



Ocean conditions influence diet and productivity in California least terns

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ABSTRACT: The California least tern *Sternula antillarum browni* (CLTE) is a federally endangered and state-listed seabird that forages and nests coastally within the California Current System. This cold-water Pacific Ocean current supports a high level of biodiversity and has experienced considerable variability in recent decades. Despite widespread nesting site management, CLTE are experiencing population declines attributed to low reproductive success. This has prompted speculation that changes in ocean conditions are disrupting CLTE prey and thus population recovery. We analyzed a 21 yr data set of egg membrane stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$), archived oceanographic data, and long-term colony monitoring reports to understand the complex relationships between diet, ocean conditions, and CLTE productivity. Our analyses suggest that variation in ocean conditions, specifically compression of nearshore cold-water habitat and upwelling strength, influenced the diet composition of pre-breeding females. We also found that changes in pre-breeding diet were linked to CLTE productivity. Higher fledge rates were observed when diet was more carbon-enriched and when lower trophic level prey was consumed. These diet shifts were observed when upwelling was more intense and cold-water habitat was more compressed against the shoreline. Our results suggest that annual variability in diet, which changes with ocean conditions, impacts annual fledge rates. This research can inform climate-resilient management of CLTE habitats, which may include restoration of foraging habitats to support prey abundance, increasing the effectiveness of population recovery efforts in light of ongoing oceanographic changes.

KEY WORDS: Seabird · Population recovery · Breeding · Climate · Prey · Stable isotopes

1. INTRODUCTION

Environmental variability has been identified as a key factor impacting population dynamics across taxonomic groups, especially in marine systems where shifts in ocean conditions can disrupt productivity and trophic relationships (Sydeman et al. 2015). In marine species, climate-driven ocean shifts have been linked to changes in prey availability, predation pressure, habitat disturbance, increased competition, and disease (Becker et al. 2007). Piscivorous migratory seabirds are especially reliant on accessible and con-

sistent prey sources near their nesting sites during the breeding season, when longer bouts of travel to obtain prey can be costly to them and to their offspring (Cohen et al. 2014, Regular et al. 2014, Sullivan et al. 2020). As a result, a growing body of research has explored the direct and indirect impacts of climate variability on seabird prey abundance and distribution (Becker et al. 2007, Wolf et al. 2009, Ainley et al. 2018) to inform and develop innovative management and recovery strategies for vulnerable seabird species.

The California least tern *Sternula antillarum browni* (CLTE) is a small, coastal seabird that mi-

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grates north from waters offshore of tropical western Mexico and Central America (Morales Flores 2024) to the west coast of North America where it breeds and nests at beaches between the San Francisco Bay and the Pacific Coast of the Baja California Peninsula to San Quintin, Baja California (Ryan et al. 2025). CLTE were listed as federally endangered in 1970 and are a fully protected species in the state of California (California Natural Diversity Database 2025). Since listing, there have been significant advances in the recovery of CLTE populations as a result of management efforts at nesting grounds (Frost 2017). During the late 1990s and early 2000s, CLTE breeding pairs increased significantly, likely due to management interventions at nesting sites, such as fence building, predator control, and habitat restoration (USFWS 2020). Despite these effective management actions, there have been declines in the number of breeding pairs, and the ratio of fledglings to breeding pairs, hereafter referred to as fledge rate, in the last decade (Sin 2021). Although the number of CLTE breeding pairs within the US breeding range has met the downlisting criteria in the USFWS (2020) recovery plan, the range-wide fledge rate is below the recovery goal of 1.0 fledgling per pair, with values less than 0.5 for the previous 17 reported breeding seasons (Fig. 1).

Reported chick die-offs and nesting failures unrelated to predation (Marschalek 2006, Frost 2017, Sin

2021) suggest that CLTE population recovery is being limited by environmental factors, specifically changes in ocean conditions. There is increasing evidence that climate change has impacted the directionality and variability of temperature and upwelling fluctuations in the California Current System (CCS) where CLTE forage (Bakun et al. 2015, Wang et al. 2015). Using a 60+ yr time series, California Cooperative Oceanic Fisheries Investigations (CalCOFI) identified significant sea surface temperature anomalies since 2014 within the CCS (Leising 2015, Peabody et al. 2018), with warmer than normal conditions across the California Current (Harvey et al. 2023). Furthermore, recent research into long-term upwelling trend modeling in the CCS predicts a decrease in summertime upwelling-favorable winds over the next century (Rykaczewski et al. 2015). Changes in upwelling strength and sea surface temperature exert bottom-up effects on primary productivity, which impact the recruitment and distribution of mid-to-low trophic level planktivorous fish, a primary food source for seabirds (Bakun et al. 2015). For example, the abundance of northern anchovy *Engraulis mordax*, an important prey species for many seabirds due to its high lipid content (Elliott et al. 2007), has exhibited significant declines along the coast of southern California over the past 20 yr due to shifts in climate conditions (MacCall et al. 2016, Sydeman et al. 2020).

Ocean conditions have been identified as putative drivers of population dynamics for several coastal seabird species, including CLTE (Golet et al. 2000, Sydeman et al. 2015, Robinette et al. 2020), primarily through changes in prey availability (Thompson et al. 2012, Ainley et al. 2018). Although CLTE diet during the breeding season can be broad (see Leicht et al. 2023), Robinette et al. (2020) found that high inter-annual variability in diet composition was an important driver of annual CLTE productivity, with higher prevalence of northern anchovy and silver-side smelt (Family Atherinopsidae) in years with better fledge rates. As central-place foragers who travel to and from feeding areas within a limited distance from the nesting colony during the breeding season (Atwood & Minsky 1983), coastal seabirds switch prey sources based on prey availability near-shore (Warzybok et al. 2018). When

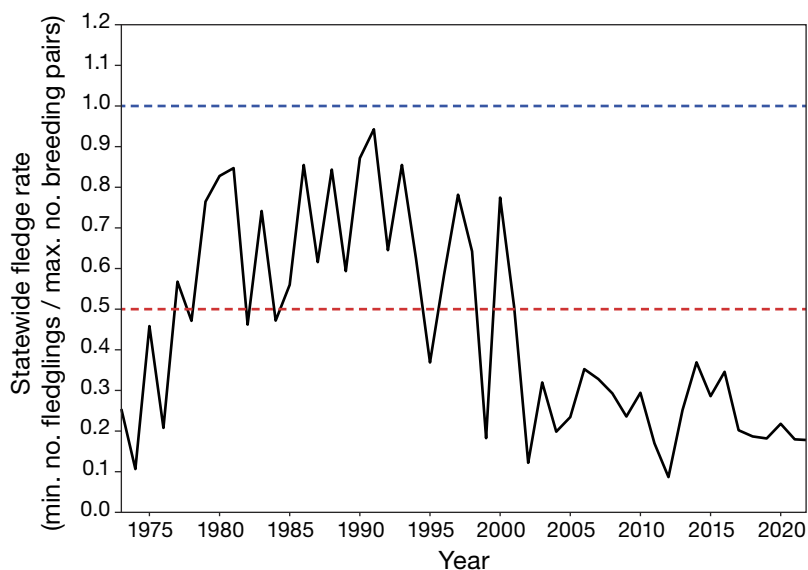


Fig. 1. California least tern annual reproductive output within its US range, calculated as the ratio of minimum estimated fledglings to maximum estimated adult breeding pairs (California Department of Fish and Wildlife unpubl. data). The dashed blue line represents the US Fish and Wildlife Service recovery goal of 1.0 fledgling per breeding pair; the dashed red line shows that since 2002, fledge rate has been below half of that recovery goal

prey distribution or abundance changes because of shifting oceanic conditions, adults may fly farther from the colony to forage or be forced to consume less nutrient-rich species (Warzybok et al. 2018). Concomitant changes in diet have been linked to a decrease in reproductive success of seabirds (Golet et al. 2000, Anderson et al. 2007, Sydeman et al. 2015), pointing to linkages among seasonal upwelling patterns, forage fish availability, and seabird population dynamics (Thompson et al. 2012).

Understanding the connections between resource availability and reproductive success requires an ability to characterize diet shifts over time. Stable isotope analysis can evaluate diet variability by using mass spectrometry to measure ratios of different isotopic forms of nitrogen and carbon (e.g. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) within consumer tissues. A growing number of diet and foraging studies measure these ratios to estimate proportions of different species consumed, based on unique $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of prey species (Hobson et al. 1994, Kelly 2000). This type of analysis can identify changes in diet over time; for example, an increase in $\delta^{15}\text{N}$ values would indicate a shift to higher trophic level prey (Kelly 2000), whereas an increase in $\delta^{13}\text{C}$ would suggest a shift in foraging habitat toward more coastal areas (Cherel & Hobson 2007). Here, we leveraged a 21 yr data set of ocean conditions, CLTE diet and foraging distance as inferred from stable isotope analysis, and CLTE productivity measures to consider whether interannual differences in CLTE diet are influenced by fluctuating ocean conditions, and whether changes in diet are linked to CLTE reproductive output. The goal of this study was to identify oceanographic conditions that significantly impact CLTE foraging and determine whether resulting shifts in diet composition affect reproductive output, thus allowing for more accurate predictions regarding CLTE population growth or decline in future climate change scenarios.

2. MATERIALS AND METHODS

2.1. Study area

We focused on 2 of the largest nesting sites in the CLTE breeding range: Marine Corps Base Camp Pendleton (hereafter Pendleton) in northern San Diego County and Naval Base Coronado (hereafter Coronado) in San Diego Bay (Fig. 2). Over the past 20 yr, these sites comprised an estimated 40% of the annual CLTE breeding population throughout California (California Department of Fish and Wildlife [CDFW]

unpubl. data). As military bases, both sites are managed in accordance with their respective Integrated Natural Resources Management Plan (Marine Corps 2007, Department of the Navy 2013) and associated Biological Opinion issued by the US Fish and Wildlife Service (USFWS 1995, 2010). Furthermore, they are both monitored by the San Diego Zoo Wildlife Alliance (SDZWA) and are part of the statewide CLTE management program overseen by CDFW. Reporting spreadsheets submitted to CDFW are standardized to ensure estimated breeding pairs and fledge rates are calculated consistently throughout the state (Sin 2021).

2.2. Data

2.2.1. Oceanographic metrics

We considered 5 metrics of ocean conditions (Table 1): sea surface temperature anomalies (SST_a), habitat compression index (HCI), coastal upwelling transport index (CUTI), biologically effective upwelling transport index (BEUTI), and pre-conditioning cumulative upwelling index (pCUI). The first 2 metrics quantify coastal water temperature and the latter 3 quantify upwelling strength. All data were obtained from the National Oceanic and Atmospheric Administration (NOAA) Environmental Research Division; Table 1 provides more detail on data sources and accessibility.

SST_a values, measured in $^{\circ}\text{C}$, are based on a 30 yr monthly climatological baseline from 1982 to 2011 (Farchadi et al. 2024), using Optimum Interpolation Sea Surface Temperature (OISST) data stored in NOAA's long-term climate records (Banzon et al. 2016, Huang et al. 2021). HCI represents the amount of available cold-water habitat, based on the proportion of modeled grid cells extending 150 km offshore with lower temperatures at 2 m depth than the monthly temperature threshold (Santora et al. 2020, Schroeder et al. 2022). CUTI measures the amount of coastal vertical transport (Jacox et al. 2018), using monthly measurements taken via a remote sensing station located at 33°N and 119°W . BEUTI measures the cumulative amount of vertical nitrate flux and is calculated using the monthly measurements taken at the same sensing station as CUTI (Jacox et al. 2018). Lastly, pCUI is calculated as the cumulative sum of only positive daily upwelling index values at 33°N and 119°W (Schroeder et al. 2013, 2022). The 3 upwelling indices each provide different information regarding ocean conditions. CUTI indicates the inten-

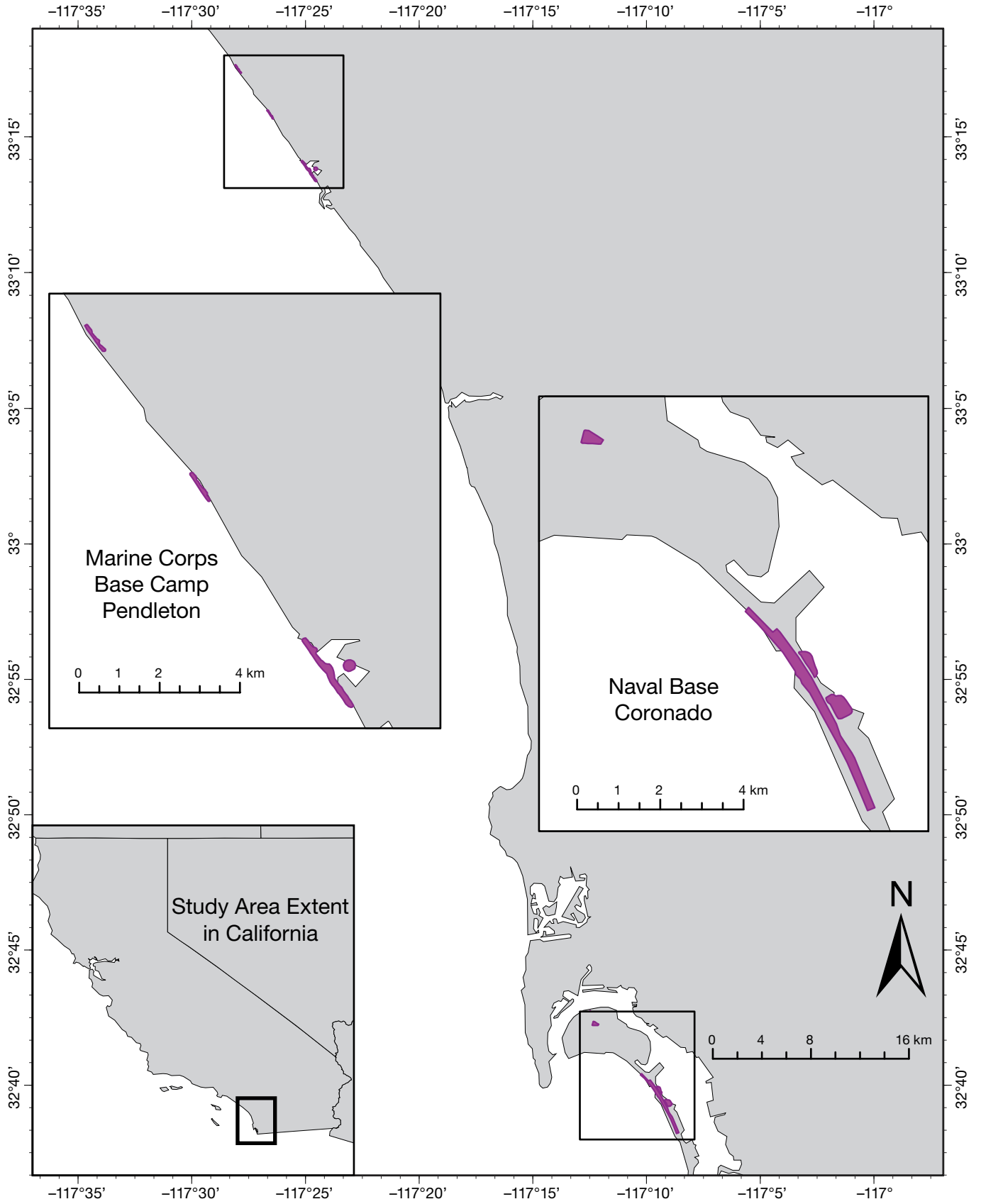


Fig. 2. CLTE nesting sites (pink areas) used in the analysis: Marine Corps Base Camp Pendleton (Pendleton) and Naval Base Coronado (Coronado). Data sources: ESRI; US Department of Commerce

Table 1. Five metrics of ocean conditions included in the analyses data were accessed from the National Oceanic and Atmospheric Administration's (NOAA) Integrated Ecosystem Assessment (IEA) webpage, served by the Environmental Research Division Data Access Program (ERDDAP) (<https://www.integratedecosystemassessment.noaa.gov/regions/california-current-iaa-indicators>). CC-IEA: California Current IEA. Dates are given as mo/d

Ocean condition metric	Measurement type	Value range	Calculation method	Time period	Measurement location	Source
Coastal upwelling transport index (CUTI)	$\text{m}^2 \text{s}^{-1}$	-0.5 to +3	Cumulative amount of coastal vertical transport (total volume of water upwelled or downwelled) between January and March, based on estimates obtained from a data-assimilative regional ocean model (Jacox et al. 2018)	1/1–3/31	Bin with 1° of latitude and extending 75 km offshore at 33° N and 119° W	CC-IEA, served from ERDDAP, filtered for 'Climate and Ocean rivers'
Biologically effective upwelling transport index (BEUTI)	$\text{mmol s}^{-1} \text{m}^{-1}$	-2 to +8	Cumulative amount of vertical nitrate flux (total quantity of nitrate upwelled or downwelled) between January and March, based on estimates obtained from a data-assimilative regional ocean model (Jacox et al. 2018)	1/1–3/31	Bin with 1° of latitude and extending 75 km offshore at 33° N and 119° W	CC-IEA, served from ERDDAP, filtered for 'Climate and Ocean Drivers'
Sea surface temperature anomaly (SST _a)	°C difference from baseline	-3 to +7	Comparison between January–March monthly average sea surface temperature (SST) for each year and a 30 yr monthly climatological baseline from 1982 to 2011 (Farchadi et al. 2024)	1/1–3/31	1/4° grids averaged within 33° N and 119° W	NOAA's Optimum Interpolation Sea Surface temperature (OISST) values are derived from multiple platforms such as satellites, ships, buoys, and Argo floats at 1/4° spatial resolution (Banzon et al. 2016; Huang et al. 2020)
Habitat compression index (HCI)	Proportion below established temperature threshold	0 to 3	3 mo cumulative amount of available cold-water habitat, based on the proportion of modeled grid cells within a total area extending from shore to 150 km offshore with 2 m depth temperatures lower than the monthly temperature threshold (Santora et al. 2020, Schroeder et al. 2022)	1/1–3/31	35.5 to 30° N, from coast to 150 km offshore	CC-IEA, served from ERDDAP; thresholds are derived from historic and near-real-time SST modeling in 4 latitudinal ranges (Schroeder et al. 2022)
Pre-conditioning cumulative upwelling index (pCUI)	$\text{m}^3 \text{s}^{-1} 100 \text{m}^{-1}$ coastline	0 to 5000	2 mo cumulative sum of only positive daily upwelling index values computed from 1 degree 6-hourly Fleet Numerical Meteorology and Oceanography Center (FNMOC) sea level pressure (Schroeder et al. 2013, 2022)	1/1–3/1	33° N and 119° W	I. Schroeder (pers. comm.)

sity of upwelling/downwelling, whereas BEUTI estimates the amount of nitrate upwelled/downwelled, affecting some biological responses differently than intensity alone. Both CUTI and pCUI are quantifications of upwelling intensity, but the latter measures upwelling potential based on wind stress during the winter pre-conditioning period, as opposed to real-time wind-driven upwelling intensity.

All oceanographic variables were calculated as 3 mo cumulative values for 2 time periods: breeding year (January to March of each year) and prior year (January to March of the preceding year) to consider the impact of both real-time and lagged ocean conditions, as previous research suggests that impacts of environmental conditions on both prey abundance and seabird productivity can exhibit time lags in some marine systems (Zador et al. 2013). Although 2 yr lags have been shown to be relevant to reproductive performance in some seabird species, we focused on a 1 yr lag to align with findings from oceanographic research, which has demonstrated the importance of winter conditions on the abundance and distribution of young-of-year forage fish species (Schroeder et al. 2013, 2022), upon which CLTE rely due to their size (Robinette 2003, Baird 2010, Hanna et al. 2021).

We identified HCI and pCUI as the 2 metrics that best represented physical oceanic conditions for CLTE and exhibited no collinearity either between metrics or between breeding year and prior year (Figs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/meps15070_supp.pdf). We chose HCI over SST_a to characterize ocean temperatures because it captured mixed-layer conditions (Schroeder et al. 2022), and we chose pCUI over CUTI and BEUTI to characterize upwelling because it better captures the sustained impacts of winter conditions on biological responses such as prey abundance or seabird phenology (Schroeder et al. 2009). Both HCI and pCUI have been shown to impact biological responses and are important early-season indicators for ecological productivity (Bograd et al. 2009, Schroeder et al. 2013, 2022). Breeding year and prior year ocean metrics were scaled to have a mean of 0 and a standard deviation of 1 before fitting models to improve convergence.

2.2.2. Diet composition

Diet composition was assessed through stable isotope analysis of unhatched eggshell membranes, a common non-invasive method in seabird diet studies (Hobson 1995, Oppel et al. 2009, Polito et al. 2009,

Quillfeldt et al. 2009). Stable isotope analysis on eggshell membranes allows for examination of the proportional contribution of each prey source in a consumer's diet during the final stage of egg production, reflecting a diet integrated 3–5 d prior to laying (Hobson 1995, Quillfeldt et al. 2009). We paired archived isotope data from 242 CLTE abandoned or non-viable unhatched eggs salvaged from Pendleton and Coronado between 2003 and 2012 (Fournier 2016) with stable isotope data from a new analysis of 179 abandoned or non-viable unhatched eggs collected at the end of each breeding season between 2013 and 2023. We analyzed 10–12 unhatched eggs per site per year, excluding 2014, 2017, and 2018 when archived samples were not available at Pendleton. Findings from Fournier (2016) indicate that isotopic values ($n = 93$) did not differ significantly between eggshell membranes from hatched versus unhatched eggs ($\delta^{15}N$ $t = 1.001$, $p = 0.323$; $\delta^{13}C$ $t = -1.6$, $p = 0.118$). Previous studies have also indicated that $\delta^{15}N$ and $\delta^{13}C$ in eggshell membranes are isotopically homogeneous (Maurer et al. 2011) and independent of egg age (Oppel et al. 2009, Fournier 2016). To avoid pseudo-replication, only 1 egg per nest was analyzed.

We employed an established technique to separate the eggshell and membrane using acetic acid solution (Torres-Mansilla & Delgado-Mejía 2017, Shi et al. 2021). We validated the membrane separation technique by comparing acetic acid versus manual separation and found no statistical difference in the isotopic values among samples (Table S1). For eggshell membrane extraction, eggs were thawed and emptied of contents (yolk, albumen, embryo, etc.), then rinsed with deionized (DI) water. The eggshell fragments with attached membranes were soaked in acetic acid to dissolve the calcium carbonate shell while preserving the membranes for stable isotope analysis. Eggshell membrane pieces were cleaned, then dried at 60–80°C. Approximately 1–1.5 mg of membrane material from each egg was loaded into tin capsules, with 2 replicates for each egg. Samples were combusted in an elemental analyzer to obtain relative concentrations of nitrogen and carbon. Resulting carbon dioxide (CO_2) and nitrogen (N_2) gases were analyzed via continuous flow isotope ratio mass spectrometer at the San Diego State University (SDSU) Ecology Analytical Lab, to obtain isotopic ratios of each element; isotope ratios are recorded in $\delta = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$. Isotope ratios were normalized to air- N_2 for $\delta^{15}N$ and Vienna PeeDee belemnite for $\delta^{13}C$. Every 12 samples were bracketed by US Geological Survey (USGS) reference material (USGS40 L-glutamic acid) to correct for instrument

drift. For quality control purposes, we re-ran samples for which $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values were unexpectedly different between 2 replicates from the same egg (Text S1) and confirmed after re-runs that there was no significant difference in stable isotope signals between replicate samples. We also corrected $\delta^{13}\text{C}$ values for the Suess effect (Clark et al. 2021), which accounts for known atmospheric carbon shifts over multi-decadal time periods. Additionally, we found there was no need for lipid normalization (Text S1).

To determine what prey items were represented by the stable isotope signatures of eggshell membranes, we considered 7 known CLTE prey species or species groups (Robinette 2003, Robinette et al. 2015, 2020, Fournier 2016): northern anchovy, Pacific saury *Cololabis saira*, juvenile rockfish (*Sebastes* spp.), topsmelt silverside *Atherinops affinis*, krill (Family Euphausiidae), killifish (Family Fundulidae), and surfperches (Family Embiotocidae). Isotopic values (Table S2) for these prey sources were obtained from stable isotope literature from the Southern California Bight (Currin et al. 2011, Madigan et al. 2012, 2018a,b, Whitcombe 2014, Fournier 2016). Based on limited data from published literature on the isotopic values in tissues of marine forage species, we found relatively little evidence of interannual variation in known CLTE prey species when comparing samples taken from similar ocean sampling locations (Table S3).

2.2.3. CLTE productivity metrics

All CLTE nesting sites use standardized reporting techniques to estimate several productivity metrics for each breeding season (CDFW unpubl. data). The most consistently reported metric for reproductive output in CDFW reports is fledge rate, calculated as the ratio of minimum estimated fledgling count divided by the maximum estimate of breeding pair count. This ratio is understood to be a conservative estimate of fledgling success (Sin 2021), i.e. it uses the maximum estimated breeding pairs as the denominator instead of the minimum to reduce potential inflation of this productivity metric. It is also highly correlated with other reproductive metrics such as fledgling:egg ratio and fledgling:nest ratio (Lewison & Deutschman 2014, E. Mills unpubl. data). Fledge rates were calculated and compiled for 2003–2023 at Pendleton and Coronado separately and for sites combined. We considered hatch rate as a potential indicator of recruitment but found there was no significant annual variation in those rates during our study period (Fig. S3).

2.3. Statistical analyses

All statistical analyses were conducted in R (R Core Team 2024) using the base 'stats' package and additional packages described below.

2.3.1. Interannual variation in egg membrane stable isotopes

CLTE diet composition was quantified based on stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) derived from 421 individual eggs collected across years and study sites. To test for significant differences in dietary isotopic signals among years, we applied a sum contrast matrix using the 'contr.sum' function. The sum contrast compares each year's isotopic values to the overall mean for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, with significant p-values indicating years that deviate significantly from these grand means. We then used generalized linear models (GLMs) with year and site as predictor variables and either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values as the response variable. We also tested for year \times site interactions to determine whether the effect of year on either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ varied by site. Sum contrast matrices and GLMs were fit in R (R Core Team 2024) using the base 'stats' package.

To further explore annual shifts in CLTE diet, we used a stable isotope mixing model ('simmr'; R package version 0.5.1.216) to identify annual shifts in proportions of different types of prey consumed (Govan & Parnell 2023). This method applies Bayesian-based mixing models to determine the most statistically probable prey sources and their relative contributions by comparing eggshell membrane isotopic signatures to those of known CLTE prey species (Table S2). Stable isotope mixing models account for uncertainty around prey sources, fractionation rates between prey and consumer tissues, and individual variability (Moore & Semmens 2008). Fractionation rates, also known as trophic discrimination factors (TDFs), have not been calculated for any type of CLTE tissues, but other seabird species have been studied using controlled feedings (Ciancio et al. 2016, Jenkins et al. 2020, Ceia et al. 2021). Furthermore, recent studies have assessed how dietary stable isotopes are assimilated into seabird eggs (Polito et al. 2009, Bond & Diamond 2010, Federer et al. 2012, Buckner et al. 2022). TDF values from a study of pigeon guillemot *Cephus columba* diet (Buckner et al. 2022) were used in this analysis. These were derived from common murre *Uria aalge* blood (Jenkins et al. 2020) and adjusted by the fractionation difference between blood and egg

albumen (-0.4 for $\delta^{15}\text{N}$ and -0.3 for $\delta^{13}\text{C}$; Bond & Diamond 2010) to come up with approximate TDFs for their study species (2.51 for $\delta^{15}\text{N}$ and 0.79 for $\delta^{13}\text{C}$).

Preliminary 'simmr' analysis revealed high uncertainty in estimates of source contributions to CLTE diet because of considerable overlap in nitrogen values among known CLTE prey species. To resolve this, we conducted a hierarchical cluster analysis and calculated a silhouette score based on k -means clustering, with higher values reflecting cluster separation (sensu Ogilvy et al. 2022). Cluster analyses were performed in R (R Core Team 2024) using the packages 'cluster' (Maechler et al. 2023), 'factoextra' (Kassambara & Mundt 2020), and 'dendextend' (Galili 2015). This approach identified the optimal number of potential clusters ($k = 2$), representing 2 prey groups denoted as 'carbon-enriched' and 'carbon-depleted' based on their $\delta^{13}\text{C}$ values (Table S2), which have been used as an indicator of foraging distance from shore (Hobson 1987, Cherel & Hobson 2007, Jaeger et al. 2010). To confirm the validity of this clustering approach, we tested the isotopic separation in these 2 resulting prey groups using Kruskal-Wallis ($\chi^2 = 4.5$, $p = 0.034$; R Core Team 2024). *A posteriori* combining of prey sources (Govan & Parnell 2023) in our 'simmr' models produced annual proportions of carbon-enriched and carbon-depleted prey in the diet of subsampled pre-breeding females at each nesting site separately and at both combined.

2.3.2. Relationships between ocean conditions, egg membrane stable isotopes, and productivity

We ran GLMs to evaluate the strength and directionality of relationships between diet composition and ocean conditions, diet composition and productivity, and the potential combined effects of ocean and diet on yearly reproductive success (see Table S4 for a list of all models tested). Three metrics derived from egg membrane stable isotope values were used to quantify diet composition for sites separately and combined (hereafter collectively referred to as 'diet metrics'): annual $\delta^{15}\text{N}$ averages, annual $\delta^{13}\text{C}$ averages, and annual proportions of carbon-enriched prey in diet. To consider the effect of ocean conditions on diet composition, we ran GLMs with diet metrics as separate response variables and with breeding year HCI and pCUI (hereafter collectively referred to as 'breeding year ocean metrics') or prior year HCI and pCUI (hereafter collectively referred to as 'prior year ocean metrics') as covariate predictors, for sites separately and combined.

GLMs examining the effects of diet composition on productivity were run with diet metrics as separate predictors and with annual fledge rate as the response variable, for sites separately and combined. GLMs examining the direct effects of ocean conditions on productivity were run with either breeding year or prior year ocean metrics as covariate predictors and annual fledge rate as the response.

To examine the possible combined effects of both diet variability and ocean conditions on CLTE productivity, we ran comprehensive GLMs for each data set (Pendleton, Coronado, and sites combined), each with 1 of the 3 yearly diet metrics and either breeding year or prior year ocean metrics as covariate predictors and with annual fledge rate as the response. Models with non-normally distributed response variables such as proportion of carbon-enriched prey in diet and annual fledge rate were fitted with beta distributions using the 'betareg' package (Cribari-Neto & Zeileis 2010) in R.

3. RESULTS

3.1. Interannual variation in egg membrane stable isotopes

Egg stable isotope values ranged from 10.10 to 17.43‰ for $\delta^{15}\text{N}$ and from -19.47 to -13.58 ‰ for $\delta^{13}\text{C}$ at Pendleton, and from 13.73 to 17.75‰ for $\delta^{15}\text{N}$ and -0.25 to -11.33 ‰ for $\delta^{13}\text{C}$ at Coronado. Results from sum contrast matrices revealed significant interannual variation in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from eggshell membranes at both sites (Figs. 3 & 4). To visualize model-estimated differences, we computed estimated marginal means (EMMs) and 95% confidence intervals using the 'emmeans' package in R (Lenth 2025). Site-specific grand means were used as baselines, and years in which confidence intervals of the EMMs did not overlap the mean ($\alpha = 0.05$) were considered significantly different. Coronado $\delta^{15}\text{N}$ values differed significantly from the site-specific grand mean in 7 of the 21 years sampled, and Pendleton $\delta^{15}\text{N}$ values differed significantly from the site-specific grand mean in 6 of the 16 years sampled (Fig. 3). Coronado $\delta^{13}\text{C}$ values differed significantly from the site-specific grand mean in 12 of the 21 years sampled, and Pendleton $\delta^{13}\text{C}$ values differed significantly from the site-specific grand mean in 7 of the 16 years sampled (Fig. 4). Overall, our results showed more variability in $\delta^{13}\text{C}$ than $\delta^{15}\text{N}$ values measured from egg membranes over the 21 yr study period.

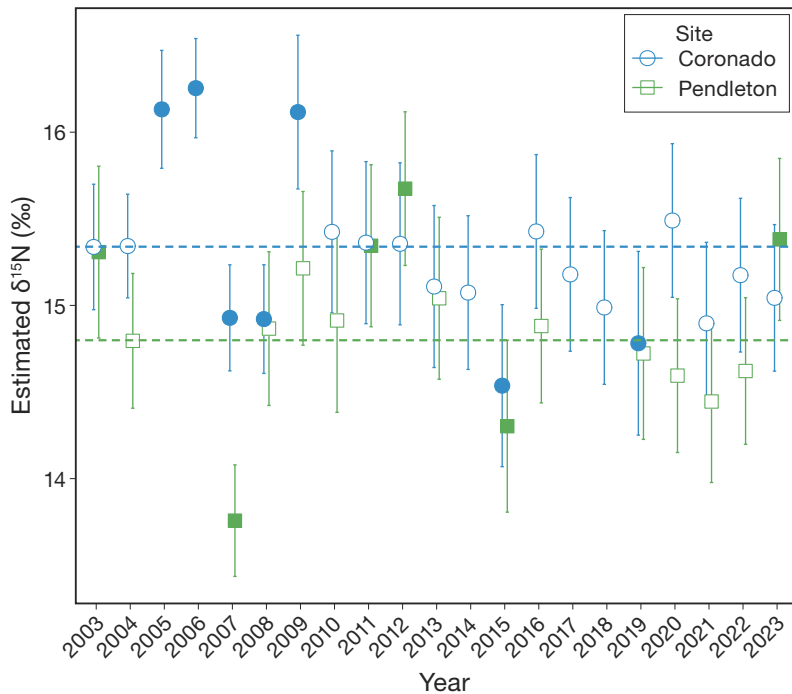


Fig. 3. Sum contrast matrices applied to a generalized linear model (GLM; $\delta^{15}\text{N} \sim \text{year} \times \text{site}$). Dashed horizontal lines represent the cumulative average $\delta^{15}\text{N}$ value for each site. Points represent estimated marginal means derived from the GLM ($\pm 95\%$ confidence intervals shown by error bars), with significance determined at $\alpha = 0.05$

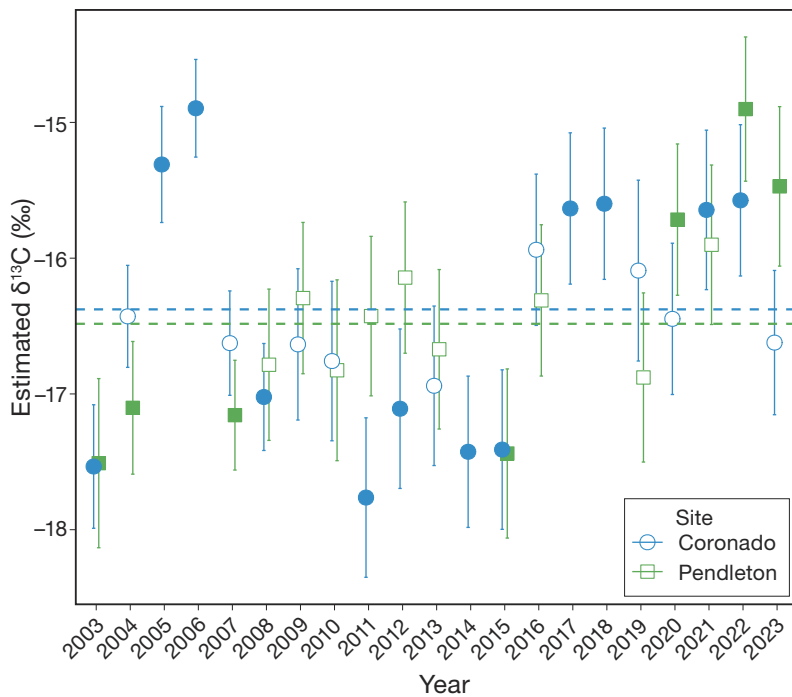


Fig. 4. Sum contrast matrices applied to a generalized linear model (GLM; $\delta^{13}\text{C} \sim \text{year} \times \text{site}$). Dashed horizontal lines represent the cumulative average $\delta^{13}\text{C}$ value for each site. Points represent estimated marginal means derived from the GLM ($\pm 95\%$ confidence intervals shown by error bars), with significance determined at $\alpha = 0.05$

Our 'simmr' analysis showed interannual variation in diet composition (Figs. S4–S6), with a tendency toward higher proportions of carbon-enriched prey sources in more recent years based on eggshell membranes from both sites (beta regression: $\beta = 0.047 \pm 0.017$ SE, $z = 2.72$, $p = 0.007$, pseudo- $R^2 = 0.28$). With isotope data from each site separately and with sites combined, all estimated \hat{R} values were between 1.00 and 1.02, indicating good convergence of the Markov chain Monte Carlo (MCMC) chains for all consumer groups as reflected by the egg samples. Posterior predictive checks on isotope mixing models with 7 distinct prey sources (Fig. S5) indicated that the proportion of observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values falling outside the 95% posterior predictive intervals was 71.7% with sites combined. Posterior predictive checks with 2 grouped prey sources (Fig. S6) indicated that the proportion of observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values falling outside the 95% posterior predictive intervals was 56.5% with sites combined. Since the ideal proportion for a well-fitting model is approximately 50%, this result also supports the use of 2 isotopically distinct clusters.

3.2. Relationships among ocean conditions, egg membrane stable isotopes, and productivity

We found evidence of linkages between CLTE egg membrane stable isotopes and coastal ocean conditions at both breeding year and prior year time-scales. Using GLMs with yearly averaged $\delta^{15}\text{N}$ values of eggshell membranes as a response variable and with ocean metrics as covariate predictors, we observed a significant positive relationship at Pendleton between breeding year HCI and $\delta^{15}\text{N}$ ($\beta = 0.237 \pm 0.107$ SE, $t_{13} = 2.214$, $p = 0.045$; Fig. 5a), and an inverse relationship at both sites combined between prior year pCUI and $\delta^{15}\text{N}$ ($\beta = -0.299 \pm 0.091$ SE, $t_{18} = -3.275$, $p = 0.004$; Fig. 5b). We also

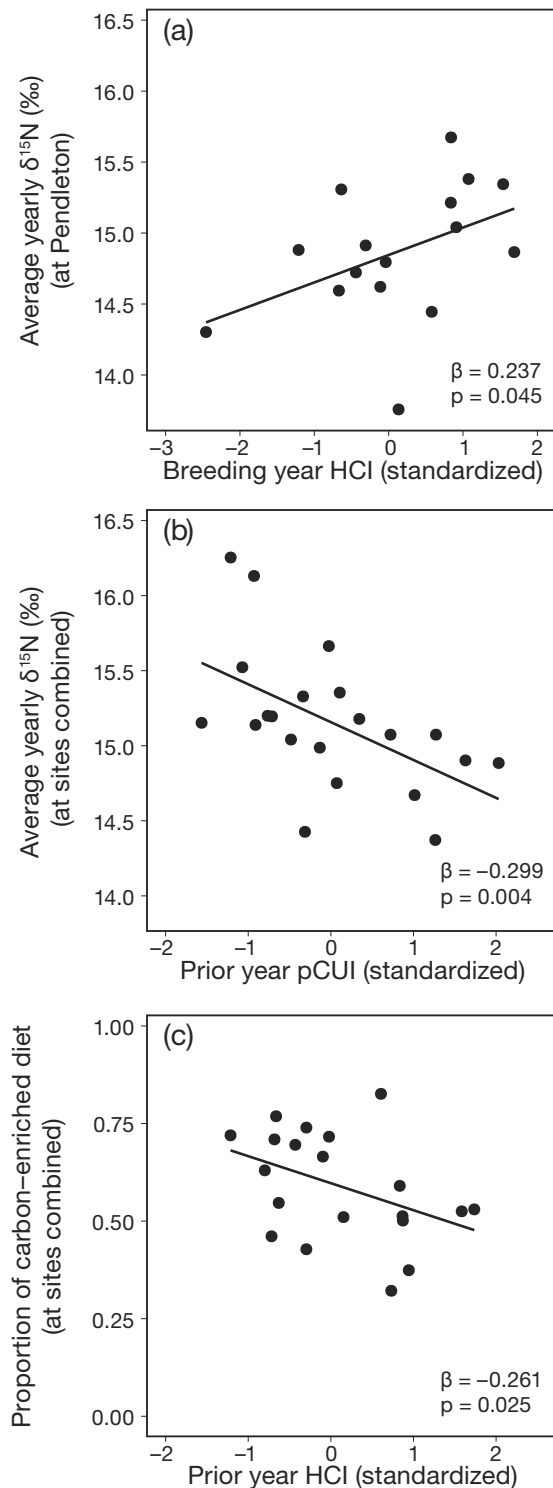


Fig. 5. Annual $\delta^{15}\text{N}$ averages from CLTE egg membranes as a function of (a) breeding year habitat compression index (HCI) and (b) prior year pre-conditioning cumulative upwelling index (pCUI), as well as proportion of carbon-enriched prey in CLTE pre-breeding diet as a function of (c) prior year HCI. Horizontal axes were scaled to have a mean of 0 and a standard deviation of 1 to improve model convergence

found evidence of significant relationships between ocean metrics and annual proportion of carbon-enriched prey in diet, with all eggshell membranes pooled across both sites. Specifically, beta regression (using the 'betareg' package in R; Cribari-Neto & Zeileis 2010) revealed a significant negative relationship between prior year HCI and carbon-enriched diet ($\beta = -0.261 \pm 0.117$ SE, $z = -2.237$, $p = 0.025$; Fig. 5c).

Our analysis also indicated that interannual variation in CLTE eggshell membrane stable isotopes was linked to reproductive success. The strongest relationships between stable isotope levels and productivity were observed at Pendleton. At this site, a higher proportion of carbon-enriched prey in diet was associated with higher fledge rates ($\beta = 3.103 \pm 1.290$ SE, $z = 2.41$, $p = 0.016$; Fig. 6), as was, to a lesser extent, lower average yearly $\delta^{15}\text{N}$ in diet ($\beta = -0.607 \pm 0.348$, $z = -1.74$, $p = 0.082$; Fig. 7). At Coronado, no significant relationships were observed (Table S4).

3.3. Combined effects of eggshell membrane stable isotopes and ocean on productivity

Although there was evidence of pairwise relationships between ocean conditions and stable isotopes and between stable isotopes and productivity, we did not find significant direct relationships linking ocean variables and fledge rate measures (Table S4). To de-

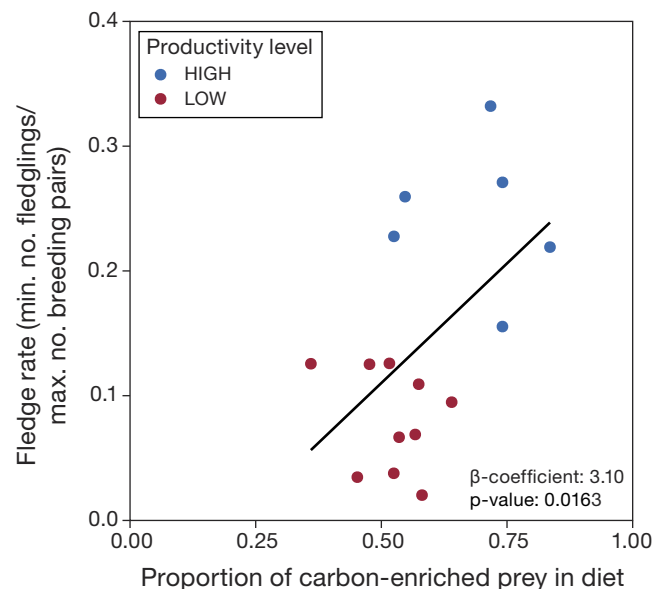


Fig. 6. Significant positive relationship between CLTE fledge rate and proportion of carbon-enriched prey in diet at Pendleton. Points are color-coded to identify fledge rates categorized as high vs. low productivity relative to a cumulative 16 yr average

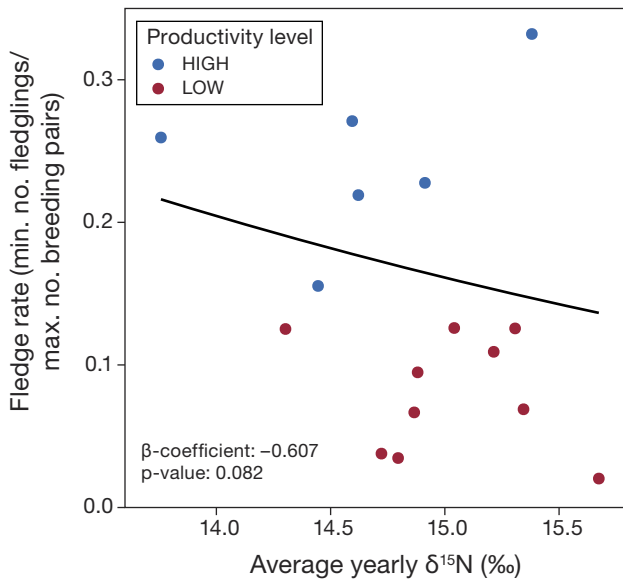


Fig. 7. Negative relationship between CLTE fledge rate and average $\delta^{15}\text{N}$ in eggshell membranes at Pendleton. Points are color-coded to identify fledge rates categorized as high vs. low productivity relative to a cumulative 16 yr average

termine whether stable isotopes and ocean conditions exert combined influences on CLTE productivity, we built GLMs (beta regressions using the 'betareg' package in R; Cribari-Neto & Zeileis 2010) that included either yearly averaged $\delta^{15}\text{N}$ values or yearly proportions of carbon-enriched prey in diet, and either breeding year or prior year metrics of cold-water habitat (HCI) and upwelling (pCUI) as covariate predictors. These relationships were not significant at Coronado or when data from both sites were combined (Table S4). At Pendleton, however, annual proportions of carbon-enriched prey in CLTE diet were positively related to site-specific annual fledge rate regardless of whether breeding year or prior year ocean metrics were included as covariates in the model ($\beta = 0.350 \pm 0.167$ SD, $z = 2.494$, $p = 0.036$ vs. $\beta = 0.361 \pm 0.170$ SD, $z = 2.126$, $p = 0.034$, respectively).

4. DISCUSSION

Using long-term data sets to assess interannual patterns between extrinsic factors and CLTE population dynamics, we found evidence that interannual changes in ocean conditions are associated with diet shifts exhibited by CLTE at 2 of the largest nesting sites in California, and that these diet shifts are associated with changes in reproductive success. We found more interannual variability in $\delta^{13}\text{C}$ levels

within diet than in $\delta^{15}\text{N}$ levels, which could indicate that CLTE varied their foraging habitat more than the types of species they were consuming (Cherel & Hobson 2007).

Two oceanographic variables, upwelling and habitat compression, were found to significantly influence diet, but at different temporal scales. The influence of upwelling was strongest over longer time scales, e.g. during the year prior to breeding, and was associated with lower trophic level prey (e.g. planktivores). Habitat compression influenced diet at both time scales—during the breeding year and in the year prior to breeding. Compressed cold-water habitat along the shoreline during the breeding year was associated with lower trophic level prey, while compressed cold-water habitat during the year prior was associated with carbon-enriched prey (i.e. prey occurring closer to shore). Overall, adult females consuming more carbon-enriched, low trophic level prey before egg-laying were associated with the highest fledge rates, i.e. higher reproductive success. Understanding the impact of ongoing and intensifying ocean changes on marine species remains a critical question for management and conservation of both common species and species of conservation concern (Lewison et al. 2012, Bakun et al. 2015, Xiu et al. 2018, Muhling et al. 2020).

4.1. Relationships between ocean and diet

Our analysis highlights complex relationships between ocean conditions and CLTE diet as measured in adult females at the start of the breeding season. We found that when there was more compression of cold-water habitat in winter months leading up to a breeding season, as indicated by a lower HCI, CLTE consumed a less nitrogen-enriched diet, suggesting that CLTE consumed greater amounts of lower trophic level prey. Conversely, the expansion of cold-water habitat was associated with consumption of higher trophic level prey.

Upwelling strength also influenced nitrogen enrichment in pre-breeding diet. For upwelling, however, stronger prior year winter upwelling was associated with less nitrogen-enriched, lower trophic level diet within the following breeding year. This relationship has been reported for other species, e.g. $\delta^{15}\text{N}$ levels of phytoplankton were found to be inversely related to upwelling strength (Lopez-Lopez et al. 2017). The age class of anchovies primarily taken by CLTE is age 1, spawned the year prior to breeding (Robinette et al. 2020), and our data suggest that mod-

erate intensity upwelling, known to promote ocean productivity (Bakun et al. 2015), could lead to increased juvenile recruitment of mid-to-low trophic level species such as anchovies or killifish the following year (Robinette et al. 2007, 2019).

The absence of strong correlations between the 2 ocean variables is likely because they represent ocean features at different spatial scales, with HCI measured over a broad latitudinal range and thus at a coarser spatial resolution versus the more location-specific measurement of pCUI values, calculated at 33° N and 119° W (Table 1). The 2 metrics also capture separate ocean processes. HCI involves measurement of temperatures within the mixed layer, not just surface conditions, and is more strongly correlated with BEUTI measurements than with the upwelling index values used to calculate pCUI (Schroeder et al. 2022).

Although our findings suggest that both compression of cold-water area (HCI) and upwelling strength (pCUI) influence CLTE diet independently, they likely interact in influencing the availability of CLTE prey. In the year prior to breeding, higher pCUI (stronger upwelling) and lower HCI (smaller, compressed area of cold-water habitat along the shoreline) may provide favorable conditions for productivity of mid-to-low trophic level planktivorous fishes and concentrate these species closer to CLTE nesting sites which could increase the availability of appropriate size prey species for CLTE foraging the following year (Fig. 5b,c). Conversely, when HCI is high and cold-water habitat is less compressed, CLTE may alter what species they consume, as is suggested by the observed relationship to $\delta^{15}\text{N}$ in their pre-breeding diet at Pendleton (Fig. 5a). Such site-specific patterns between ocean conditions and diet at our 2 study sites could be linked to differences in coastal topography or rugosity which influence distribution or abundance of prey species (e.g. Robinette et al. 2019).

4.2. Relationship between diet and fledge rates

Our analyses revealed direct relationships between diet composition and CLTE productivity, with $\delta^{13}\text{C}$ exhibiting more variability than $\delta^{15}\text{N}$ in this 21 yr data set. We found that greater proportions of carbon-enriched species in CLTE pre-breeding diet, which could indicate years when CLTE foraged in more nearshore areas (sensu Cherel & Hobson 2007), were associated with relatively higher fledge rates. Foundational studies in seabird stable isotopes have suggested that $\delta^{13}\text{C}$ provides information on seabird foraging locations relative to the shoreline (Hobson et al.

1994, Cherel & Hobson 2007). Similar relationships between foraging location and reproduction are reported in seabird literature, e.g. thick-billed murres in the North Pacific had greater fledging success when chicks were fed nearshore prey, as opposed to offshore prey with similar energetic content (Renner et al. 2014). In CLTE, the relationship between proportion of carbon-enriched prey in diet and fledge rate could reflect similar benefits of highly abundant nearshore prey or the indirect benefits of seabirds foraging closer to shore, i.e. more frequent chick provisioning and higher adult colony attendance leading to better nest defense (Robinette et al. 2020).

It is also possible that carbon-enrichment within CLTE diet reflects changes in the base of the marine food web (Kurle & McWhorter 2017), which could affect the isotopic values of the prey species. However, a similar study of a large marine predator (humpback whale *Megaptera novaeangliae*) found consistent $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in krill, sardine, and anchovy collected between 1993 and 2009 in the California Current System, suggesting that baseline prey signatures can remain relatively stable over multi-decadal study periods (Fleming et al. 2016). Irrespective, our results suggest that annual shifts in prey composition for pre-breeding females are linked to CLTE productivity, although further research is needed to evaluate the underlying mechanism of observed shifts in isotopic signatures.

Although some seabird diet research suggests that a more nitrogen-enriched diet is associated with better reproductive output (Kowalczyk et al. 2014), in other species, lower trophic level prey is associated with better body condition and earlier egg-laying (Janssen et al. 2009, Morrison et al. 2014). The trend observed at the Pendleton nesting site toward higher productivity with lower $\delta^{15}\text{N}$ levels in diet has also been observed in marbled murrelets, where reproductive success correlates with low and mid-trophic level species in their pre-breeding diet (Becker et al. 2007).

It is worth noting that even the highest annual value observed during our study period (0.365 fledglings per pair at Pendleton in 2006) is still very low compared to fledge rates observed at more northern sites (Robinette et al. 2020). In fact, fledge rates in southern California (where >80% of the US CLTE population breeds) have been chronically low since the late 1990s, and there is a positive relationship between annual fledge rate and latitude of breeding site in California (Schuetz 2011, Lewison & Deutschman 2014). Robinette et al. (2020) hypothesized that chronically low fledge rates in southern California are largely driven by documented declines in prey availability. Koslow et al. (2015) showed a 72–78% decline in fish taxa across

multiple trophic guilds since the 1970s, particularly affecting species with cold-water preferences. This declining trend in fish abundance is correlated with a suite of factors largely impacted by climate change, including hypoxic conditions nearshore, high variability in ocean temperature, and a long-term decline in zooplankton abundance throughout the Southern California Bight (Siegelman-Charbit et al. 2018). Furthermore, Howard et al. (2020) showed that the northern anchovy distribution within the California Current System is shifting due to changes in the extent of aerobic habitat suitable for anchovy metabolism. They showed that as hypoxia increases with rising temperatures in coastal waters, anchovy distribution is shifting offshore and to the north. They predicted a loss of 30–50% of this aerobic habitat by 2100. As this trend continues, CLTE will have to travel farther offshore to catch prey, which could result in lower adult colony attendance and lower chick provisioning rates.

Robinette et al. (2020) also hypothesized that prey availability drives fledge rate through chick provisioning rates and adult colony attendance. Their results suggested that, as prey becomes less available close to the colony, adults spend more time away from the colony on foraging bouts. Bertrand et al. (2012) and Pichegru et al. (2012) showed that seabirds can respond to local prey depletion around breeding sites by increasing their foraging range, resulting in more time spent away from the breeding colony. Increased time foraging can lead to decreased chick provisioning rates and subsequent decreases in chick growth rates and survival (Regular et al. 2014). Additionally, longer foraging bouts can decrease the amount of time adults attend and defend the colony from predators (Sullivan et al. 2020). Similarly, our findings suggest that foraging location (i.e. distance from the breeding site inferred from $\delta^{13}\text{C}$ levels in diet) may have a larger influence on productivity than the trophic level of the prey. Though more research is needed to fully understand the relationships between fledge rate, diet composition, chick provisioning rates, and adult colony attendance, focus on restoration of nearshore and estuarine foraging areas could positively impact CLTE productivity if such efforts enhance the abundance of prey close to the breeding site before and during the breeding season.

4.3. Other site-specific factors that may influence diet and productivity

In addition to ocean conditions and diet, there are other site-specific factors that are known to directly

influence CLTE recruitment. Predation and human-mediated disturbances on a colony likely have a substantial influence on annual reproductive success as well (Carney & Sydeman 1999, Riensche et al. 2012). For CLTE, the relative impact of these factors compared across sites and years can be difficult to assess because predation and disturbance data are not consistently recorded and are inherently difficult to measure. Efforts, coordinated by CDFW, are underway to compile more standardized data on predator presence by species and guilds at all monitored sites from 1997 onward, as well as to record yearly site-specific predation mortality counts for CLTE of different age classes (chick, fledgling, adult). More mortality and predation data have been made available on CDFW's Biogeographic Information Observation System (BIOS). Mortalities directly caused by humans (i.e. nest trampling, vehicle strike) are also identified in this data set. Another confounding factor that obscures the impact of site-specific factors at a nesting site is the amount and type of predator control implemented at a given site, which varies widely based on acreage, proximity to public areas, and regulations on deployment of different types of lethal or non-lethal control measures. Accounting for site-specific variability in predator management and other human disturbances will be an essential next step to more fully understand which extrinsic factors are enabling or limiting CLTE population recovery.

5. CONCLUSION

Results from this study suggest that ocean conditions influence CLTE diet and highlight the importance of prey composition in CLTE reproductive success. These findings have meaningful implications for management and population recovery of this endangered species. The influence of a more carbon-enriched diet on fledge rates suggests potential benefits of restoring and conserving habitats close to shore (e.g. estuaries and kelp beds) to provide reliable access to prey sources that can support CLTE reproductive output. Future research that includes multiple diet characterization methods, such as observations of chick provisioning events, fecal analysis of diet during the chick-rearing period, or direct tracking of foraging individuals, can provide additional information on how both adult and chick diet affect reproductive output. Furthermore, using a statistical approach that can consider complex direct and indirect relationships among ocean conditions, CLTE diet, and productivity, such as structural equation modeling,

may be needed to account for indirect interaction effects among factors (Lefcheck 2016). Identifying the variables that have the strongest impacts on CLTE reproductive success will be crucial to determining how to maximize the effectiveness of future monitoring and management efforts.

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