diet, and post-breeding dispersal, perhaps in conjunction with surveys of prey availability, is required to directly link egg size with resource availability during the breeding and non-breeding seasons.

We found mixed results regarding the relevant temporal scale of covariates. Support was greatest for unlagged effects of SST and NPGO (both 6-mo unlagged), and ANCHL. However, support was greatest for lagged effects of PDO and ONI (both 6-mo lagged) and BEUTI (12-mo lagged), suggesting that oceanographic conditions in the prior year may have important effects on breeders. Ainley & Hyrenbach (2010) found that current, as well as winter conditions, can affect the prevalence of several species in the central portion of the CCS. High quality pre-breeding diet has been linked to larger eggs and laying date for the Cassin's Auklet (Sorensen *et al.* 2009).

One consistent and important effect supported by all our competitive models was laying sequence, with second eggs substantially larger than first eggs. The relationship between laying sequence and egg size is well-studied in other species such as *Eudyptes* penguins (e.g., Stein & Williams 2013), where the egg size difference is much more pronounced, and the first egg rarely produces a fledged chick. Intra-clutch egg size dimorphism is less extreme for murrelets; Murray *et al*. (1983) found that the second egg of a murrelet clutch was ~1 g heavier on average than the first, and here our measurements of second eggs were, on average, 1.9% larger than first eggs. Murrelet females leave the nest unattended for about 8 d after laying the first

egg before returning to lay the second egg (Murray *et al*. 1980). This extended laying interval helps to reduce the daily cost of egg production (Astheimer 1985), and the inter-egg foraging period may be key to murrelets producing a larger second egg (Murray *et al*. 1983). However, this period of temporary egg neglect also comes at a cost. Island deer mice will depredate murrelet eggs when nests are unattended, with especially high predation during droughts when vegetation is sparse (Murray *et al*. 1980, Thomsen & Green 2019). Given the risk of egg depredation, murrelets may benefit from investing more energy in the second egg. However, if the frequency of drought years increases in the Channel Islands with climate change, the ability of murrelets to withstand mice depredation may be compromised.

Egg measurements have been collected at SBI since the 1990s without any indication of their importance to the conservation of murrelets. Our analysis provides some support for a positive relationship between murrelet egg size and available food resources, indicating that egg size may prove to be a sensitive and relatively easily collected metric through which to understand the degree to which prey conditions may be changing. However, murrelets are long-lived species that will delay or forgo breeding during low prey availability years (Goodman 1974, Hunt & Butler 1980); such a strategy is characteristic of most CCS seabirds (Ainley & Boekelheide 1990). Therefore, egg size may only be a valuable metric of oceanographic conditions above a certain threshold of prey availability. Given the relatively large size of eggs produced by murrelets, which is necessary to support precociality, investment in egg production requires a large amount of nutrient and energy input (Robins 1981, Williams 2005, Nager 2006). Egg size can influence offspring fitness and survival (Krist 2011, Lee *et al*. 2012, Marchisio *et al*. 2021). Monitoring the relationship between egg size and hatching success or chick survival would be a valuable step in understanding how murrelet populations cope, and might continue to cope, with the highly variable CCS.

REFERENCES

AINLEY, D.G., BOEKELHEIDE, B.J., MORRELL, S.H. & STRONG, C.S. 1990. Cassin's Auklet. In: AINLEY, D.G. & BOEKELHEIDE, B.J. (Eds.) *Seabirds of the Farallon Islands: Dynamics of an Upwelling System Community*. Stanford, USA: Stanford University Press, pp. 306–338.

AINLEY, D.G. & HYRENBACH, K.D. 2010. Top-down and bottom-up factors affecting seabird population trends in the California current system (1985–2006). *Progress in Oceanography* 84: 242–254.

AINLEY, D.G., SYDEMAN, W.J. & NORTON, J. 1995. Upper-trophic level predators indicate interannual negative and positive anomalies in the California Current food web. *Marine Ecology Progress Series* 118: 69–79.

ANDERSON D.W., GRESS, F. & KELLY, P.R. 1980. Brown Pelicans as anchovy stock indicators and their relationships to commercial fishing. *California Cooperative Oceanic Fishery Investigations, Reports* 21: 54–61.

ASTHEIMER, L.B. 1985. Long laying intervals: A possible mechanism and its implications. *The Auk* 102: 401–409. doi:10.2307/4086789

BAKUN, A., BLACK, B.A., BOGRAD, S.J. ET AL. 2015. Anticipated effects of climate change on coastal upwelling ecosystems. *Current Climate Change Reports* 1: 85–93. doi:10.1007/s40641-015-0008-4

BARRETT, R., NILSEN, E. & ANKER-NILSSEN, T. 2012. Long-term decline in egg size of Atlantic Puffins *Fratercula arctica* is related to changes in forage fish stocks and climate conditions. *Marine Ecology Progress Series* 457: 1–10. doi:10.3354/meps09813

BATES, D., MÄCHLER, M., BOLKER, B. & WALKER, S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48. doi:10.18637/jss.v067.i01

BENNETT, J.L., JAMIESON, E.G., RONCONI, R.A. & WONG, S.N.P. 2017. Variability in egg size and population declines of Herring Gulls in relation to fisheries and climate conditions. *Avian Conservation and Ecology* 12: 16. doi:10.5751/ACE-01118-120216

BOGRAD, S.J. & LYNN, R.J. 2001. Physical-biological coupling in the California Current during the 1997–99 El Niño-La Niña Cycle. *Geophysical Research Letters* 28: 275–278. doi:10.1029/2000GL012047

BRADY, R.X., ALEXANDER, M.A., LOVENDUSKI, N.S. & RYKACZEWSKI, R.R. 2017. Emergent anthropogenic trends in California Current upwelling. *Geophysical Research Letters* 44: 5044–5052. doi:10.1002/2017GL072945

CARTER, H.R., MCCHESNEY, G.J., JAQUES, D.L. ET AL. 1992. *Breeding populations of seabirds in California, 1989–1991, volume 1 population estimates*. Dixon, USA: US Fish and Wildlife Service, Northern Prairie Wildlife Research Center; Newark, USA: US Fish and Wildlife Service San Francisco Bay National Wildlife Complex.

CHAVEZ, F.P., RYAN, J., LLUCH-COTA, S.E. & NIQUEN C., M. 2003. From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. *Science* 299: 217–221. doi:10.1126/science.1075880

CHECKLEY, D.M., ASCH, R.G. & RYKACZEWSKI, R.R. 2017. Climate, anchovy, and sardine. *Annual Review of Marine Science* 9: 8.1–8.25.

CHECKLEY, D.M. & BARTH, J.A. 2009. Patterns and processes in the California Current System. *Progress in Oceanography* 83: 49–64. doi:10.1016/j.pocean.2009.07.028

CHENILLAT, F., RIVIÈRE, P., CAPET, X., LORENZO, E.D. & BLANKE, B. 2012. North Pacific Gyre Oscillation modulates seasonal timing and ecosystem functioning in the California Current upwelling system. *Geophysical Research Letters* 39: L01606. doi:10.1029/2011GL049966

CLIMATE PREDICTION CENTER INTERNET TEAM. 2021. *Cold & Warm Episodes by Season*. College Park, USA: National Weather Service. [Accessed at https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php on 15 July 2021.]

FIEDLER, P.C., METHOT, R.D. & HEWITT, R.P. 1986. Effects of California El Niño 1982–1984 on the northern anchovy. *Journal of Marine Research* 44: 317–338. doi:10.1357/002224086788405365

GOODMAN, D. 1974. Natural selection and a cost ceiling on reproductive effort. *American Naturalist* 108: 247–268.

GJERDRUM, C., VALLÉE, A.M.J., CLAIR, C.C.S., BERTRAM, D.F., RYDER, J.L. & BLACKBURN, G.S. 2003. Tufted Puffin reproduction reveals ocean climate variability. *Proceedings of the National Academy of Sciences* 100: 9377–9382. doi:10.1073/pnas.1133383100

HAMILTON, C.D., CARTER, H.R. & GOLIGHTLY, R.T. 2004. Diet of Xantus's Murrelets in the Southern California Bight. *The Wilson Bulletin* 116: 152–157.

HAMILTON, C.D., GOLIGHTLY, R.T. & TAKEKAWA, J.Y. 2011. Relationships between breeding status, social-congregation attendance, and foraging distance of Xantus's Murrelets. *The Condor* 113: 140–149. doi:10.1525/cond.2011.100040

HIPFNER, J.M. 2008. Matches and mismatches: Ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. *Marine Ecology Progress Series* 368: 295–304. doi:10.3354/meps07603

HIPFNER, J.M. 2012. Effects of sea-surface temperature on egg size and clutch size in the Glaucous-winged Gull. *Waterbirds* 35: 430–436. doi:10.1675/063.035.0307

HUNT, G.L. JR. & J.L. BUTLER. 1980. Reproductive ecology of Western Gulls and Xantus's Murrelets with respect to food resources in the Southern California Bight. *California Cooperative Oceanic Fisheries Investigation, Reports* 21: 62–67.

JACOX, M.G., EDWARDS, C.A., HAZEN, E.L. & BOGRAD, S.J. 2018. Coastal upwelling revisited: Ekman, Bakun, and improved upwelling indices for the U.S. West Coast. *Journal of Geophysical Research: Oceans* 123: 7332–7350. doi:10.1029/2018JC014187

JACOX, M.G., HAZEN, E.L. & BOGRAD, S.J. 2016. Optimal environmental conditions and anomalous ecosystem responses: Constraining bottom-up controls of phytoplankton biomass in the California Current System. *Scientific Reports* 6: 27612. doi:10.1038/srep27612

KARNOVSKY, N.J., SPEAR, L.B., CARTER, H.R. ET AL. 2005. At-sea distribution, abundance and habitat affinities of Xantus's Murrelets. *Marine Ornithology* 33: 89–104.

KRIST, M. 2011. Egg size and offspring quality: A meta-analysis in birds. *Biological Reviews of the Cambridge Philosophical Society* 86: 692–716. doi:10.1111/j.1469-185X.2010.00166.x

LEE, D.E., WARZYBOK, P.M. & BRADLEY, R.W. 2012. Recruitment of Cassin's Auklet (*Ptychoramphus aleuticus*): Individual age and parental age effects. *The Auk* 129: 124–132. doi:10.1525/auk.2012.10224

LORENZO, E.D., SCHNEIDER, N., COBB, K.M. ET AL. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters* 35: L08607. doi:10.1029/2007GL032838

MACCALL, A.D., SYDEMAN, W.J., DAVISON, P.C. & THAYER, J.A. 2016. Recent collapse of northern anchovy biomass off California. *Fisheries Research* 175: 87–94. doi:10.1016/j.fishres.2015.11.013

MARCHISIO, N., BARRIONUEVO, M. & FRERE, E. 2021. Compensatory effect of egg size dimorphism on hatching asynchrony in Magellanic Penguin. *Journal of Avian Biology* 52: 1–11. doi:10.1111/jav.02673

MURRAY, K.G., WINNETT-MURRAY, K. & HUNT, G.L. 1980. Egg neglect in Xantus' Murrelet. *Proceedings of the Colonial Waterbird Group* 3: 186–195.

MURRAY, K.G., WINNETT-MURRAY, K., EPPLEY, Z.A. & SCHWARTZ, D.B. 1983. Breeding biology of the Xantus' Murrelet. *The Condor* 85: 12–21. doi:10.2307/1367880

NAGER, R. 2006. The challenges of making eggs. *Ardea-Wageningen* 94: 323–346.

NOAA [National Oceanic and Atmospheric Association]. California Current Integrated Ecosystem Assessment website. Washington, USA. [Accessed at https://www.integratedecosystemassessment.noaa.gov/regions/california-current on 05 September 2021.]

POZO BUIL, M., JACOX, M.G., FIECHTER, J. ET AL. 2021. A dynamically downscaled ensemble of future projections for the California Current System. *Frontiers in Marine* Science 8: 612874. doi:10.3389/fmars.2021.612874

R CORE TEAM. 2021. *R: A Language and Environment for Statistical Computing.* Vienna, Austria: The R Foundation for Statistical Computing. [Accessed at https://www.R-project.org/ on 01 June 2021.]

ROBBINS, C.T. 1981. Estimation of the relative protein cost of reproduction in birds. *The Condor* 83: 177–179. doi:10.2307/1367424

ROTH, J.E., SYDEMAN, W.J. & MARTIN, P.L. 2005. Xantus's Murrelet breeding relative to prey abundance and oceanographic conditions in the Southern California Bight. *Marine Ornithology* 33: 115–121.

SCHAFFNER, F.C. 1986. Trends in Elegant Tern and northern anchovy populations in California. *Ornithological Applications* 88: 347–354. doi:10.2307/1368882

SCHEIPL, F., GREVEN, S. & KÜCHENHOFF, H. 2008. Size and power of tests for a zero random effect variance or polynomial regression in additive and linear mixed models. *Computational Statistics & Data Analysis* 52: 3283–3299. doi:10.1016/j.csda.2007.10.022

SEALY, S.G. 1975. Egg size of murrelets. *The Condor* 77: 500. doi:10.2307/1366104

SIPLE, M.C., ESSINGTON, T.E., BARNETT, L.A.K. & SCHEUERELL, M.D. 2020. Limited evidence for sardine and anchovy asynchrony: Re-examining an old story. *Proceedings of the Royal Society B* 287: 20192781. doi:10.1098/rspb.2019.2781

SORENSEN, M.C., HIPFNER, J.M., KYSER, T.K. & NORRIS, D.R. 2009. Carry-over effects in a Pacific seabird: Stable isotope evidence that pre-breeding diet quality influences reproductive success. *Journal of Animal Ecology* 78: 460–467. doi:10.1111/j.1365-2656.2008.01492.x

STEIN, R.W. & WILLIAMS, T.D. 2013. Extreme intraclutch egg-size dimorphism in Eudyptes penguins, an evolutionary response to clutch-size maladaptation. *The American Naturalist* 182: 260–270. doi:10.1086/670929

SYDEMAN, W.J., DEDMAN, S., GARCÍA-REYES, M. ET AL. 2020. Sixty-five years of northern anchovy population studies in the southern California Current: A review and suggestion for sensible management. *ICES Journal of Marine Science* 77: 486–499. doi:10.1093/icesjms/fsaa004

THOMSEN, S.K. & GREEN, D.J. 2019. Predator-mediated effects of severe drought associated with poor reproductive success of a seabird in a cross-ecosystem cascade. *Global Change Biology* 25: 1642–1652. doi:10.1111/gcb.14595

THORNE, L.H., HAZEN, E.L., BOGRAD, S.J. ET AL. 2015. Foraging behavior links climate variability and reproduction in North Pacific albatrosses. *Movement Ecology* 3: 27. doi:10.1186/s40462-015-0050-9

WEN, C., KUMAR, A. & XUE, Y. 2014. Factors contributing to uncertainty in Pacific Decadal Oscillation index. *Geophysical Research Letters* 41: 7980–7986. doi:10.1002/2014gl061992

WHITWORTH, D.L., TAKEKAWA, J.Y., CARTER, H.R., NEWMAN, S.H., KEENEY, T.W. & KELLY, P.R. 1995. *Foraging Distribution and Post-Breeding Dispersal of the Xantus' Murrelets in the Southern California Bight.* Unpublished report. Vallejo and Dixon, USA: National Biological Service and California Pacific Science Center; Point Mugu, USA: Naval Air Weapons Station.

WILLIAMS, T.D. 2005. Mechanisms underlying the costs of egg production. *BioScience* 55: 39–48. doi:10.1641/0006-3568(2005)055[0039:MUTCOE]2.0.CO;2