



Contribution to the Theme Section 'How do marine heatwaves impact seabirds?'

# Resilience to a severe marine heatwave at two Pacific seabird colonies

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**ABSTRACT:** A severe marine heat wave (MHW) persisted in the California Current ecosystem from 2014 through 2016. The MHW featured record-high sea surface temperatures in 2015, with 2014 to 2016 being the warmest 3 yr period on record. Our decade-long (2010–2019) breeding and diet monitoring of the rhinoceros auklet *Cerorhinca monocerata*, a burrow-nesting seabird, at significant breeding colonies on Destruction Island (California Current) and Protection Island (Salish Sea) allowed us to compare reproductive and dietary responses to this MHW. Although the colonies are relatively close to each other, and their reproductive output is, on average, similar, the auklets' responses to the MHW differed. At Destruction Island, burrow occupancy rates were lower during the MHW ( $0.54 \pm 0.02$  vs.  $0.61 \pm 0.02$  [mean  $\pm$  SE] in non-MHW years), suggesting that birds skipped breeding, but fledging success rates did not differ ( $0.85 \pm 0.02$  vs.  $0.89 \pm 0.03$ ). At Protection Island, burrow occupancy remained at non-MHW levels ( $0.72 \pm 0.02$  vs.  $0.69 \pm 0.02$ ), but reproductive success declined ( $0.71 \pm 0.03$  vs.  $0.82 \pm 0.02$ ). Chick provisioning also showed different patterns. The energy (kJ) per bill load at Destruction Island showed no clear MHW effect, while at Protection Island, it was reduced. At the same time, bill-load prey item count rose at Protection Island, indicating increased foraging effort and/or a reduction in diet quality. Our results further suggest rhinoceros auklets may be more resilient than other seabird species to major climate perturbations. However, with MHWs predicted to become more frequent and severe, the auklets' ability to maintain these levels of breeding success will be tested.

**KEY WORDS:** Rhinoceros auklet · *Cerorhinca monocerata* · Alcids · Climate change · Forage fish · Marine heatwaves

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## 1. INTRODUCTION

Climate change has led to an increase in the frequency of extreme events in marine systems, including marine heatwaves (MHWs) (Hobday et al. 2016, Oliver et al. 2018, Jacox et al. 2020). Defined as extended periods of significantly elevated sea surface temperatures (SSTs) over large areas (Benthuisen

et al. 2020), MHWs have been linked to reduced ocean productivity (Wernberg et al. 2013, Smale et al. 2019), shifts in the geographic distribution of organisms (Mills et al. 2013, Goddard et al. 2018), increased frequency of harmful algal blooms (Roberts et al. 2019), local extinctions (Thomsen et al. 2019), unusual mortality events for both marine mammals and seabirds (McClatchie et al. 2016, Piatt et al.

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2020), and negative effects on breeding phenology and reproductive success in seabirds (Fromant et al. 2021, Glencross et al. 2021).

One of the most recent and severe MHWs occurred in the NE Pacific Ocean (Smith et al. 2023). In late 2013/early 2014, a large patch of anomalously warm water formed in the Gulf of Alaska due to low rates of heat loss and weak cold advection in the upper ocean (Bond et al. 2015). Over the next 2 yr, the patch of warm water spread to cover more than 2.5 million km<sup>2</sup>, extending from southern Alaska (USA) to Baja California (Mexico) (Smale et al. 2019), and became known colloquially as ‘The Blob’ (Kintisch 2015). Off-shore SSTs were more than 3 standard deviations above normal during the winter of 2013–2014, with elevated SSTs lasting through the summer of 2016; at their peak in 2015, SST anomalies were 3–6°C above the 1981–2010 climatology (Bond et al. 2015, Gentemann et al. 2017). All of these factors combined at the time to make the NE Pacific MHW the largest documented MHW in terms of duration, geographic extent, and magnitude since recording began in 1982 (Hobday et al. 2018, Oliver et al. 2018).

Elevated temperatures during the NE Pacific MHW led to increased stratification of the upper ocean, lowering nutrient supplies at the surface and resulting in declines in net primary productivity (NPP), prey availability, and community production (Whitney 2015, Yang et al. 2018). The 2014–2016 NE Pacific MHW has been linked to mass mortality events in both marine mammals (Savage 2017) and birds (Jones et al. 2018, 2019, Piatt et al. 2020), as well as other significant ecological disruptions for organisms over a range of trophic levels (e.g. Leising et al. 2015, Cavole et al. 2016, McCabe et al. 2016, Peterson et al. 2017, Brodeur et al. 2019, Jones et al. 2021). However, some of the consequences of the NE Pacific MHW have been more subtle, and their full breadth is still being explored.

Understanding climate–biology relationships in marine systems is critical for conservation and resource management, and seabirds, as conspicuous and widespread top predators, are good sentinels to detect shifts in marine systems (Parrish et al. 2007, Hazen et al. 2019). In this paper, we draw on a long-term monitoring study to compare the responses of the rhinoceros auklet *Cerorhinca monocerata*, a colonial burrow-nesting seabird, to the NE Pacific MHW at 2 major breeding colonies: one at Destruction Island on the outer coast of Washington, USA, in the California Current Large Marine Ecosystem, and the other at Protection Island, in the Strait of Juan de Fuca (part of the Salish Sea), a fjord estuary complex

that includes the interior waters of Washington and southern British Columbia (Canada). Although the 2 colonies are less than 150 linear km apart, the systems in which they sit are subject to distinct physical forcing mechanisms (e.g. MacCready et al. 2021). The most extreme effects of the NE Pacific MHW, for example, may have been buffered in the Salish Sea due to increased freshwater inputs, and peak temperature anomalies were elevated just 2.3°C above average (Khangaonkar et al. 2021). Auklets at the 2 colonies also rely on different prey bases (Wilson & Manuwal 1986).

We hypothesized that the responses of auklets on the 2 islands would be neither uniform nor synchronous, despite their geographic proximity. Due in part to the more severe marine conditions faced by auklets at Destruction Island during the NE Pacific MHW, we predicted they would experience more pronounced disruptions than auklets at Protection Island. These disruptions would manifest in the form of lower burrow occupancy and fledging success rates, and bill-load characteristics indicative of poor prey quality and/or greater compensatory foraging effort (cf. Schrimpf et al. 2012). By relating breeding metrics (burrow occupancy, hatching success, and fledging success) and diet metrics (prey species composition, bill-load weight, energy, prey item count, fish condition) to marine conditions at the 2 colonies, we aimed to detect shifts that indicate how the NE Pacific MHW affected a sentinel species.

## 2. MATERIALS AND METHODS

### 2.1. Study sites and species

The rhinoceros auklet is a medium-sized alcid whose breeding and non-breeding ranges encompass much of the northern Pacific. In the NE Pacific and the Salish Sea, it is a year-round resident. Adults return to breeding colonies in March and April, where pairs either re-occupy existing burrows or excavate new ones. The female lays 1 egg in early to mid-May (Leschner 1976, Wilson & Manuwal 1986), and mates share incubation duties for approximately 45 d. After the chick hatches, one or both adults bring back a single bill load of fish per night for approximately 50 d until the chick fledges (Wilson 1977).

Since 2010, we have been monitoring breeding metrics at 2 major colonies in Washington. Protection Island (48.1270° N, 122.9275° W) is a 143 ha island about 3 km off the mouth of Discovery Bay at the eastern end of the Strait of Juan de Fuca in the Salish



Fig. 1. Rhinoceros auklet *Cerorhinca monocerata* colonies included in this study: Protection Island ( $48.1270^{\circ}$  N,  $122.9275^{\circ}$  W), in the Salish Sea, hosts ~36 000 breeding pairs per year, while on the outer coast, Destruction Island ( $47.6760^{\circ}$  N,  $124.4831^{\circ}$  W), in the California Current, hosts ~6500 breeding pairs

Sea (Fig. 1). Along its perimeter, the island contains beach and spit habitats that give way to cliffs and steep slopes, while the interior of the island is flat or rolling. Approximately 36 000 breeding pairs nest in burrows on grass-dominated habitats on cliff edges and steeper slopes (Pearson et al. 2013). Destruction Island ( $47.6760^{\circ}$  N,  $124.4831^{\circ}$  W) is located 4.8 km west of the Olympic Peninsula and the mouth of the Hoh River (Fig. 1). The 15 ha flat-topped island is part of an extensive sandstone reef (Wilson & Manuel 1986) and is surrounded by rocky islets. Approximately 6500 auklet pairs nest in burrows on cliff tops and steep slopes in grass, shrub, and willow habitats (Pearson et al. 2013).

## 2.2. Breeding metrics

On Protection Island, we established multiple study sites and monitored all burrows within a 2.5 m radius from the center of each. We randomly located sites in habitats dominated by grass and flowering plants (see Pearson et al. 2013). More than 95% of all auklet burrows on Protection Island occur in these habitats, and burrow occupancy does not differ among them (Pearson et al. 2013). On Destruction

Island, we established study sites and monitored individually marked burrows in all habitat types occupied by auklets (grass-, willow-, and salmonberry-dominated) on the south and southwestern sides of the island (see Pearson et al. 2013).

We monitored breeding activity from 2010 to 2019 on both islands, timing our sampling trips to phenological patterns reported by Leschner (1976) for Destruction Island and Wilson (1977) for Protection Island. On an initial trip in late May/early June, we assessed breeding activity by examining all burrows in our study areas using infrared camera probes. We defined a burrow as any excavation that contained both a tunnel and at least 1 nesting chamber. A burrow with an adult and/or egg on 2 consecutive days during that initial trip was considered occupied by a breeding pair. During a second trip in mid/late June (except for 2012), we assessed hatching success. On a third trip in mid/late July (except for 2012), we assessed chick survival and presumed fledging success by scoring chicks according to plumage development; the stages included downy chicks, chicks with partial feathering, and chicks that were either mostly or fully feathered. Chicks absent on the final trip that had been recorded as at least partially feathered on the pre-

vious trip were assumed to have fledged; similarly, we assumed that chicks that were at least partially feathered on the last trip would survive to fledge. Any burrow occupied on the first visit was rechecked on the last visit, even if it had no contents on the second visit. This ensured we would account for missed chicks.

### 2.3. Diet sampling

#### 2.3.1. Bill-load collection and diet metrics

After chicks hatch, adult auklets return to the colony after dark to deliver bill loads of one to many prey items. We collected bill loads from adults using a spotlighting method for 7 seasons on Protection Island (2010, 2013, 2015–2019) and 6 seasons on Destruction Island (2010, 2013, 2016–2019). For analysis, we used only bill loads verified as entire bill loads ('complete confirmed').

Diet sampling was done during the second and third visits to each colony, so we could detect differences in bill-load size during early and late chick provisioning (e.g. Bertram & Kaiser 1993, Hedd et al. 2006). Collection sites at each colony were varied within trips and between trips to ensure that few, if any, chicks were not deprived of more than 1 meal over the course of the season, and also that we did not collect samples from the same adults.

#### 2.3.2. Prey species identification and energy content

We weighed and measured prey either in the field the morning after collection or in the lab within a week of collection, after storing bill loads in a freezer. We recorded standard length (SL, from the tip of the snout to the end of the last vertebra), fork length (FL, from the tip of the snout to the middle of the caudal fin rays), and total length (TL, from the tip of the snout to the end of the longer caudal fin lobe) to the nearest millimeter, and wet mass to the nearest 0.1 g. Some taxa, including juvenile rockfish (*Sebastes* spp.) and juvenile greenling (*Hexagrammos* spp.), were treated as single taxa in the analysis. Although rare, fish too badly mangled to obtain a reliable species ID were identified to the lowest possible taxon.

Energy densities ( $\text{J g}^{-1}$  wet mass) were calculated in 2008 and 2009 by bomb calorimetry on a representative subset of samples as described by Schrimpf et al. (2012) (see Table S1 in Supplement 1 at [www.int-res.com/articles/suppl/m737p101\\_supp1.xlsx](http://www.int-res.com/articles/suppl/m737p101_supp1.xlsx) and Text S1 in Supplement 2 at [www.int-res.com/articles/suppl/m737p101\\_supp2.pdf](http://www.int-res.com/articles/suppl/m737p101_supp2.pdf)) for energy densities and a more detailed methods description).

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### 2.4. Principal component analysis (PCA) of marine conditions

To test whether and how breeding and diet metrics correlated with marine conditions at Destruction Island in the California Current and Protection Island in the Salish Sea, we performed a PCA using basin-wide, regional-scale, and local environmental predictors. For basin-wide predictors, we used the Pacific Decadal Oscillation (PDO) index (NASA Extended Reconstructed Sea Surface Temperature [ERSST] V.3b, <https://psl.noaa.gov/pdo/>) and Multivariate ENSO Index (MEI v.2) (<https://psl.noaa.gov/enso/mei/>). For the PDO and the MEI, we took the average of the indices from September through August so that the values encompassed the whole auklet breeding cycle, i.e. the start of the non-breeding season to the end of the breeding season.

At the regional scale, we used 2 indices to account for annual spring cold-water upwelling, the main driver of regional productivity (Hickey 1989). The first is the onset of the biological spring transition (day of year) (Northwest Fisheries Science Center, <https://www.fisheries.noaa.gov/west-coast/science-data/local-biological-indicators>), which begins the day the northern cold-water copepod community first appears at NH 05, a sampling station about 5 miles offshore along the Newport Line (44.6517° N, 124.1770° W)—a signal that upwelling has begun. Second, as a measure of upwelling intensity, we used the Biologically Effective Upwelling Transport Index (BEUTI) (<https://mjacox.com/upwelling-indices/>), averaging the monthly means of daily indices for March to July. BEUTI is an estimate of the total quantity of nitrate upwelled or downwelled during a given period (Jacox et al. 2018). We preferred BEUTI to other upwelling indices because it quantifies both the intensity of upwelling and the nutrient quality of the waters being upwelled (Jacox et al. 2018), rather than just the former.

For local predictors, we used monthly SSTs, area-averaged by the MODIS-Aqua satellite at 4 km spatial resolution around both Protection Island and Destruction Island as a proxy, since the precise foraging locations for auklets from both colonies are unknown. Using the NASA Giovanni tool (<https://giovanni.gsfc.nasa.gov/giovanni/>), we delimited boxes

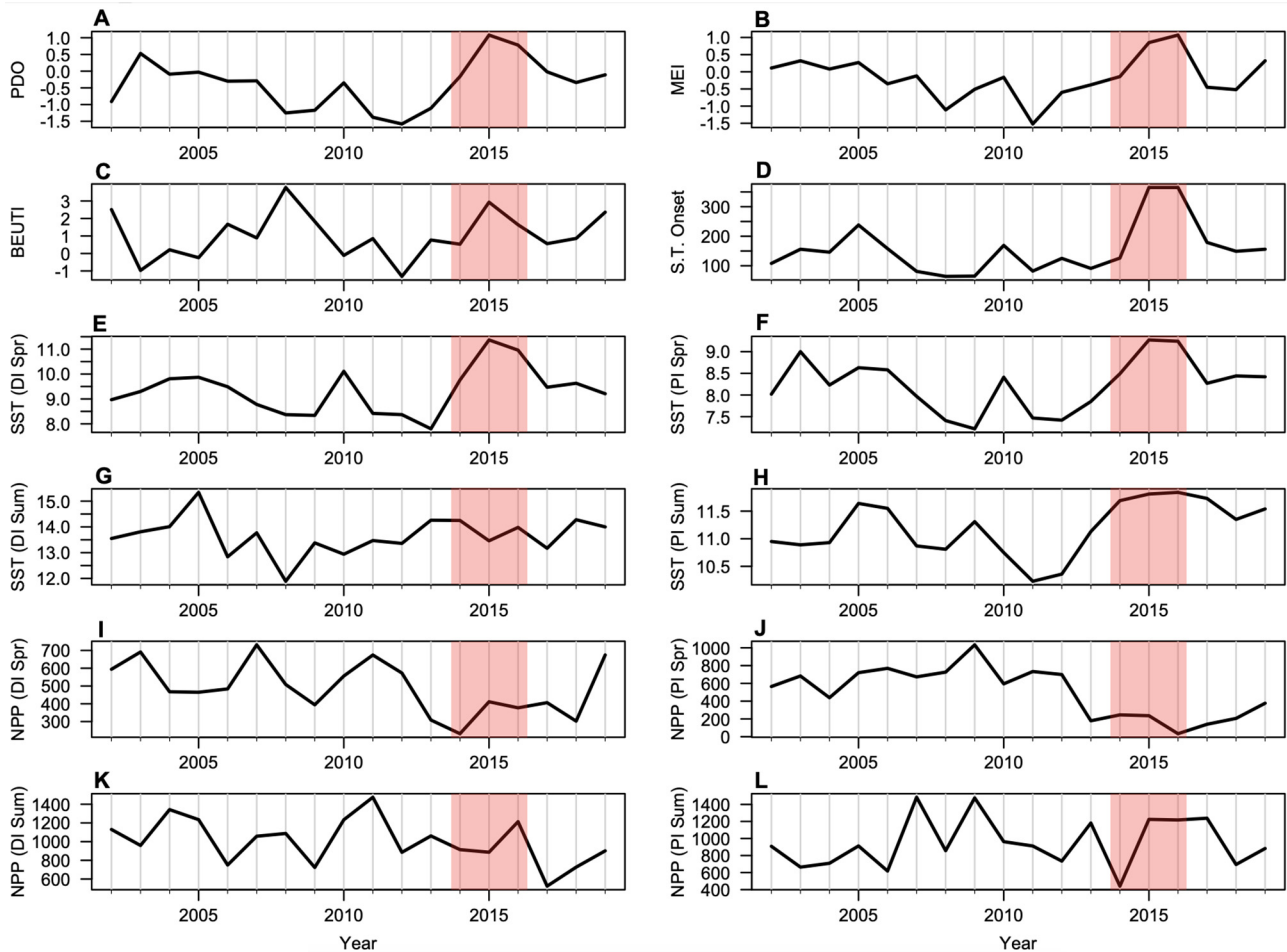


Fig. 2. Environmental predictors included in principal component analysis (PCA). All years used to build the PCA are shown, starting in 2002; the study years were 2010–2019. Red columns bracket the years affected by the NE Pacific marine heatwave (2014–2016). Predictor and data source: (A) Pacific Decadal Oscillation (PDO); (B) Multivariate El Niño Index (MEI); (C) Biologically Effective Upwelling Transport Index (BEUTI); (D) onset of the spring transition (S.T. Onset); (E–H) island-specific sea surface temperature (SST) from February through April (DI/PI Spr, where DI: Destruction Island, PI: Protection Island) and May through August (DI / PI Sum); (I–L) island-specific values from Carbon-based Productivity Model of Net Primary Production (NPP) with the same seasonal ranges as SST. See Section 2.4 for sources and a description of how predictors were tabulated

from 47.6042° N, 124.562° W to 47.7292° N, 124.479° W (roughly 24 km<sup>2</sup> around Destruction) and 48.1458° N, 123.146° W to 48.3958° N, 122.937° W (roughly 30 km<sup>2</sup> around Protection Island). As a proxy for food quality and availability, we used island-specific monthly values from the Carbon-based Productivity Model of Net Primary Production (CbPM-NPP), a model-based dataset of primary production from the Oregon State University Ocean Productivity Group (<http://sites.science.oregonstate.edu/ocean.productivity/>). CbPM-NPP estimates phytoplankton carbon concentration and uses that as a metric for biomass rather than chlorophyll *a*. NPP is therefore described as the product of carbon biomass and growth rate, rather than the traditional product of chlorophyll and photosynthetic efficiencies (Behrenfeld et al. 2005, Westberry et al.

2008). For both Protection and Destruction Islands, we averaged values for spring SST and CbPM-NPP from February through April, to match the spring conditions affecting their prey base; and for summer SST and CbPM-NPP from May through August, to match the auklet breeding season (see Fig. 2 for a time series of all indicators).

All predictors were scaled and normalized using the mean and SD of the study period (2002–2019). The sign of each index was standardized so that the direction associated with conditions favorable to ocean productivity was always positive, ensuring that the indices could be interpreted together. All indices were then combined in a PCA to create summary variables that captured the overall interannual environmental fluctuations (Fig. 3).

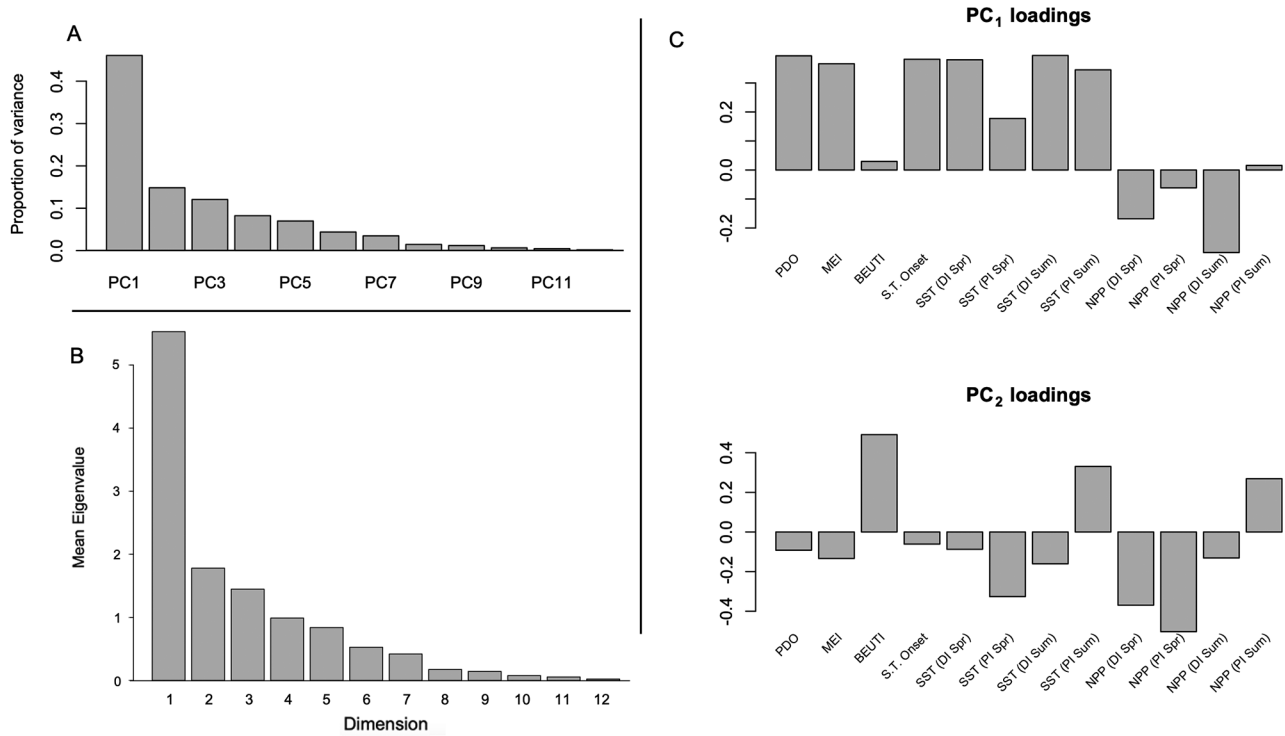


Fig. 3. Principal component (PC) scores and loadings of environmental predictors. See Section 2.4 for more detailed descriptions of the environmental predictors. (A) Proportion of variance explained by each PC. (B) Mean eigenvalues. (C) Loadings for the first 2 PCs. Abbreviations as in Fig. 2. PC<sub>1</sub> accounts for 45% of the variance and depicts the conditions found during the NE Pacific marine heatwave: positive PDO and MEI, higher SSTs, a delayed spring transition onset (or no transition at all), etc. PC<sub>2</sub> accounts for 16% of the variance and captures more generally moderate marine conditions

### 2.5. Statistical analysis

#### 2.5.1. Models for breeding metrics and marine condition

To test for differences in burrow occupancy, hatching success, and fledging success, both between the colonies and in different marine conditions, we fit a generalized linear mixed model (GLMM; Bolker et al. 2009) using a hierarchical Bayesian framework for inference. Response variables were modeled as binomial with a logit link function. For burrow occupancy, the sample size  $N$  was the total number of viable burrows, and successes ( $y$ ) were burrows in which a pair attempted to breed (i.e. laid an egg). For hatching,  $N$  was the number of burrows containing an egg, and  $y$  was the number of chicks that hatched. For fledging,  $N$  was the number of eggs and  $y$  the number of chicks that were either observed or presumed to have fledged. All models included random intercepts grouped by site-within-island and year, with a year-varying effect of island. Thus the full model for observation  $i$  in site  $j[i]$  and year  $k[i]$  was:

$$y_i \sim \text{Bin}(N_i, \pi_i)$$

$$\text{logit}(\pi_i) = \alpha + a_{j[i]} + a_{k[i]} + (\beta + b_{k[i]})I_i + \gamma_1 \text{PC}_{1i} + \gamma_2 \text{PC}_{2i} + \varphi_1 I_i \text{PC}_{1i} + \varphi_2 I_i \text{PC}_{2i}$$

$$a_j \sim \text{N}(0, \sigma_{\text{site}})$$

$$\begin{bmatrix} a_k \\ b_k \end{bmatrix} \sim \text{N}(\mathbf{0}, \Sigma_{\text{year}}) \tag{1}$$

where  $I$  is a dummy indicator for island, and PC<sub>1</sub> and PC<sub>2</sub> are the first and second principal components, with interactions between island, PC<sub>1</sub>, and PC<sub>2</sub> (but no 3-way interaction). We did not conduct model selection to compare restricted models to the full model, as the terms included represent a parsimonious description of known sources of variation; instead, we focused on interpreting the posterior distributions of parameters and quantities of interest in the full model (Gelman & Rubin 1995).

To draw samples from the posterior distributions of model parameters, we used the ‘rstanarm’ package, which is an R interface to Stan, a probabilistic programming language for Bayesian estimation (Gabry & Goodrich 2018). The ‘rstanarm’ package allows fitting

many of the most common applied regression models using Markov chain Monte Carlo (MCMC), in this case Hamiltonian Monte Carlo (Monnahan et al. 2017). All prior distributions were selected to be weakly informative, with  $N(0, 5)$  priors on the intercept and regression coefficients. We ran 3 independent chains for 5000 iterations after a warmup of 1000 iterations. MCMC convergence was assessed using the potential scale reduction factor diagnostic ( $\hat{R} \leq 1.05$ ; Gelman et al. 2013) and visual inspection of chains.

### 2.5.2. Nonmetric multidimensional scaling of prey species composition

To analyze differences in prey species composition between islands and years, we used a nonmetric multidimensional scaling (NMDS) ordination with the ‘vegan’ package in R, based on Bray-Curtis distances (Oksanen et al. 2013). Prey data from both islands were combined, and 2 axes were selected for each ordination based on the least-stress ordination configuration after 200 randomizations. Stress values reflect goodness-of-fit, or how well the ordination summarizes the observed differences between the samples. Due to the small sample size and wide range in relative abundances (from  $<0.01$  to  $>0.75$ ), the data were square-root transformed and then submitted to a Wisconsin double standardization, the standard transformation in ‘vegan.’ We used Shepherd stress plots to determine the reliability of these analyses by plotting the relationship and computing the correlation between actual dissimilarities and ordination distances (linear  $R^2 = 0.918$  and non-metric  $R^2 = 0.987$ ; stress = 0.11, indicating good ordination fit).

We followed this with a permutational multivariate analysis of variance (PERMANOVA) using the ‘adonis’ function in the ‘vegan’ package in R to test if there were multivariate community differences both between the 2 islands and between years.

### 2.5.3. Models for diet metrics and marine conditions, and fish condition

As with the breeding metrics, we used hierarchical Bayesian regression models to test for differences in average bill-load mass (g), and count of prey items per bill load (as a proxy for adult foraging effort; e.g. Fayet et al. 2021), and average energy content (kJ) per bill load, both between the colonies and in different marine conditions. We used linear mixed models for bill-load mass and energy content, and a Poisson

GLMM for prey item count. These models did not include site-within-island as a random effect since birds were caught opportunistically outside of the study areas, but did include a random effect of the number of weeks since 1 June to account for changes in chick age and size, which can influence the amount of food a parent brings back as a season progresses (Leschner 1976, Wilson 1977). Year was also a random effect, again with the intercept and inter-island differences varying across years. For bill-load mass and energy content, the full model for observation  $i$  in week  $j[i]$  and year  $k[i]$  was:

$$\begin{aligned}
 y_i &\sim N(\mu_i, \sigma) \\
 \mu_i &= \alpha + a_{j[i]} + a_{k[i]} + (\beta + b_{k[i]})I_i + \gamma_1 PC_{1i} + \gamma_2 PC_{2i} \\
 &\quad + \varphi_1 I_i PC_{1i} + \varphi_2 I_i PC_{2i} \\
 a_j &\sim N(0, \sigma_{\text{week}}) \\
 \begin{bmatrix} a_k \\ b_k \end{bmatrix} &\sim N(\mathbf{0}, \mathbf{\Sigma}_{\text{year}})
 \end{aligned} \tag{2}$$

The model for prey item count was identical, but with a Poisson observation model and linear predictor on the log link scale, i.e.  $y_i \sim \text{Pois}(e^{\mu_i})$ .

To test whether the average size of individual fish in a bill load increased during a season, we fit a linear mixed model in a Bayesian framework. Average prey item size per bill load (i.e. the bill-load mass divided by the prey count) was the response variable, the number of weeks since 1 June (log-transformed) and the first 2 PCs were main effects, and inter-island differences varying across years was a random effect.

Finally, to test whether the condition of major prey species varied among years, we used Fulton’s body condition factor  $K$  (Fulton 1904):

$$K = \frac{10^6 \times W}{L^3} \tag{3}$$

where  $W$  is the weight (g) and  $L$  the standard length (mm), using only whole, intact fish. This factor assumes that heavier fish of a given length are in better condition (Sutton et al. 2000). We separated bill loads by island and tested for annual differences in  $K$  using a linear mixed-effects model (with year as a factor rather than a continuous variable), where number of weeks since 1 June was a random effect. For species whose models had significant results, we did a post hoc pairwise comparison of the least-square means.

All analyses were performed using R version 4.2.0 (R Core Team 2022).

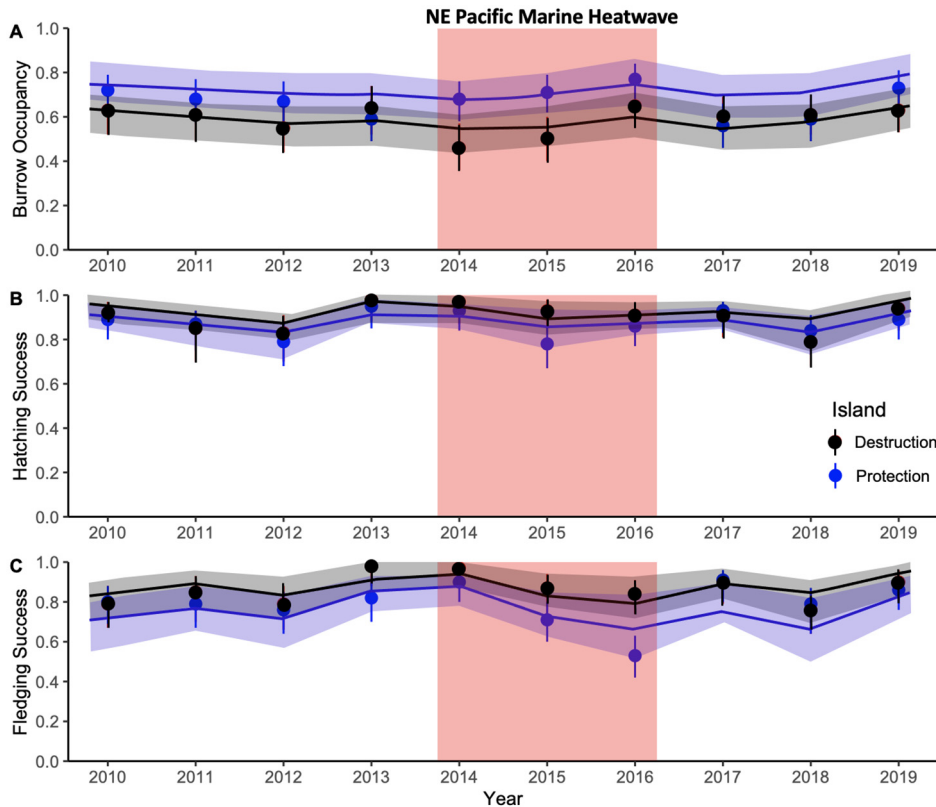


Fig. 4. Times series plots for rhinoceros auklet breeding metrics at Protection Island (Salish Sea) and Destruction Island (California Current). (A) Burrow occupancy; (B) hatching success; (C) fledging success. Points are the annual observed proportions of burrow occupancy, hatching success, and fledging success rates, with error bars showing sample binomial 95% confidence intervals. The solid line is the posterior median of the fitted values and the shaded ribbon is the 95% credible interval. Red columns indicate the 3 seasons (2014–2016) of the NE Pacific marine heat wave

### 3. RESULTS

#### 3.1. Breeding metrics and marine conditions

During the 10 yr of our study, we checked an average ( $\pm$ SE) of  $87.9 \pm 4.4$  burrows per year at Destruction Island (DI), and  $95.4 \pm 2.6$  burrows at Protection Island (PI). Over all years, the 2 colonies differed in burrow occupancy (DI:  $0.59 \pm 0.02$ ; PI:  $0.67 \pm 0.02$ ) and fledging success rates (DI:  $0.87 \pm 0.02$ ; PI:  $0.79 \pm 0.04$ ), but not hatching success rates (DI:  $0.90 \pm 0.02$ ; PI:  $0.87 \pm 0.02$ ; Fig. 4, Table 1).

The islands also responded differently to the NE Pacific MHW. During the MHW years (2014–2016), average burrow occupancy rates declined at Destruction Island ( $0.54 \pm 0.01$  vs.  $0.61 \pm 0.02$  in non-MHW years), but increased at Protection Island ( $0.72 \pm 0.04$  vs.  $0.65 \pm 0.03$  in non-MHW years) due to sharp declines in the years immediately following the MHW (2017: 0.56; 2018: 0.59). Hatching success rates did not differ at either island between the MHW and non-MHW years (Fig. 4B, Table 1). Fledging rates at Destruction Island did not differ between MHW and non-MHW years ( $0.85 \pm 0.02$  vs.  $0.89 \pm 0.05$ ), but at Protection Island they were lower in MHW years ( $0.71 \pm 0.03$  vs.  $0.82 \pm 0.02$ ).

The first 2 PCs accounted for 61% of the observed variation in the environmental variables (Fig. 3). PC<sub>1</sub> (46% of variation) described years when all conditions were unfavorable (e.g. late or absent spring transition, higher SSTs in both spring and summer and lower NPP at both locations, weak coastal upwelling, positive PDO and MEI), in effect capturing the effects of the NE Pacific MHW. PC<sub>2</sub> (15% of variation) described conditions that were more moderate (e.g. PDO and MEI closer to neutral or negative, average SST spring/summer temperatures, and comparatively increased NPP at both locations, although note that NPP and to a lesser extent SST were separated between the outer coast and the Salish Sea). The annual values for the PCs detected an initial overall ocean warming in 2014 and by 2015 and 2016 showed a strong MHW signal (Table S2 in Supplement 2). Prior to 2014, the PCs describe marine conditions that were closer to the mean. Conditions remained warmer once the MHW had dissipated.

By themselves, PC<sub>1</sub> and PC<sub>2</sub> did not correlate with auklet breeding metrics, but there were interactions with the island term, although not consistently. For burrow occupancy, PC<sub>1</sub> had a strong positive interaction with island, while PC<sub>2</sub> had a strong negative



Table 1. Mean parameter estimates (95 % credible interval [CI] in parentheses) from binomial generalized linear mixed models (GLMMs) for rhinoceros auklet breeding metrics at Protection Island (Salish Sea) and Destruction Island (California Current). Positive main effect values: increased effect at Protection Island. Hierarchical variance components are  $\sigma_{\text{site}}$ : among-site intercept SD;  $\sigma_{\text{year}}^{\alpha}$ : interannual SD of the intercept;  $\sigma_{\text{year}}^{\beta}$ : island effect;  $\rho_{\text{year}}$ : interannual correlation between  $\sigma_{\text{year}}^{\alpha}$  and  $\sigma_{\text{year}}^{\beta}$ . PC: principal component. **Bold** indicates 95 % CIs of main effects that did not overlap with zero, indicating strong support. *Italics* indicate main effects whose 80 % CIs did not overlap with zero, indicating weak support

Parameter	Burrow occupancy	Hatching success	Fledging success
Intercept ( $\alpha$ )	0.39 (0.12, 0.66)	2.3 (1.75, 2.91)	1.91 (1.44, 2.43)
Island ( $\beta$ )	<i>0.31 (-0.04, 0.66)</i>	-0.29 (-0.91, 0.30)	<i>-0.45 (-1.02, 0.08)</i>
PC <sub>1</sub> ( $\gamma_1$ )	-0.02 (-0.18, 0.14)	0.14 (-0.39, 0.64)	-0.07 (-0.52, 0.38)
PC <sub>2</sub> ( $\gamma_2$ )	-0.05 (-0.29, 0.19)	0.11 (-0.63, 0.89)	0.36 (-0.24, 1.03)
Island $\times$ PC <sub>1</sub> ( $\varphi_1$ )	<b>0.26 (0.04, 0.49)</b>	-0.32 (-0.83, 0.17)	<i>-0.38 (-0.81, 0.08)</i>
Island $\times$ PC <sub>2</sub> ( $\varphi_2$ )	<b>-0.35 (-0.67, -0.03)</b>	0.20 (-0.55, 0.94)	0.21 (-0.47, 0.88)
$\sigma_{\text{site}}$	0.27 (0.12, 0.48)	0.31 (0.02, 0.67)	0.26 (0.02, 0.58)
$\sigma_{\text{year}}^{\alpha}$	0.09 (0.01, 0.30)	0.55 (0.16, 1.15)	0.47 (0.11, 1.04)
$\sigma_{\text{year}}^{\beta}$	0.09 (0.01, 0.32)	0.33 (0.05, 0.88)	0.38 (0.05, 0.96)
$\rho_{\text{year}}$	-0.2 (-0.98, 0.92)	-0.12 (-0.95, 0.92)	-0.19 (-0.94, 0.89)

interaction (Table 1), meaning that when marine conditions were warmer and/or less moderate, burrow occupancy rates were higher at Protection Island than at Destruction Island. Neither PC correlated with hatching success rates, but with fledging rates, PC<sub>1</sub> had a weak negative interaction with island, meaning that when marine conditions were warmer, breeding success was lower at Protection Island (Table 1). There was no interaction with PC<sub>2</sub> (Table 1).

### 3.2. Diet metrics

#### 3.2.1. Prey species composition

Over 7 seasons at Protection Island, we collected 231 complete confirmed bill loads (range: 13–56 per season) composed of 1498 individual prey items from at least 13 species. In 6 seasons at Destruction Island, we collected 184 complete confirmed bill loads (range: 15–53 per season) composed of 679 individual prey items from at least 16 species.

The NMDS and PERMANOVA showed that the 2 colonies differed in the fish prey taxa that adults brought back to chicks in all years (PERMANOVA: Island:  $F = 19.9$ ,  $R^2 = 0.62$ ,  $p = 0.001$ ; Year:  $F = 4.1$ ,  $R^2 = 0.14$ ,  $p = 0.04$ , Fig. 5). At Protection Island, the 2 most abundant species in all years were Pacific sand lance *Ammodytes hexapterus* (mean 70%, range 52–79%), followed by Pacific herring *Clupea pallasii* (mean 25%, range 11–44%). No other single species had an overall average of >2%, and other than juve-

nile salmon, which made up 7% of prey items in 2010, no other species had an average of >5% in a single year (Fig. 6A).

Prey species composition at the Destruction Island colony was much more variable over time (Fig. 6B). Northern anchovy *Engraulis mordax* was the most abundant species in all years (40%), with peaks in 2010 (72%) and 2013 (81%); however, it declined in proportion from 46% in 2016 to just 3% in 2019. Anchovy was replaced largely by smelt species, which increased from 17% of prey items in 2010 to 58% in 2019. Major prey species (mean abundance >5%) also included Pacific sand lance (mean 12%, range 0–33%), Pacific herring (mean 12%, range 0–33%), and juvenile rockfish (mean 6%, range 0–28%). No other species made up >5% of prey items in a single year.

#### 3.2.2. Diet metrics, fish condition, and marine conditions

Although bill loads from the 2 colonies differed in prey species composition, their mass (DI:  $27.9 \pm 1.1$  g, PI:  $29.0 \pm 1.0$  g) and energy content (DI:  $138.0 \pm 7.8$  kJ, PI:  $147.9 \pm 8.5$  kJ) were similar (Figs. 5C & 7A, Table 2). However, auklets from Protection Island brought more prey items per bill load in all sample years (DI:  $3.63 \pm 0.4$ , PI:  $6.54 \pm 0.8$ , Fig. 7B, Table 2). Between 2015 and 2016, the peak years of the NE Pacific MHW, bill-load energy content at Protection Island declined by more than 50% even as the number of prey items

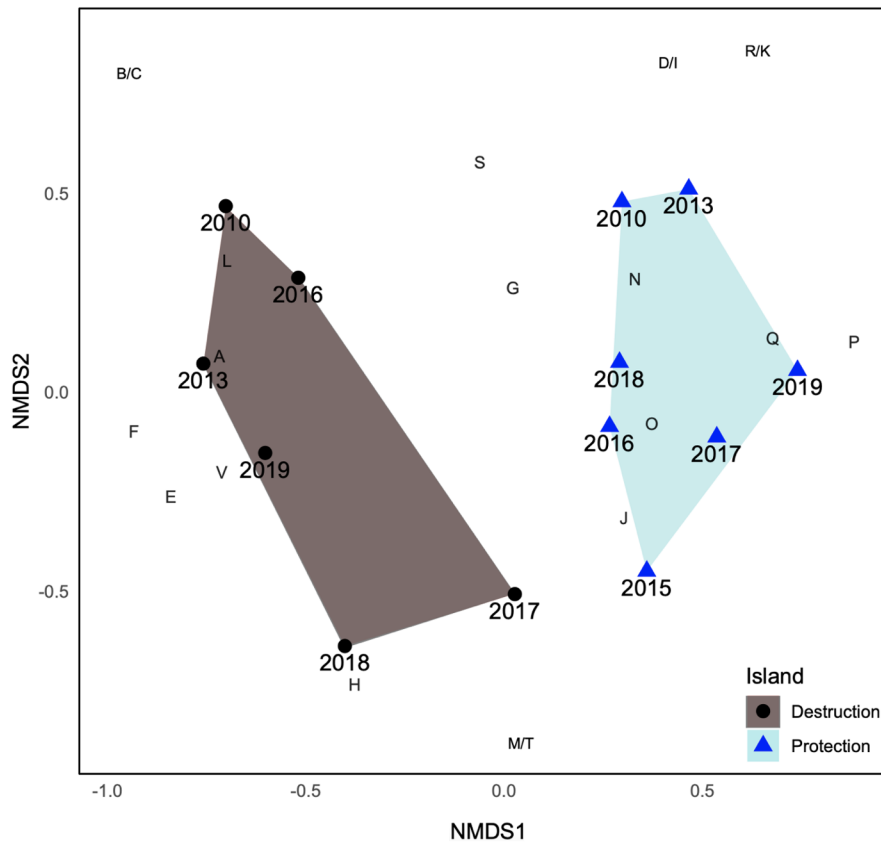


Fig. 5. Hull plot showing nonmetric multidimensional scaling (NMDS) ordinations for annual differences in prey species composition for rhinoceros auklets at Destruction Island (California Current) and Protection Island (Salish Sea). Convex hulls show items in a class (here, the islands' distinct compositions). For the purposes of clarity, letters denote species' names to lowest identifiable taxonomic level: (A) northern anchovy *Engraulis mordax*; (B) slender barracudina *Lestidium ringens*; (C) eulachon *Thaleichthys pacificus*; (D) fiery armhook squid *Gonatus pyrus*; (E) unknown flatfish (Pleuronectidae); (F) unknown greenling spp. (*Hexagrammos* spp.); (G) Pacific lamprey *Lampetra tridentatus*; (H) northern lampfish *Stenobranchius leucopsarus*; (I) market squid *Doryteuthis opalescens*; (J) Pacific herring *Clupea pallasii*; (K) snake prickleback *Lumpenus sagitta*; (L) unknown rockfish juveniles (Sebastinae); (M) search *Bathymaster signatus*; (N) unknown salmonid (Salmonidae); (O) Pacific sand lance *Ammodytes hexapterus*; (P) shiner perch *Cymatogaster aggregata*; (Q) unknown squid (Order: Teuthida); (R) three-spined stickleback *Gasterosteus aculeatus*; (S) surf smelt *Hypomesus pretiosus*; (T) unknown hexagrammid (Hexagrammidae); (U) whitebait smelt *Allosmerus elongatus*; (V) other. Letters separated by a slash (/) would otherwise occupy the same space

per bill load more than doubled. The average mass of individual prey items in bill loads was also less at Protection Island in all years, but increased at both islands as a season progressed, indicating that, generally, adults brought larger prey items to their chicks as they grew (Table 3).

We only collected bill loads at Destruction Island during one of the MHW years, and for 2 years at Protection Island, and the PCs had little explanatory power; the only relationship was  $PC_2$ , which had a strong negative effect on prey item count, meaning that the more moderate marine conditions were, the fewer prey items auklets brought back to their chicks (Table 2). There were no interactions between the islands and the PCs.

Of the 6 major prey species at Destruction Island, only Pacific sand lance and smelt showed any inter-annual variation in average fish condition. For sand lance, individuals in 2019 were in better condition than individuals in 2016, with no differences among the other years; for smelt, individuals in 2018 and 2019 were in better condition than individuals in 2013 (Fig. 8, Table 4; Table S3 in Supplement 2). At Protection Island, Pacific sand lance and Pacific herring showed marked interannual variation in condition (Fig. 9, Table 4; Table S3). Notably, individuals of both species captured by auklets were in the poorest condition in 2013 and 2017, i.e. the 2 years that bracketed the NE Pacific MHW; they were in the highest condition in 2015, during the MHW.

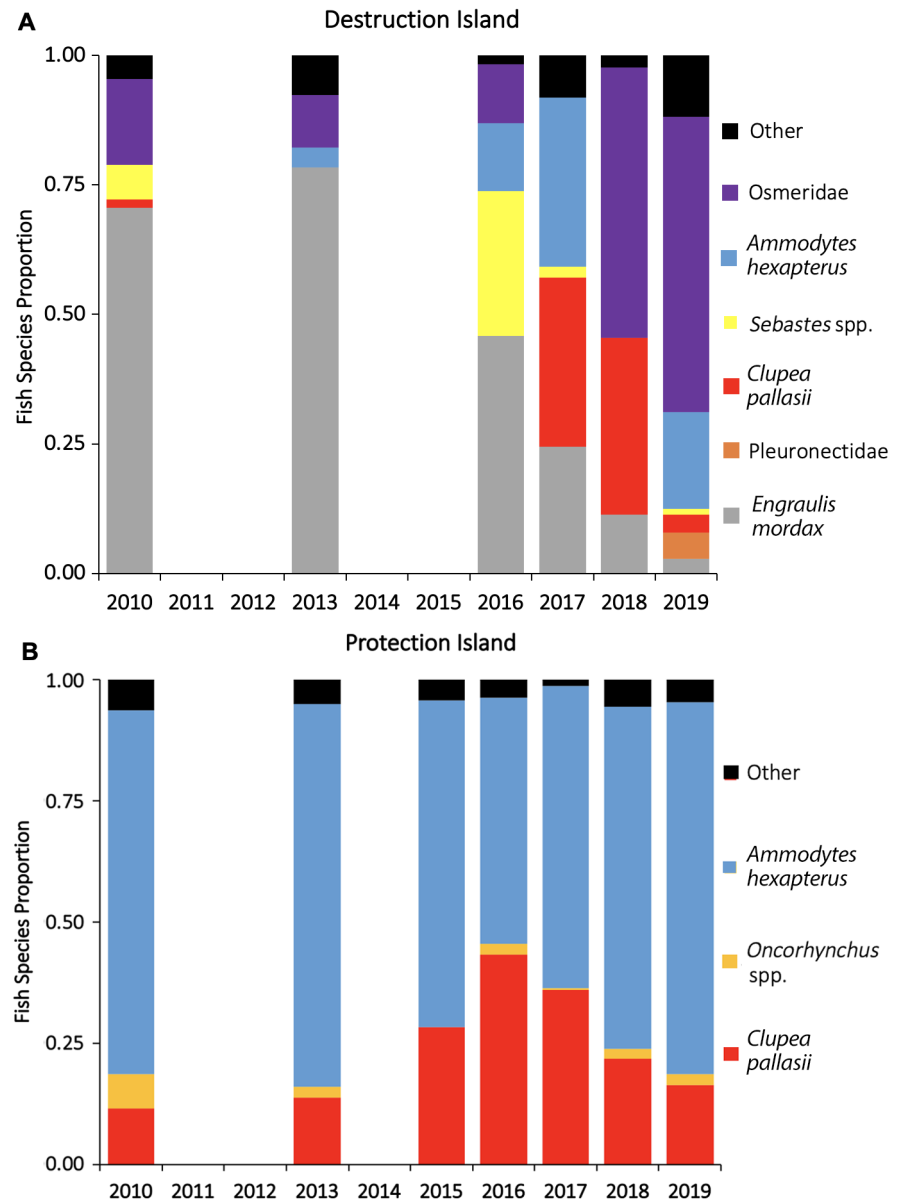


Fig. 6. Major prey species in rhinoceros auklet bill loads from (A) Destruction Island (California Current) and (B) Protection Island (Salish Sea). Major prey species were defined as those present in >5% of bill loads for at least 1 yr of the sample period. See Table S1 in Supplement 1 for a full list of species found in auklet bill loads

## 4. DISCUSSION

### 4.1. Differing responses in breeding metrics without catastrophic declines

This study showed the degree to which a species' responses to a large MHW can vary even on relatively small spatial scales. Our hypothesis that the consequences of the NE Pacific MHW for the 2 colonies might not be identical was supported. However, our prediction that Destruction Island, owing to its location on the outer coast where conditions are more extreme, would be more significantly affected both in terms of burrow occupancy/egg

production and fledging success rates, was not supported. Finally, our study suggests that the rhinoceros auklet may have a greater capacity to withstand significant climate perturbations than many other seabirds, particularly other alcids (see Suryan et al. 2021).

Breeding metrics at the 2 islands generally covaried positively in non-MHW years, but during the NE Pacific MHW, the islands had differing responses. At Destruction Island, the main effect of the MHW was an immediate ~30% decline in burrow occupancy/egg production rates in 2014 and 2015, before they returned to the pre-MHW average in 2016, where they remained. Chick fledging rates dipped some-

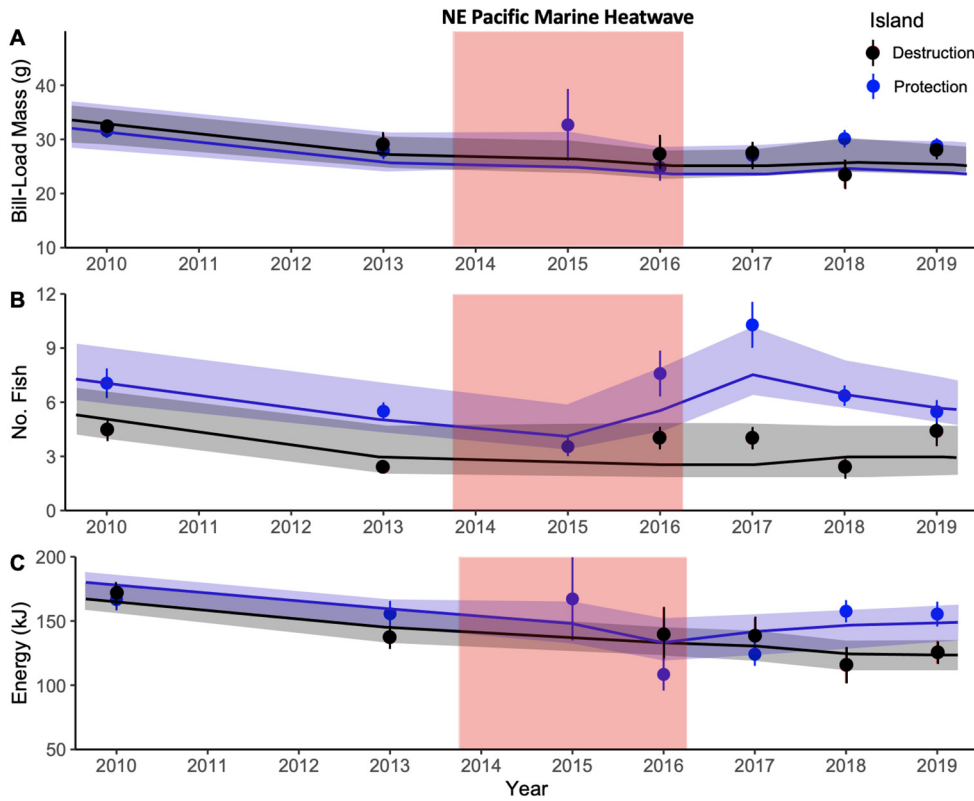


Fig. 7. Time series of diet metrics for rhinoceros auklet colonies on Protection Island (Salish Sea) and Destruction Island (California Current). (A) Average bill-load mass; (B) average number of prey items per bill load; (C) average bill-load energy content. Points are annual means; error bars show sample 95% confidence intervals. The solid line is the posterior median of the fitted values, and the shaded ribbon is the 95% credible interval. Red columns show the 3 seasons (2014–2016) affected by the NE Pacific marine heat wave

what, but the decline during the MHW did not depart substantially from general interannual variation. At Protection Island, the response was almost the reverse. There, fledging success rates declined by nearly 50% from 2015 to 2016 before returning to pre-MHW levels in 2017. Occupancy rates declined as well, but neither as steeply nor during the MHW years, reaching a low in the same season that fledging rates recovered, before returning to more typical levels by 2019.

Since burrow occupancy and egg production rates declined at Destruction Island while fledging rates remained steady, adults at that colony likely skipped breeding due to unfavorable marine conditions, a well-known phenomenon in seabirds (Bradley et al. 2000, Cubaynes et al. 2011). The NE Pacific MHW may not have affected the nearshore environment off the Washington coast until 2015 (e.g. Jones et al. 2018), but auklets wintering in offshore waters may have still encountered suboptimal conditions (e.g.

Table 2. As in Table 1, but for GLMMs of rhinoceros auklet bill-load metrics.  $\sigma_{\text{week}}$ : among-week intercept SD.  $R^2$  values are given for the weight and energy content models, which are linear, but not for prey item count, which was a Poisson observation model

Parameter	Weight	Prey item count	Energy content
Intercept ( $\alpha$ )	13.29 (-0.55, 27.03)	1.25 (0.70, 1.78)	1.69 (-9.50, 12.97)
Island ( $\beta$ )	-0.12 (-3.78, 3.03)	<b>0.62 (0.19, 1.09)</b>	0.35 (-8.30, 8.95)
PC <sub>1</sub> ( $\gamma_1$ )	0.23 (-2.70, 3.99)	-0.01 (-0.52, 0.48)	0.37 (-7.74, 8.50)
PC <sub>2</sub> ( $\gamma_2$ )	-1.32 (-4.19, 2.38)	-0.17 (-0.75, -0.39)	-3.76 (-12.25, 5.36)
Island × PC <sub>1</sub> ( $\varphi_1$ )	0.68 (-2.88, 4.06)	-0.11 (-0.61, 0.31)	-0.11 (-8.66, 8.39)
Island × PC <sub>2</sub> ( $\varphi_2$ )	0.48 (-4.19, 2.38)	0.23 (-0.29, 0.71)	-0.73 (-9.36, 8.06)
$\sigma_{\text{week}}$	15.45 (2.86, 33.86)	0.13 (0.01, 0.39)	146.07 (91.33, 236.86)
$\sigma_{\text{year}}^{\alpha}$	2.04 (0.04, 12.90)	0.44 (0.17, 1.02)	12.74 (0.60, 34.61)
$\sigma_{\text{year}}^{\beta}$	1.64 (0.04, 6.50)	0.37 (0.10, 0.92)	11.36 (0.52, 34.42)
$\rho_{\text{year}}$	-0.10 (-0.97, 0.94)	-0.06 (-0.85, 0.81)	-0.04 (-0.20, 0.08)
$R^2$	0.07 (0.05, 0.09)	-	0.1 (0.08, 0.12)

Table 3. As in Table 1, but for a linear mixed model of average prey item size per rhinoceros auklet bill load by island as the breeding season progressed

Parameter	Size
Intercept ( $\alpha$ )	6.65 (1.04, 11.89)
<b>Island (<math>\beta_1</math>)</b>	<b>-4.14 (-7.32, -0.73)</b>
<b>Log(Week) (<math>\beta_2</math>)</b>	<b>2.87 (0.52, 5.18)</b>
PC <sub>1</sub> ( $\gamma_1$ )	0.86 (-2.39, 4.67)
PC <sub>2</sub> ( $\gamma_2$ )	0.44 (-4.01, 5.29)
$\sigma_{\text{year}}^{\alpha}$	5.11 (1.74, 11.66)
$\sigma_{\text{year}}^{\beta}$	5.33 (2.6, 9.91)
$\rho_{\text{year}}$	-0.59 (-0.98, -0.34)
R <sup>2</sup>	0.23 (0.03, 0.5)

Black et al. 2010, Schroeder et al. 2013). What is notable, then, is that auklets returning to Protection Island as the MHW approached its peak in 2015 either did not receive the same non-breeding season

signal as those at Destruction Island (e.g. Crossin et al. 2022), or did not heed it, being in good enough body condition to attempt to breed regardless. If this was the case, then it may be because auklets from the 2 colonies overwinter in different areas (Hipfner et al. 2020).

The resulting pattern at Protection Island of decreasing reproductive success for 2 years followed by a ~20% decrease in burrow occupancy rates in 2017 further suggests that carry-over effects from the NE Pacific MHW may have extended by a year for those auklets and their prey (PSEMP Marine Waters Workgroup 2017, 2018). Although the MHW signature had disappeared by late 2016 from surface waters in Queen Charlotte Sound, British Columbia, for example, warmer temperatures persisted below the surface mixed layer at least through 2018 (Jackson et al. 2018). Additionally, auklets in the Salish Sea underwent an unusual mortality event in 2016 due to an outbreak of septicemia (Knowles et al. 2019). Autop-

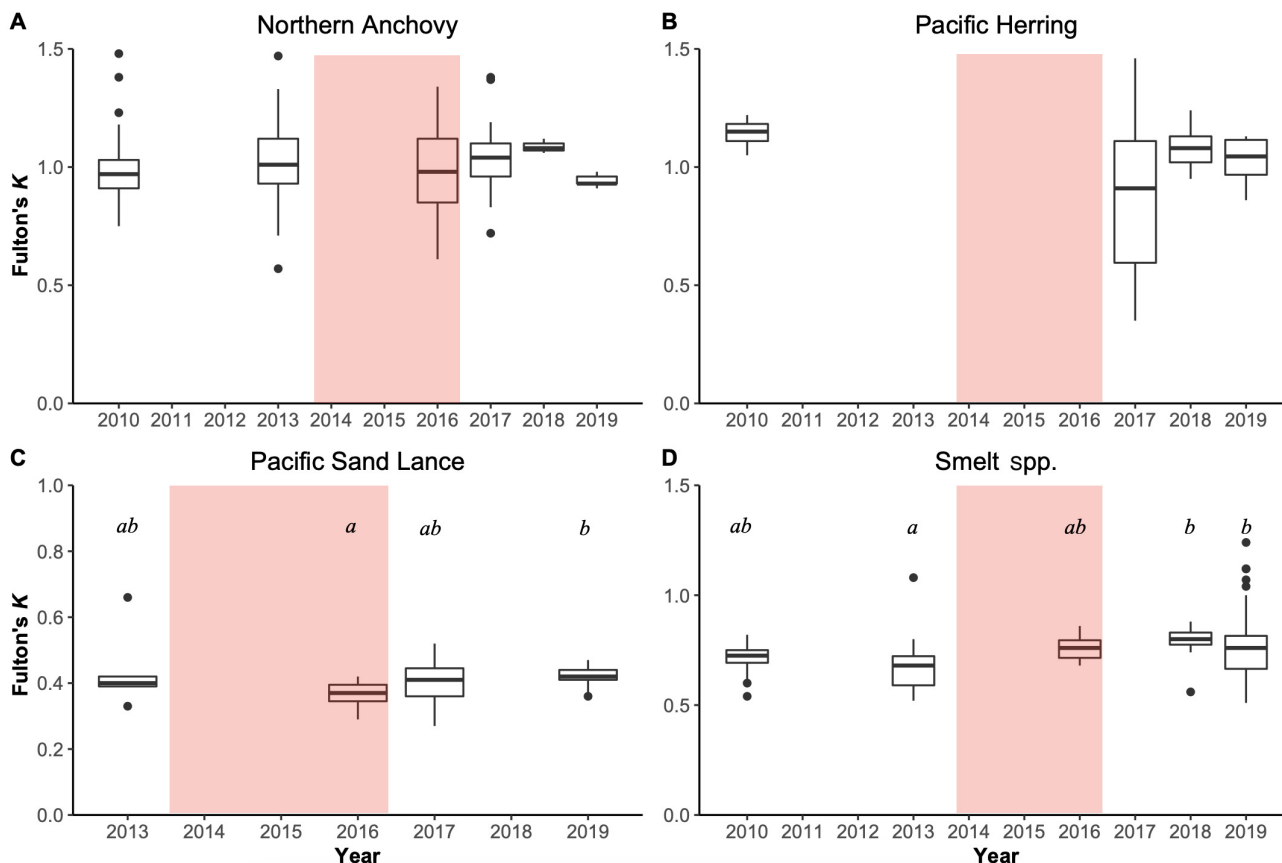


Fig. 8. Average annual Fulton's  $K$  factor scores for 4 major prey species at the Destruction Island colony: (A) northern anchovy; (B) Pacific herring; (C) Pacific sand lance; (D) smelt species. Red columns indicate years affected by the NE Pacific marine heatwave. Boxplots show medians and upper and interquartile range (IQR). Whiskers show largest/smallest values  $\pm 1.5$  (IQR). Black dots show outliers. Letters indicate years that differ according to pairwise least-square means tests, such that any 2 years sharing one or more letters do not differ from one another; if a plot has no letters, condition did not differ among years. See Table S3 in Supplement 2 for statistical summaries

Table 4. Results from linear mixed-effects models on annual average Fulton’s *K* factor scores for major prey species of rhinoceros auklets at Destruction and Protection Islands. Species in **bold** had significant results, and the pairwise least-square means for each year were then compared (see Table S3 in Supplement 2)

Island	Species	Variable	df	SS	MS	<i>F</i>	<i>p</i>
Destruction Island	Northern anchovy	Year	5	0.16	0.03	1.62	0.16
		Residuals	251	4.87	0.02		
	Pacific herring	Year	3	0.03	0.01	0.03	0.99
		Residuals	50	15.44	0.31		
	<b>Pacific sand lance</b>	Year	3	0.02	0.008	2.63	<b>0.04</b>
		Residuals	75	0.35	0.005		
<b>Smelt spp.</b>	Year	4	0.17	0.05	3.27	<b>0.01</b>	
	Residuals	166	2.21	0.01			
Protection Island	<b>Pacific sand lance</b>	Year	6	0.55	0.09	25.3	<b>&lt;0.00001</b>
		Residuals	976	3.55	0.004		
	<b>Pacific herring</b>	Year	6	1.73	0.29	8.73	<b>&lt;0.00001</b>
		Residuals	262	8.63	0.03		

sied adults were often emaciated, but whether it was a result of reduced prey quality and/or availability, weak foraging ability due to illness, or both is uncertain (S. F. Pearson unpubl.). However, disease outbreaks in marine environments could increase with warming conditions (e.g. Burge et al. 2014).

Seabird breeding success frequently declines in response to MHWs, as we observed at Protection Island. Fairy prions *Pachyptila turtur* and common diving petrels *Pelecanoides urinatrix* both showed delayed laying dates, slower chick growth, and reduced breeding success during MHWs in Aus-

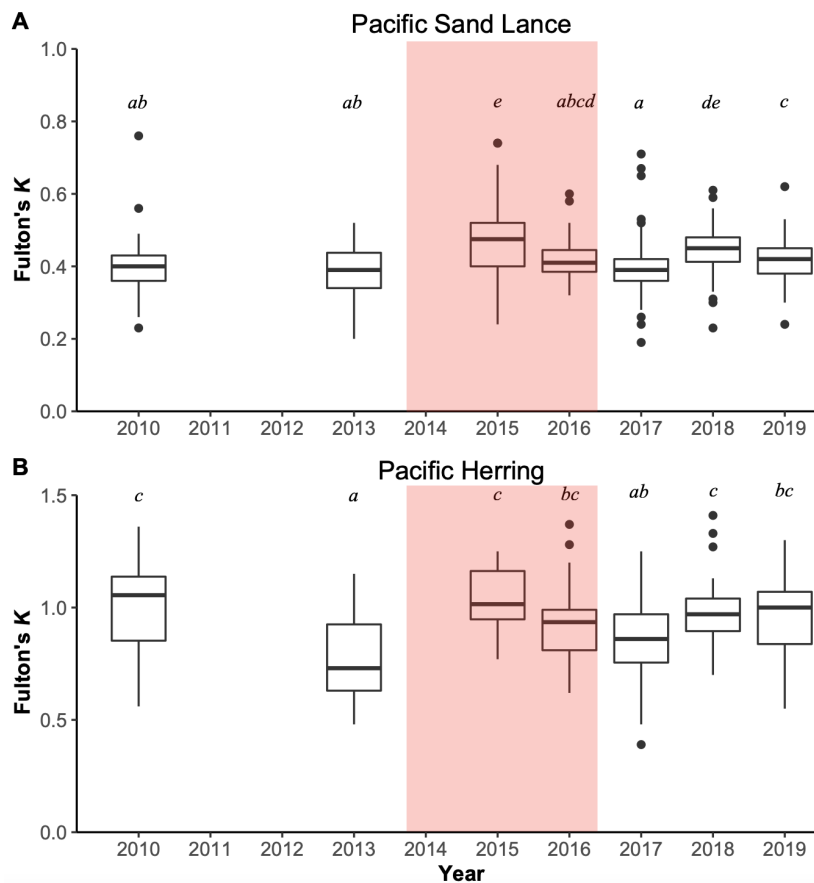


Fig. 9. As in Fig. 8, but for 2 major prey species at Protection Island: (A) Pacific sand lance; (B) Pacific herring

tralia, although the effects were not as pronounced for the prions (Eizenberg et al. 2021). Short-tailed shearwaters *Ardenna tenuirostris* exhibited both delayed breeding onset and reduced breeding success in response to an MHW in southern Australia, before being subject to a die-off in response to an MHW in 2019 in the NE Pacific (Glencross et al. 2021).

Of note is that, even as rhinoceros auklets at both islands experienced declines in breeding metrics during the NE Pacific MHW, the consequences of the MHW were not nearly as catastrophic as they were to other species, even other alcids (e.g. Jones et al. 2018, Piatt et al. 2020). Additionally, the dynamic we observed at Destruction Island is the first instance we know of where we see a decline in burrow occupancy and egg production rates without concurrent declines in breeding success. We will explore possible mechanisms for this pattern in the next section, but we recognize that our chick survey methods hinge on visual inspection, which may overestimate fledging success rates. In auklet chicks, the partial feathering stage can last a long time depending on chick feeding and development rates (e.g. Harfenist 1995). Because we did not measure or weigh auklet chicks, we could not know the condition of those present on our last visit, i.e. whether they were close to a minimum fledging weight.

#### 4.2. Diet shifts to mitigate climate impacts

Auklet bill loads for chicks from Destruction Island differed from those at Protection Island both in terms of dominant prey species and overall species composition, consistent with historical studies (Wilson & Manuwal 1986). In all years of this study, auklets at Protection Island depended on Pacific sand lance and Pacific herring, but prey species composition at Destruction Island was highly variable across years, shifting from a diet dominated by northern anchovy through 2013 to one made up of mostly smelt species by 2019. Whether the NE Pacific MHW drove this shift is unknown, but anchovy abundance in the California Current was variable during this period (e.g. Harvey et al. 2020).

The ability to take advantage of an expanded prey pool may serve to insulate auklets at Destruction Island against extreme events that affect the abundance or condition of 1 or 2 prey species (Kondoh 2003). Auklets eat mostly pelagic forage fish, but as generalists, adults in this study brought back squid, juvenile rockfish, and other species more commonly

associated with benthic nearshore environments (e.g. Hexagrammidae spp.). Auklets may also specialize more in a particular foraging location than on a target species in an effort to maximize bill-load mass and energy, resulting in the capture of more variable prey species (Cunningham et al. 2018). Additionally, Suryan et al. (2002) suggested that interannual variation in environmental forcing creates a threshold above which the parental behavior of a seabird can flexibly accommodate shifts in the prey base.

At Protection Island, there was no such shift in prey species composition. During the 2 years that sampling overlapped with the NE Pacific MHW, sand lance and herring comprised ~90% of auklet bill loads, as they did in other years. This dependence suggests that the Salish Sea is a wasp-waisted system (Cury et al. 2000, Therriault et al. 2009), in which an intermediate trophic level controls the abundance of predators through a bottom-up interaction. Although sand lance and herring have different life history strategies (e.g. timing of spawning, being migratory or non-migratory), the NE Pacific MHW may have overwhelmed their capacity to buffer against environmental variance (e.g. Arimitsu et al. 2021).

Both sand lance and herring in the Salish Sea fluctuate in abundance depending on their environment, with pronounced declines in fish condition due to anomalous warming (Baker et al. 2019); herring in particular underwent steep population declines during the NE Pacific MHW and did not apparently recover until 2019 (Frick et al. 2022). Because rhinoceros auklets only deliver on average 1 bill load per parent to their chick each night (Wilson 1977), they do not have the opportunity to compensate with more bill loads per day should prey be difficult to find or of poor quality, unlike diurnal-provisioning common murre *Uria aalge* and tufted puffins *Fratercula cirrhata* (Schrimpf et al. 2012, but see Gjerdrum et al. 2003). One way for rhinoceros auklets to offset a poorer energy-per-prey-item relationship is to bring back more items per bill load, in which case there is likely a physical limit to the amount of prey they can effectively carry (e.g. Watanuki et al. 2022). Alternatively, they could try to capture more energy-rich species, although doing so could confer an energetic cost to adults, as they may have to fly farther to reach optimal foraging sites or spend more time hunting once they get there (e.g. Ballance et al. 1997, Davoren 2000).

We only sampled diets during one of the MHW seasons at Destruction Island in the California Current, but bill-load characteristics did not differ from

other years, and reproductive success rates were similar. At Protection Island, however, bill load characteristics showed a clear effect of the MHW. Even though the condition of the sand lance and herring captured by auklets did not immediately decline compared to non-MHW years, the individual fish were smaller. Sand lance and herring condition was highest in 2015, which is evidence that auklets were able to target higher-condition prey in that year at least, since nearby beach seine surveys found sand lance condition to be poor relative to pre-MHW baseline data (Baker et al. 2019). However, as fish size declined, the number of fish per auklet bill load doubled in 2016 and then nearly tripled in 2017 compared to 2015. At the same time, the average bill load energy content relative to 2015 was 35% lower in 2016 and 25% lower in 2017—a sign that increased foraging effort was not yielding an energetic payoff. All of this coincided with the lowest fledging success rates of this colony.

#### 4.3. Resilience in the face of unfavorable marine conditions

Alcids were among several seabird families to be hard hit during the NE Pacific MHW (e.g. Jones et al. 2019, Tate et al. 2021, Van Hemert et al. 2021). Previous research has suggested a correlation between physical forcing in general and reproductive success and periodic die-offs in seabirds. The foraging ranges of black-legged kittiwakes *Rissa tridactyla* increased in years of poor food availability, for example, and led to declines in breeding success (Hatch 2013). An abnormally late spring transition to upwelling conditions in 2005 led to severely reduced NPP (Barth et al. 2007), which resulted in breeding failures in marbled murrelets *Brachyramphus marmoratus* in British Columbia (Ronconi & Burger 2008) and nest abandonment in Cassin's auklets *Ptycho-ramphus aleuticus* throughout the California Current (Sydeman et al. 2006). Similarly, from California, USA, to British Columbia, Canada, Cassin's auklets experienced an unusual mortality event as a result of warm-water intrusions from the NE Pacific MHW into the nearshore environment. This led to a shift in the zooplankton community composition away from a northern copepod assemblage to smaller southern copepods, as well as reducing the mean size of adult euphausiids and overall abundance (Jones et al. 2018, Phillips et al. 2022).

While the NE Pacific MHW clearly affected both breeding and diet metrics at the 2 auklet colonies, it

did not do so consistently, synchronously, or even that strongly. We thus did not find a pronounced relationship between these metrics and a PCA of marine conditions. Where breeding metrics are concerned, this was likely because the effects of the MHW were evident for only 2 of its 3 years at each island, and then with different stages: burrow occupancy rates at Destruction Island in 2014 and 2015, and fledging success rates at Protection Island in 2015 and 2016. Subsequent declines in burrow occupancy at Protection Island took place after the MHW was supposed to have ended; furthermore, occupancy rates were higher during parts of the NE Pacific MHW, making it appear that MHW-like conditions increased burrow occupancy. However, the decline in breeding success at Protection Island was enough to result in a negative relationship between ocean warming and breeding performance, consistent with many other studies.

Rhinoceros auklets have occasionally shown an idiosyncratic relationship with marine conditions (e.g. Morrison et al. 2011). For example, Bertram et al. (1991) found that while there could be substantial interannual variation in provisioning and chick growth rates at breeding colonies in British Columbia, those variations did not necessarily reflect fluctuations in the marine environment. On the other hand, Hedd et al. (2006) found a clear association between spring SSTs and auklet reproduction at Triangle Island, British Columbia, as chick growth rates decreased with increasing SSTs. They hypothesized this was due to temperature-dependent recruitment of sand lance, since years with high auklet breeding success were linked to sand lance-dominated chick diets. In another study of the same colony, Borstad et al. (2011) found that the relationship between breeding success and SST may have been correlative rather than causal and that an early spring transition date was more predictive. Breeding colonies in the southern portion of the California Current have also exhibited a relationship between bill load mass and SSTs (Thayer & Sydeman 2007). Finally, auklets have shown behavioral flexibility in the past when confronted with poor marine conditions. Their chick-rearing period of ~50 d is long compared to other alcids (e.g. ~48 d for tufted puffins, a larger species; Piatt & Kitaysky 2002). During the 1997/98 El Niño, for example, auklets at the Protection Island colony were able to maintain average rates of fledging success by extending that rearing period still more, even as chick average growth rates were significantly lower (Wilson 2005).



#### 4.4. Conclusions

Rhinoceros auklets in Washington withstood the major environmental shifts of the NE Pacific MHW without experiencing significant or durable declines in breeding performance. Their capacity to do this, whether by skipping breeding, relying on an expanded prey portfolio, increasing foraging effort, and/or extending the chick-rearing period, varied between the 2 colonies we studied. As indicated by the higher diversity of prey items at Destruction Island, the California Current is a prey-rich system, and auklets there could change their diet without a substantial effect on breeding success. In the wasp-waisted Salish Sea, however, the energy available to chicks was constrained by the abundance and condition of Pacific sand lance and herring (Bertram & Kaiser 1993, Therriault et al. 2009, Selleck et al. 2015).

Although auklets at Protection Island have weathered poor marine conditions in the past (e.g. the 1997/98 El Niño, Wilson 2005), and suffered no apparent ill effects in the first year of the NE Pacific MHW, by its final year, the combination of decreased food availability/quality and the rise of a lethal bacterial pathogen (Knowles et al. 2019) proved too much to endure without some consequence to breeding metrics. The subsequent decrease in burrow occupancy rates after the MHW and unusual mortality event suggests a possible population-level decline, i.e. a lack of available breeders, as opposed to adult birds simply choosing not to breed. Still, auklets at both colonies showed the ability to adapt to the NE Pacific MHW. Whether they can endure the more frequent, intense, or longer-lasting MHWs predicted to occur under future climate scenarios remains an open question.

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