1   Resilience to a severe marine heatwave at two Pacific seabird colonies
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20   Running head: Seabird responses to marine heatwave

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 three-year period on record. Our decade-long (2010-2019) breeding and diet monitoring of the rhinoceros auklet (*Cerorhinca mococerata*), a burrow-nesting seabird, at significant breeding colonies on Destruction Island (in the California Current) and Protection Island (in the 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 similar on average, the auklets' responses to the MHW differed. At Destruction Island, burrow occupancy rates were lower during the MHW (0.54 ± 0.02 v. 0.61 ± 0.02 in non-MHW years), suggesting that birds skipped breeding, but fledging success rates did not differ (0.85 ± 0.02 v. 0.89 ± 0.03). At Protection Island, burrow occupancy remained at non-MHW levels (0.72 ± 0.02 v. 0.69 ± 0.02), but reproductive success declined (0.71 ± 0.03 v. 0.82 ± 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. With marine heat waves predicted to become more frequent and severe, however, the auklets' ability to maintain these levels of breeding success will be tested.

Keywords: alcids, climate change, forage fish, marine heatwaves

1. INTRODUCTION

43
44 Climate change has led to an increase in the frequency of extreme events in marine
45 systems, including marine heatwaves (MHWs) (Hobday et al. 2016, Oliver et al. 2018, Jacox et
46 al. 2020). Defined as extended periods of significantly elevated sea surface temperatures (SSTs)
47 over large areas (Benthuysen et al. 2020), MHWs have been linked to reduced ocean
48 productivity (Wernberg et al. 2013, Smale et al. 2019), shifts in the geographic distribution of
49 organisms (Goddard et al. 2016, Mills et al. 2013), increased frequency of harmful algal blooms
50 (Robert et al. 2019), local extinctions (Thomsen et al. 2019), unusual mortality events for both
51 marine mammals and seabirds (McClatchie et al. 2016, Piatt et al. 2020), and negative effects on
52 breeding phenology and reproductive success in seabirds (Fromant et al. 2021, Glencross et al.
53 2021).
54 One of the most recent and severe MHWs occurred in the northeast Pacific Ocean (Smith
55 et al. 2023). In late 2013/early 2014, a large patch of anomalously warm water formed in the
56 Gulf of Alaska due to low rates of heat loss and weak cold advection in the upper ocean (Bond et
57 al. 2015). Over the next two years, the patch of warm water spread to cover more than 2.5
58 million km^2, extending from southern Alaska to Baja California (Smale et al. 2019) and
59 becoming known colloquially as The Blob (Kintisch 2015). Offshore SSTs were more than three
60 standard deviations above normal during the winter of 2013 – 2014, with elevated SSTs lasting
61 through the summer of 2016; at their peak in 2015, SST anomalies were 3 – 6 ºC above the 1981
62 – 2010 climatology (Bond et al. 2015, Gentemann et al. 2017). All of this combined at the time
63 to make the NE Pacific MHW the largest documented MHW in terms of duration, geographic
64 extent, and magnitude since recording began in 1982 (Oliver et al. 2018).
65 Elevated temperatures during the NE Pacific MHW led to increased stratification of the
66 upper ocean, lowering nutrient supplies at the surface and resulting in declines in net primary
67 productivity (NPP), prey availability, and community production (Whitney 2015, Yang et al.
68 2018). The 2014-16 NE Pacific MHW has been linked to mass mortality events in both marine
69 mammals (Savage 2017) and birds (Jones et al. 2018, Jones et al. 2019, Piatt et al. 2020), as well
70 as other significant ecological disruptions for organisms over a range of trophic levels (e.g.,
71 Cavole et al. 2016, Leising et al. 2016, McCabe et al. 2016, Peterson et al. 2017, Brodeur et al
72 2019, Jones et al. 2021). Some of the NE Pacific MHW's consequences, however, have been
73 more subtle, and their full breadth is still being explored.
74 Understanding climate-biology relationships in marine systems is critical for
75 conservation and resource management, and seabirds, as conspicuous and widespread top
76 predators, are good sentinels to detect shifts in marine systems (Parrish et al. 2007, Hazen et al.
77 2019). In this paper, we draw on a long-term monitoring study to compare the responses of the
78 rhinoceros auklet (*Cerorhinca monocerata*), a colonial burrow-nesting seabird, to the NE Pacific
79 MHW at two major breeding colonies. One is it at Destruction Island on the outer coast of
80 Washington, USA, in the California Current Large Marine Ecosystem. The other is at Protection
81 Island, in the Strait of Juan de Fuca, and is part of the Salish Sea, a fjord estuary complex that
82 includes the interior waters of Washington and southern British Columbia, Canada. Although the
83 two colonies are less than 150 linear km apart, the systems in which they sit are subject to
84 distinct physical forcing mechanisms (e.g., MacCready et al. 2021). The NE Pacific MHW's
85 most extreme effects, for example, may have been buffered in the Salish Sea due to increased
86 freshwater inputs, and peak temperature anomalies were elevated just 2.3 ºC above average
87 (Khangaonkar et al. 2021). Auklets at the two colonies also rely on different prey bases (Wilson
88 & Manuwal 1986).

89   We hypothesized that auklets' responses on the two islands would be neither uniform nor
90   synchronous, despite their geographic proximity. Due in part to the more severe marine
91   conditions auklets at Destruction Island faced during the NE Pacific MHW, we predicted they
92   would experience more pronounced disruptions than auklets at Protection Island. These
93   disruptions would manifest in the form of lower burrow occupancy and fledging success rates,
94   and bill load characteristics indicative of poor prey quality and / or greater compensatory
95   foraging effort (*cf.* Schrimpf et al. 2012). By relating breeding metrics (burrow occupancy, hatch
96   success, and fledge success) and diet metrics (prey species composition, bill load weight, energy,
97   prey item count, fish condition) to marine conditions at the two colonies, we aim to detect shifts
98   that indicate how the NE Pacific MHW affected a sentinel species.
99
100   2. MATERIALS & METHODS
101   2.1. Study Sites and Species
102   The rhinoceros auklet is a medium-sized alcid whose breeding and non-breeding ranges
103   encompass much of the northern Pacific. In the northeast Pacific and the Salish Sea it is a year-
104   round resident. Adults return to breeding colonies in March and April, where pairs either re-
105   occupy existing burrows or excavate new ones. The female lays one egg in early- to mid-May
106   (Leschner 1976, Wilson & Manuwal 1986), and mates share incubation duties for approximately
107   45 days. After the chick hatches, one or both adults bring back a single bill load of fish per night
108   for approximately 50 days until the chick fledges (Wilson 1977).
109   Since 2010, we have been monitoring breeding metrics at two major colonies in
110   Washington, USA. Protection Island (48°08'N, 122°55'W) is a 143-ha island about 3 km off the
111   mouth of Discovery Bay at the eastern end of the Strait of Juan de Fuca in the Salish Sea. Along
112   its perimeter, the island contains beach and spit habitats that give way to cliffs and steep slopes,
113   while the interior of the island is flat or rolling. Approximately 36,000 breeding pairs nest in
114   burrows on the island's grass-dominated habitats on cliff edges and steeper slopes (Pearson et al.
115   2013). Destruction Island (47°40'N, 124°24'W) is located 4.8 km west of the Olympic Peninsula
116   and the mouth of the Hoh River (Figure 1). The 15-ha flat-topped island is part of an extensive
117   sandstone reef (Wilson & Manuwal 1986) and is surrounded by rocky islets. Approximately
118   6,500 auklet pairs nest in burrows on cliff tops and the island's steep slopes in grass, shrub, and
119   willow habitats (Pearson et al. 2013).
120
121   2.2. Breeding Metrics
122   On Protection Island, we established multiple study sites and monitored all burrows
123   within a 2.5-m radius from the center of each. We randomly located sites in habitats dominated
124   by grass and flowering plants (see Pearson et al. 2013). More than 95% of all auklet burrows on
125   Protection Island occur in these habitats, and burrow occupancy does not differ among them
126   (Pearson et al. 2013). On Destruction Island, we established study sites and monitored
127   individually marked burrows in all habitat types occupied by auklets (grass-, willow-, and
128   salmonberry-dominated) on the south and southwestern sides of the island (see Pearson et al.
129   2013).
130   We monitored breeding activity from 2010 – 2019 on both islands, timing our sampling
131   trips to phenological patterns reported in Leschner (1976) for Destruction Island and Wilson
132   (1977) for Protection Island. On an initial trip in late May/early June, we assessed breeding
133   activity by examining all burrows in our study areas using infra-red camera probes. We defined a
134   burrow as any excavation that contained both a tunnel and at least one nesting chamber. A

burrow with an adult and/or egg on two 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
hatch 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 chick, chick 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 previous 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
seven seasons on Protection Island (2010, 2013, 2015 – 2019) and six 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 one 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 vertebrae), 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 gram.
Some taxa, including juvenile rockfish (Sebastes spp.) and juvenile greenling (Hexagrammos
spp.), were treated each 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 (J/g wet mass) were calculated in 2008 and 2009 by bomb calorimetry
on a representative subset of samples as described in Schrimpf et al. (2012) (See Table S1 for
energy densities and a more detailed methods description).

2.4. Principal Components Analysis 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 principal component analysis (PCA) using basin-wide, regional-scale, and local
environmental predictors. For basin-wide predictors, we used the Pacific Decadal Oscillation
(PDO) index and Multivariate ENSO Index (MEI v.2). For the PDO the MEI, we took the
average of the indices from September through August so that the values encompassed the whole
of an auklet breeding cycle, i.e., the start of the non-breeding season to the end of the breeding
season.

181   At the regional scale, we used two indices to account for annual spring cold-water
182 upwelling, the main driver of regional productivity (Hickey 1989). The first is the onset of the
183 biological spring transition (day of year), which begins the day the northern cold-water copepod
184 community first appears at NH 05, a sampling station about five miles offshore along the
185 Newport Line (44.6517N, 124.1770W)—a signal that upwelling has begun. Second, as a
186 measure of upwelling intensity, we used the Biologically Effective Upwelling Transport Index
187 (BEUTI), averaging the monthly means of daily indices for March – July. BEUTI is an estimate
188 of the total quantity of nitrate upwelled or downwelled during a given period (Jacox et al. 2018).
189 We preferred BEUTI to other upwelling indices because it quantifies both the intensity of
190 upwelling and the nutrient quality of the waters being upwelled (Jacox et al. 2018), rather than
191 just the former.
192   For local predictors, we used monthly SSTs, area-averaged by the MODIS-Aqua satellite
193 at 4 km spatial resolution around both Protection Island and Destruction Island as a proxy, since
194 the precise foraging locations for auklets from both colonies are unknown. Using the NASA
195 Giovanni tool (https://giovanni.gsfc.nasa.gov/giovanni/), we delimited boxes from 47.6042N,
196 124.562W to 47.7292N, 124.479W (roughly 24 km^2 around Destruction) and 48.1458N,
197 123.146W to 48.3958N, 122.937W (roughly 30 km^2 around Protection). As a proxy for food
198 quality and availability, we used island-specific monthly values from the Carbon-based
199 Productivity Model of Net Primary Production (CbPM-NPP), a model-based dataset of primary
200 production from the Oregon State University Ocean Productivity Group
201 (http://sites.science.oregonstate.edu/ocean.productivity/). CbPM-NPP estimates phytoplankton
202 carbon concentration and uses that as a metric for biomass rather than chlorophyll a. NPP is
203 therefore described as the product of carbon biomass and growth rate, rather than the traditional
204 product of chlorophyll and photosynthetic efficiencies (Behrenfield et al. 2005, Westberry et al.
205 2008). For both Protection and Destruction islands, we averaged values for spring SST and
206 CbPM-NPP from February through April, to match the spring conditions affecting their prey
207 base; and for summer SST and CbPM-NPP from May through August, to match the auklet
208 breeding season (see Figure 2 for a time series of all indicators).
209   All predictors were scaled and normalized using the mean and standard deviation of the
210 study period (2002 – 2019). The sign of each index was standardized so that the direction
211 associated with conditions favorable to ocean productivity was always positive, ensuring that the
212 indices could be interpreted together. All indices were then combined in a PCA to create
213 summary variables that captured the overall interannual environmental fluctuations (Figure 3).
214
215 2.5. Statistical Analysis
216 2.5.1. Models for Breeding Metrics and Marine Condition
217   To test for differences in burrow occupancy, hatch success, and fledging success, both
218 between the colonies and in different marine conditions, we fit a generalized linear mixed model
219 (GLMM; Bolker et al. 2009) using a hierarchical Bayesian framework for inference. Response
220 variables were modeled as binomial with a logit link function. For burrow occupancy, the sample
221 size N was the total number of viable burrows and successes y were burrows in which a pair
222 attempted to breed (i.e., laid an egg). For hatching, N was the number of burrows containing an
223 egg and y was the number of chicks that hatched. For fledging, N was the number of eggs and y
224 the number of chicks that were either observed or presumed to have fledged. All models included
225 random intercepts grouped by site-within-island and year, with a year-varying effect of island.
226 Thus the full model for observation i in site $j[i]$ and year $k[i]$ was

227

229
$$y_i \sim \text{Bin}(N_i, \pi_i)$$
230
$$\text{logit}(\pi_i) = \alpha + a_{j[i]} + a_{k[i]} + (\beta + b_{k[i]})I_i + \gamma_1 \text{PC}_{1i} + \gamma_2 \text{PC}_{2i} + \varphi_1 I_i PC_{1i} + \varphi_2 I_i PC_{2i}$$
231
$$a_j \sim \text{N}(0, \sigma_{\text{site}})$$
232
$$\begin{bmatrix} a_k \\ b_k \end{bmatrix} \sim \text{N}(\mathbf{0}, \mathbf{\Sigma}_{\text{year}}), \qquad\qquad\qquad [1]$$

228

233 where I is a dummy indicator for island and PC_1 and PC_2 are the first and second principal
234 components, with interactions between island, PC_1, and PC_2 (but no three-way interaction). We
235 did not conduct model selection to compare restricted models to the full model, as the terms
236 included represent a parsimonious description of known sources of variation; instead we focused
237 on interpreting the posterior distributions of parameters and quantities of interest in the full
238 model (Gelman & Rubin 1995).
239   To draw samples from the posterior distributions of model parameters we used the
240 *rstanarm* package, which is an R interface to Stan, a probabilistic programming language for
241 Bayesian estimation (Gabry & Goodrich 2018). The *rstanarm* package allows fitting many of the
242 most common applied regression models using Markov chain Monte Carlo – in this case
243 Hamiltonian Monte Carlo (Monnahan et al. 2017). All prior distributions were selected to be
244 weakly informative, with N(0, 5) priors on the intercept and regression coefficients. We ran three
245 independent chains for 5000 iterations after a warmup of 1000 iterations. MCMC convergence
246 was assessed using the potential scale reduction factor diagnostic ($\hat{R} \leq 1.05$; Gelman et al. 2014)
247 and visual inspection of chains.

248

249 2.5.2. NMDS of Prey Species Composition
250   To analyze differences in prey species composition between islands and years, we used a
251 nonmetric multidimensional scaling (NMDS) ordination with the *vegan* package in R, based on
252 Bray-Curtis distances (Oksanen et al. 2017). Prey data from both islands were combined and two
253 axes were selected for each ordination based on the least-stress ordination configuration after
254 200 randomizations. Stress values reflect goodness-of-fit, or how well the ordination summarizes
255 the observed differences between the samples. Due to the small sample size and wide range in
256 relative abundances (from < 0.01 to > 0.75), the data were square-root-transformed and then
257 submitted to a Wisconsin double standardization, the standard transformation in *vegan*. We used
258 Shepherd stress plots to determine the reliability of these analyses by plotting the relationship
259 and computing the correlation between actual dissimilarities and ordination distances (linear $R^2 =$
260 0.918 and non-metric $R^2 = 0.987$; stress = 0.11, indicating good ordination fit).
261   We followed this with a permutational multivariate analysis of variance (PERMANOVA)
262 using the *adonis* function in the *vegan* package in R to test if there were multivariate community
263 differences both between the two islands and between years.

264

265 2.5.3. Models for Diet Metrics and Marine Conditions, and Fish Condition
266   As with the breeding metrics, we used hierarchical Bayesian regression models to test for
267 differences in average bill load mass (g), and count of prey items per bill load (as a proxy for
268 adult foraging effort (e.g., Fayet et al. 2021)), and average energy content per bill load (kJ), both
269 between the colonies and in different marine conditions. We used linear mixed models for bill
270 load mass and energy content, and a Poisson GLMM for prey item count. These models did not
271 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 June 1 to account for changes in chick age and size, which can influence the amount of food a parent brought 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

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

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

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 June 1 (log-transformed) and the first two principal components 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 June 1 was a random effect. For species whose models had significant results, we did a post-hoc pairwise comparison on the least-square means.

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

3. RESULTS

3.1. Breeding Metrics and Marine Conditions

During the 10 years of our study, we checked an average of 87.9±4.4 burrows per year at Destruction Island (DI), and 95.4±2.6 burrows at Protection Island (PI). Over all years, the two colonies differed in burrow occupancy (DI: 0.59±0.02; PI: 0.67±0.02) and fledging success rates (DI: 0.87±0.02; PI: 0.79±0.04), but not hatching success rates (DI: 0.90±0.02; PI: 0.87±0.02, Figure 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±0.01 vs. 0.61±0.02 in non-MHW years), but *increased* at Protection Island (0.72±0.04 vs. 0.65±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 (Figure 4B, Table 1). Fledging rates at Destruction Island did not differ

between MHW and non-MHW years (0.85±0.02 vs. 0.89±0.05), but at Protection Island they were lower in MHW years (0.71±0.03 vs. 0.82±0.02).

The first two principal components accounted for 61% of the observed variation in the environmental variables (Figure 3). The first principal component (PC_1, 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. The second principal component (PC_2, 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 Salish Sea). The annual values for the principal components detected an initial overall ocean warming in 2014 and by 2015 and 2016 showed a strong MHW signal (Table S2). Prior to 2014, the principal components describe marine conditions that were closer to the mean. Conditions remained warmer once the MHW had dissipated.

By themselves, PC_1 and PC_2 did not correlate with auklet breeding metrics, but there were interactions with the island term, although not consistently. For burrow occupancy, PC_1 had a strong positive interaction with island, while PC_2 had a strong negative 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 hatch success rates, but with fledging rates, PC_1 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_2 (Table 1).

3.2. Diet Metrics
3.2.1. Prey Species Composition

Over seven 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 six 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 analyses showed the two 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: $F = 4.1$, $R^2 = 0.14$, $P = 0.04$, Figure 5). At Protection Island, the two 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 greater than 2%, and other than juvenile salmon, which made up 7% of prey items in 2010, no other species had an average of >5% in a single year (Figure 6A).

Prey species composition at the Destruction Island colony was much more variable over time (Figure 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.

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362
363   3.2.2. Diet Metrics, Fish Condition, and Marine Conditions
364   Although bill loads from the two colonies differed in prey species composition, their
365   mass (DI: 27.9±1.1 g, PI: 29.0±1.0 g) and energy content (DI: 138.0±7.8 kJ, PI: 147.9±8.5 kJ)
366   were similar (Figure 7A, 5C, Table 2). Auklets from Protection Island brought more prey items
367   per bill load in all sample years, however (DI: 3.63±0.4, PI: 6.54±0.8, Figure 7B, Table 2).
368   Between 2015 and 2016, the peak years of the NE Pacific MHW, bill load energy content at
369   Protection Island declined by more than 50% even as the number of prey items per bill load more
370   than doubled. The average mass of individual prey items in bill loads was also less at Protection
371   Island in all years, but increased at both islands as a season progressed, indicating that, generally,
372   adults brought larger prey items to their chicks as they grew (Table 3).
373   We only collected bill loads at Destruction Island during one of the MHW years, and for
374   two years at Protection Island, and the principal components had little explanatory power: the
375   only relationship was PC$_2$, which had a strong negative effect on prey item count, meaning that
376   the more moderate marine conditions were, the fewer prey items auklets brought back to their
377   chicks (Table 2). There were no interactions between the islands and the PCs.
378   Of the six major prey species at Destruction Island, only Pacific sand lance and smelt
379   spp. showed any interannual variation in average fish condition. For sand lance, individuals in
380   2019 were in better condition than 2016 individuals, with no differences among the other years;
381   for smelts, individuals in 2018 and 2019 were in better condition than individuals in 2013
382   (Figure 8, Table 4, Table S3). At Protection Island, Pacific sand lance and Pacific herring
383   showed marked interannual variation in condition (Figure 9, Table 4, Table S3). Notably,
384   individuals of both species that auklets captured were in the poorest condition in 2013 and
385   2017—the two years that bracketed the NE Pacific MHW; they were in the highest condition in
386   2015, during the MHW.
387
388   4. DISCUSSION
389   4.1. Differing Responses in Breeding Metrics Without Catastrophic Declines
390   This study showed the degree to which a species' responses to a large MHW can vary
391   even on relatively small spatial scales. Our hypothesis that the consequences of the NE Pacific
392   MHW for the two colonies might not be identical was supported. However, our prediction that
393   Destruction Island, owing to its location on the outer coast where conditions were more extreme,
394   would be more significantly affected both in terms of burrow occupancy/egg production and
395   fledging success rates, was not supported. Finally, our study suggests that the rhinoceros auklet
396   may have a greater capacity to withstand significant climate perturbations than many other
397   seabirds—particularly other alcids (see Suryan et al. 2021).
398   Breeding metrics at the two islands generally covaried positively in non-MHW years, but
399   during the NE Pacific MHW the islands had differing responses. At Destruction Island, the
400   MHW's main effect was an immediate ~30% decline in burrow occupancy/egg production rates
401   in 2014 and 2015, before they returned to the pre-MHW average in 2016, where they remained.
402   Chick fledging rates dipped somewhat, but the decline during the MHW did not depart
403   substantially from general interannual variation. At Protection Island the response was almost the
404   reverse. There, fledging success rates declined by nearly 50% from 2015 to 2016 before
405   returning to pre-MHW levels in 2017. Occupancy rates declined as well, but neither as steeply
406   nor during the MHW years, reaching a low in the same season that fledging rates recovered,
407   before returning to more typical levels by 2019.

10

408   Since burrow occupancy and egg production rates declined at Destruction Island while
409 fledging rates remained steady, adults at that colony likely skipped breeding due to unfavorable
410 marine conditions, a well-known phenomenon in seabirds (Bradley et al. 2000, Cubaynes et al.
411 2010). The NE Pacific MHW may not have affected the nearshore environment off the
412 Washington coast until 2015 (e.g., Jones et al. 2018), but auklets wintering in offshore waters
413 may have still encountered suboptimal conditions (e.g., Black et al. 2010, Schroeder et al. 2012).
414 What is notable, then, is that auklets returning to Protection Island as the MHW approached its
415 peak in 2015 either did not receive the same non-breeding season signal as those at Destruction
416 Island (e.g., Crossin et al. 2022), or did not heed it, being in good enough body condition to
417 attempt to breed regardless. If this was the case, then it may be because auklets from the two
418 colonies overwinter in different areas (Hipfner et al. 2020).
419   The resulting pattern at Protection Island of decreasing reproductive success for two
420 years followed by a ~20% decrease in burrow occupancy rates in 2017 further suggests that
421 carry-over effects from the NE Pacific MHW may have extended by a year for those auklets and
422 their prey (PSEMP 2017, PSEMP 2018). Although the MHW signature had disappeared by late
423 2016 from surface waters in the Queen Charlotte Sound, British Columbia, for example, warmer
424 temperatures persisted below the surface mixed layer at least through 2018 (Jackson et al. 2018).
425 Additionally, auklets in the Salish Sea underwent an unusual mortality event in 2016 due to an
426 outbreak of septicemia (Knowles et al. 2019). Autopsied adults were often emaciated, but
427 whether it was a result of reduced prey quality and/or availability, weak foraging ability due to
428 illness, or both is uncertain (Pearson et al. *in prep*). Disease outbreaks in marine environments
429 could increase, however, with warming conditions (e.g., Burge et al. 2014).
430   Seabird breeding success frequently declines in response to MHWs, as we observed at
431 Protection Island. Fairy prions (*Pachyptila turtur*) and common diving petrels (*Pelecanoides*
432 *urinatrix*) both showed delayed laying dates, slower chick growth, and reduced breeding success
433 during MHWs in Australia, although the effects were not as pronounced for the prion (Eizenberg
434 et al. 2021). Short-tailed shearwaters (*Ardenna tenuirostris*) exhibited both delayed breeding
435 onset and reduced breeding success in response to a MHW in southern Australia, before being
436 subject to a die-off in response to a MHW in 2019 in the NE Pacific (Glencross et al. 2021).
437   Of note is that, even as rhinoceros auklets at both islands experienced declines in
438 breeding metrics during the NE Pacific MHW, the MHW's consequences were not nearly as
439 catastrophic as they were to other species—even other alcids (e.g., Jones et al. 2018, Piatt et al.
440 2020). Additionally, the dynamic we observed at Destruction Island is the first instance we know
441 of where we see a decline in burrow occupancy and egg production rates without concurrent
442 declines in breeding success. We will explore possible mechanisms for this pattern in the next
443 section, but we recognize that our chick survey methods hinge on visual inspection, which may
444 overestimate fledging success rates. In auklet chicks, the partial feathering stage can last a long
445 time depending on chick feeding and development rates (e.g., Harfenist, 1995). Because we did
446 not measure or weigh auklet chicks, we could not know the condition of those present on our last
447 visit, *i.e.*, whether they were close to a minimum fledging weight.
448
449 4.2. Diet Shifts to Mitigate Climate Impacts
450   Auklet bill loads for chicks from Destruction Island differed from those at Protection
451 Island both in terms of dominant prey species and overall species composition, consistent with
452 historical studies (Wilson & Manuwal 1986). In all years of this study, auklets at Protection
453 Island depended on Pacific sand lance and Pacific herring, but prey species composition at

454 Destruction Island was highly variable across years, shifting from a diet dominated by northern
455 anchovy through 2013 to one made up of mostly smelt species by 2019. Whether the NE Pacific
456 MHW drove this shift is unknown, but anchovy abundance in the California Current has been
457 variable during this period (e.g., Harvey et al. 2020).
458   The ability to take advantage of an expanded prey pool may serve to insulate auklets at
459 Destruction Island against extreme events that affect the abundance or condition of one or two
460 prey species (Kondoh 2003). Auklets eat mostly pelagic forage fish, but as generalists, adults in
461 this study brought back squid, juvenile rockfish, and other species more commonly associated
462 with benthic nearshore environments (e.g., Hexagrammidae spp.). Auklets may also specialize
463 more in a particular foraging location than on a target species in an effort to maximize bill load
464 mass and energy, resulting in the capture of more variable prey species (Cunningham et al.
465 2018). Additionally, Suryan et al. (2002) suggested that interannual variation in environmental
466 forcing creates a threshold above which a seabird's parental behavior can flexibly accommodate
467 shifts in the prey base.
468   At Protection Island, there was no such shift in prey species composition. During the two
469 years that sampling overlapped with the NE Pacific MHW, sand lance and herring comprised
470 ~90% of auklet bill loads, as they did in other years. This dependence suggests the Salish Sea is a
471 wasp-waisted system (Cury et al. 2000, Therriault et al. 2009), in which an intermediate trophic
472 level controls the abundance of predators through a bottom-up interaction. Although sand lance
473 and herring have different life history strategies (e.g., timing of spawning, being migratory or
474 non-migratory), the NE Pacific MHW may have overwhelmed their capacity to buffer against
475 environmental variance (e.g., Arimitsu et al. 2022).
476   Both sand lance and herring in the Salish Sea fluctuate in abundance depending on their
477 environment, with pronounced declines in fish condition due to anomalous warming (Baker et al.
478 2019); herring in particular underwent steep population declines during the NE Pacific MHW
479 and did not apparently recover until 2019 (Frick et al. 2022). Because rhinoceros auklets only
480 deliver on average one bill load per parent to their chick each night (Wilson 1977), they do not
481 have the opportunity to compensate with more bill-loads per day should prey be difficult to find
482 or of poor quality, unlike diurnal provisioning common murres (*Uria aalge*) and tufted puffins
483 (*Fratercula cirrhata*) (Schrimpf et al. 2012, but see Gjerdrum et al. 2003). One way for
484 rhinoceros auklets to offset a poorer energy-per-prey-item relationship is to bring back more
485 items per bill load, in which case there is likely a physical limit to the amount of prey they can
486 effectively carry (e.g., Watanuki et al. 2022). Alternatively, they could try to capture more
487 energy-rich species, although doing so could confer an energetic cost to adults, as they may have
488 to fly farther to reach optimal foraging sites or spend more time hunting once they get there (*e.g.*,
489 Ballance et al. 1997, Davoren 2000).
490   We only sampled diets during one of the MHW seasons at Destruction Island in the
491 California Current, but bill-load characteristics did not differ from other years and reproductive
492 success rates were similar. At Protection Island, however, bill load characteristics showed a clear
493 effect of the MHW. Even as the condition of the sand lance and herring auklets captured did not
494 immediately decline compared to non-MHW years, the individual fish were smaller. Sand lance
495 and herring condition was highest in 2015, which is evidence that auklets were able to target
496 higher-condition prey in that year at least, since nearby beach seine surveys found sand lance
497 condition to be poor relative to pre-MHW baseline data (Baker et al. 2019). However, as fish
498 size declined, the number of fish per auklet bill load doubled in 2016 and then nearly tripled in
499 2017 compared to 2015. At the same time, the average bill load energy content relative to 2015

500 was 35% lower in 2016 and 25% lower in 2017—a sign that increased foraging effort was not
501 yielding an energetic payoff. All of this coincided with the colony's lowest fledging success
502 rates.
503
504 4.3. Resilience in the Face of Unfavorable Marine Conditions
505   Alcids were among several seabird families to be hard-hit during the NE Pacific MHW
506 (e.g., Jones et al. 2019, Tate et al. 2021, Van Hemert et al. 2021). Previous research has
507 suggested a correlation between physical forcing in general and reproductive success and
508 periodic die-offs in seabirds. The foraging ranges of black-legged kittiwakes (*Rissa tridactyla*)
509 increased in years of poor food availability, for example, and led to declines in breeding success
510 (Hatch 2013). An abnormally late spring transition to upwelling conditions in 2005 led to
511 severely reduced NPP (Barth et al. 2007), which resulted in breeding failures in marbled
512 murrelets (*Brachyramphus marmoratus*) in British Columbia (Ronconi & Burger 2008) and nest
513 abandonment in Cassin's auklets (*Ptychoramphus aleuticus*) throughout the California Current
514 (Sydeman et al. 2006). Similarly, from California, U.S.A. to British Columbia, Canada, Cassin's
515 auklets experienced an unusual mortality event as a result of warm-water intrusions from the NE
516 Pacific MHW into the nearshore environment. This led to a shift in the zooplankton community
517 composition away from a northern copepod assemblage to smaller southern copepods, as well as
518 reducing the mean size of adult euphausiids and overall abundance (Jones et al. 2018, Phillips et
519 al. 2022).
520   While the NE Pacific MHW clearly affected both breeding and diet metrics at the two
521 auklet colonies, it did not do so consistently, synchronously, or even that strongly. We thus did
522 not find a pronounced relationship between these metrics and a PCA of marine conditions.
523 Where breeding metrics are concerned, this was likely because the MHW's effects were evident
524 for only two of its three years at each island, and then with different stages: burrow occupancy
525 rates at Destruction Island in 2014 and 2015, and fledging success rates at Protection Island in
526 2015 and 2016. Subsequent declines in burrow occupancy at Protection Island took place after
527 the MHW was supposed to have ended; furthermore, occupancy rates were higher *during* parts
528 of the NE Pacific MHW, making it appear MHW-like conditions increased burrow occupancy.
529 However, the decline in breeding success at Protection Island was enough for there to be a
530 negative relationship between ocean warming and breeding performance, consistent with many
531 other studies.
532   Rhinoceros auklets have shown a sometimes idiosyncratic relationship with marine
533 conditions (*e.g.*, Morrison et al. 2011). Bertram et al. (1991), for example, found that while there
534 could be substantial interannual variation in provisioning and chick growth rates at breeding
535 colonies in British Columbia, those variations did not necessarily reflect fluctuations in the
536 marine environment. Hedd et al. (2006), on the other hand, found a clear association between
537 spring SSTs and auklet reproduction at Triangle Island, British Columbia, as chick growth rates
538 decreased with increasing SSTs. They hypothesized this was due to temperature-dependent
539 recruitment of sand lance, since years with high auklet breeding success were linked to sand
540 lance-dominated chick diets. In another study of the same colony, Borstad et al. (2011) found
541 that the relationship between breeding success and SST may have been correlative rather than
542 causal and that an early spring transition date was more predictive. Breeding colonies in the
543 southern portion of the California Current have also exhibited a relationship between bill load
544 mass and SSTs (Thayer & Sydeman 2007). Finally, auklets have shown behavioral flexibility in
545 the past when confronted with poor marine conditions. Their chick-rearing period of ~50 d is

546 long compared to other alcids (e.g., ~48 d for tufted puffins, a larger species; Piatt & Kitaysky
547 2002). During the 1997/98 El Niño, for example, auklets at the Protection Island colony were
548 able to maintain average rates of fledging success by extending that rearing period still more,
549 even as chick average growth rates were significantly lower (Wilson 2005).
550
551 4.4 Conclusions
552   Rhinoceros auklets in Washington withstood the NE Pacific MHW's major
553 environmental shifts without experiencing significant or durable declines in breeding
554 performance. Their capacity to do this—whether by skipping breeding, relying on an expanded
555 prey portfolio, increasing foraging effort, and / or extending their chicks' rearing period—varied
556 between the two colonies we studied. As indicated by the higher diversity of prey items at
557 Destruction Island, the California Current is a prey-rich system, and auklets there could change
558 their diet without a substantial effect on breeding success. In the wasp-waisted Salish Sea,
559 however, the energy available to chicks was constrained by the abundance and condition of
560 Pacific sand lance and herring (Bertram & Kaiser 1993, Therriault et al 2009, Selleck et al.
561 2015).
562   Although auklets at Protection Island have weathered poor marine conditions in the past
563 (e.g., the 1997/98 El Niño, Wilson 2005), and suffered no apparent ill effects in the first year of
564 the NE Pacific MHW, by its final year, the combination of decreased food availability/quality
565 and the rise of a lethal bacterial pathogen (Knowles et al. 2019, Pearson et al. *in prep*) proved too
566 much to endure without some consequence to breeding metrics. The subsequent decrease in
567 burrow occupancy rates *after* the MHW and unusual mortality event suggests a possible
568 population-level decline, *i.e.*, a lack of available breeders, as opposed to adult birds simply
569 choosing not to breed. Still, auklets at both colonies showed the ability to adapt to the NE Pacific
570 MHW. Whether they can endure the more frequent, intense, or longer-lasting MHWs predicted
571 to occur under future climate scenarios remains an open question.

TABLES

Table 1. Parameter estimates (mean and 95% credible interval [CI] in parentheses) from binomial GLMMs for rhinoceros auklet breeding metrics at Protection Island and Destruction Island. Positive main effect values: increased effect at Protection Island. Hierarchical variance components — σ_{site}: among-site intercept SD; σ^{α}_{year}: interannual SD of the intercept; σ^{β}_{year}: island effect; ρ_{year}: interannual correlation between σ^{α}_{year} and σ^{β}_{year}. Bold: 95% Cis of main effects that did not overlap with zero, indicating strong support. Italics: 95% CIs of main effects that only slightly overlapped with zero, indicating weak support.

Parameter	Burrow occupancy	Hatching success	Fledging success
Intercept (α)	0.39 (0.12, 0.66)	2.3 (1.75, 2.91)	1.91 (1.44, 2.43)
Island (β)	*0.31 (-0.04, 0.66)*	-0.29 (-0.91, 0.30)	*-0.45 (-1.02, 0.08)*
PC$_1$ (γ_1)	-0.02 (-0.18, 0.14)	0.14 (-0.39, 0.64)	-0.07 (-0.52, 0.38)
PC$_2$ (γ_2)	-0.05 (-0.29, 0.19)	0.11 (-0.63, 0.89)	0.36 (-0.24, 1.03)
Island x PC$_1$ (φ_1)	**0.26 (0.04, 0.49)**	-0.32 (-0.83, 0.17)	*-0.38 (-0.81, 0.08)*
Island x PC$_2$ (φ_2)	**-0.35 (-0.67, -0.03)**	0.20 (-0.55, 0.94)	0.21 (-0.47, 0.88)
σ_{site}	0.27 (0.12, 0.48)	0.31 (0.02, 0.67)	0.26 (0.02, 0.58)
σ^{α}_{year}	0.09 (0.01, 0.30)	0.55 (0.16, 1.15)	0.47 (0.11, 1.04)
σ^{β}_{year}	0.09 (0.01, 0.32)	0.33 (0.05, 0.88)	0.38 (0.05, 0.96)
ρ_{year}	-0.2 (-0.98, 0.92)	-0.12 (-0.95, 0.92)	-0.19 (-0.94, 0.89)

Table 2. As in Table 1, but for GLMMs of rhinoceros auklet bill load metrics. 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 (α)	13.29 (-0.55, 27.03)	1.25 (0.70, 1.78)	1.69 (-9.50, 12.97)
Island (β)	-0.12 (-3.78, 3.03)	**0.62 (0.19, 1.09)**	0.35 (-8.30, 8.95)
PC$_1$ (γ_1)	0.23 (-2.70, 3.99)	-0.01 (-0.52. 0.48)	0.37 (-7.74, 8.50)
PC$_2$ (γ_2)	-1.32 (-4.19, 2.38)	-0.17 (-0.75 -0.39)	-3.76 (-12.25, 5.36)
Island x PC$_1$ (φ_1)	0.68 (-2.88, 4.06)	-0.11 (-0.61, 0.31)	-0.11 (-8.66, 8.39)
Island x PC$_2$ (φ_2)	0.48 (-4.19, 2.38)	0.23 (-0.29, 0.71)	-0.73 (-9.36, 8.06)
σ_{week}	15.45 (2.86, 33.86)	0.13 (0.01, 0.39)	146.07 (91.33, 236.86)
σ_{year}^{α}	2.04 (0.04, 12.90)	0.44 (0.17, 1.02)	12.74 (0.60, 34.61)
σ_{year}^{β}	1.64 (0.04, 6.50)	0.37 (0.10, 0.92)	11.36 (0.52, 34.42)
ρ_{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)

610 Table 3. As in Table 1, but for a linear mixed model of average prey item size per bill load by
611 island as the breeding season progressed. Hierarchical variance components — σ^{α}_{year}:
612 interannual SD of the intercept; σ^{β}_{year}: island effect; ρ_{year}: interannual correlation between σ^{α}_{year}
613 and σ^{β}_{year}. Bold: 95% Cis of fixed effects that did not overlap with zero.
614

Parameter	*Size*
Intercept (α)	6.65 (1.04, 11.89)
Island (β_1)	**-4.14 (-7.32, -0.73)**
Log(Week) (β_2)	**2.87 (0.52, 5.18)**
PC$_1$ (γ_1)	0.86 (-2.39, 4.67)
PC$_2$ (γ_2)	0.44 (-4.01, 5.29)
σ^{α}_{year}	5.11 (1.74, 11.66)
σ^{β}_{year}	5.33 (2.6, 9.91)
ρ_{year}	-0.59 (-0.98, -0.34)
R^2	0.23 (0.03, 0.5)

615
616

617 Table 4. Results from linear mixed-effects models on annual average Fulton's *K* factor scores for
618 major prey species at Destruction and Protection Island. Species in bold had significant results,
619 and the pairwise least-square means for each year were then compared (see Table S3).
620

| *Island*	*Species*	*Variable*	*Df*	*Sum Sq*	*Mean Sq*	*F*	*P*
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		
	Pacific Sand Lance	Year	3	0.02	0.008	2.63	**0.04**
		Residuals	75	0.35	0.005		
	Smelt spp.	Year	4	0.17	0.05	3.27	**0.01**
		Residuals	166	2.21	0.01		
Protection Island	**Pacific Sand Lance**	Year	6	0.55	0.09	25.3	**<0.00001**
		Residuals	976	3.55	0.004		
	Pacific Herring	Year	6	1.73	0.29	8.73	**<0.00001**
		Residuals	262	8.63	0.03		

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623   FIGURES
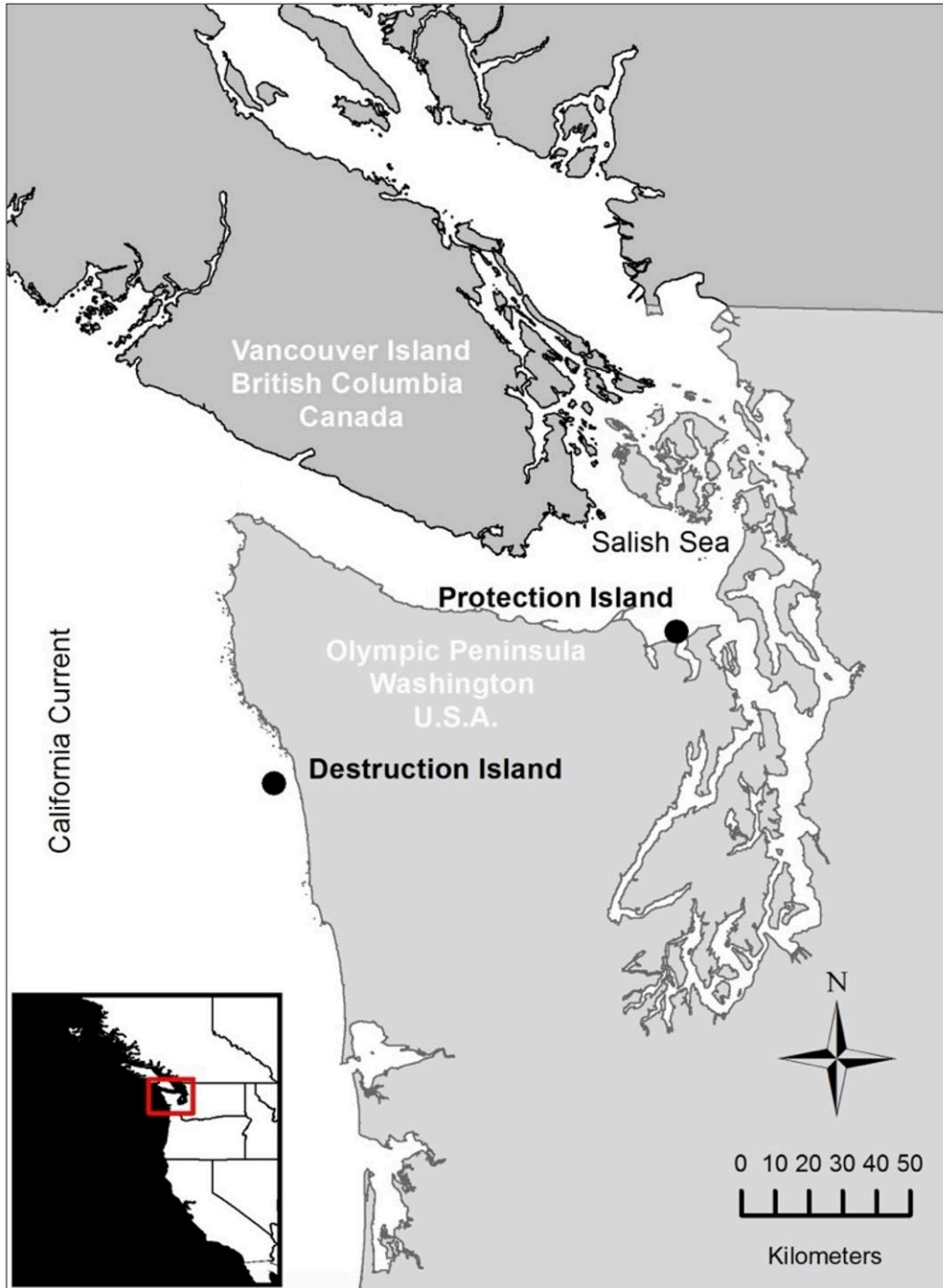
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626   Figure 1. The two rhinoceros auklet (*Cerorhinca monocerata*) colonies included in this study.
627   Protection Island (48°08'N, 122°55'W), in the Salish Sea, hosts ~36,000 breeding pairs per year,
628   while on the outer coast, Destruction Island (47°40'N, 124°24'W), in the California Current,
629   hosts ~6,500 breeding pairs.
630
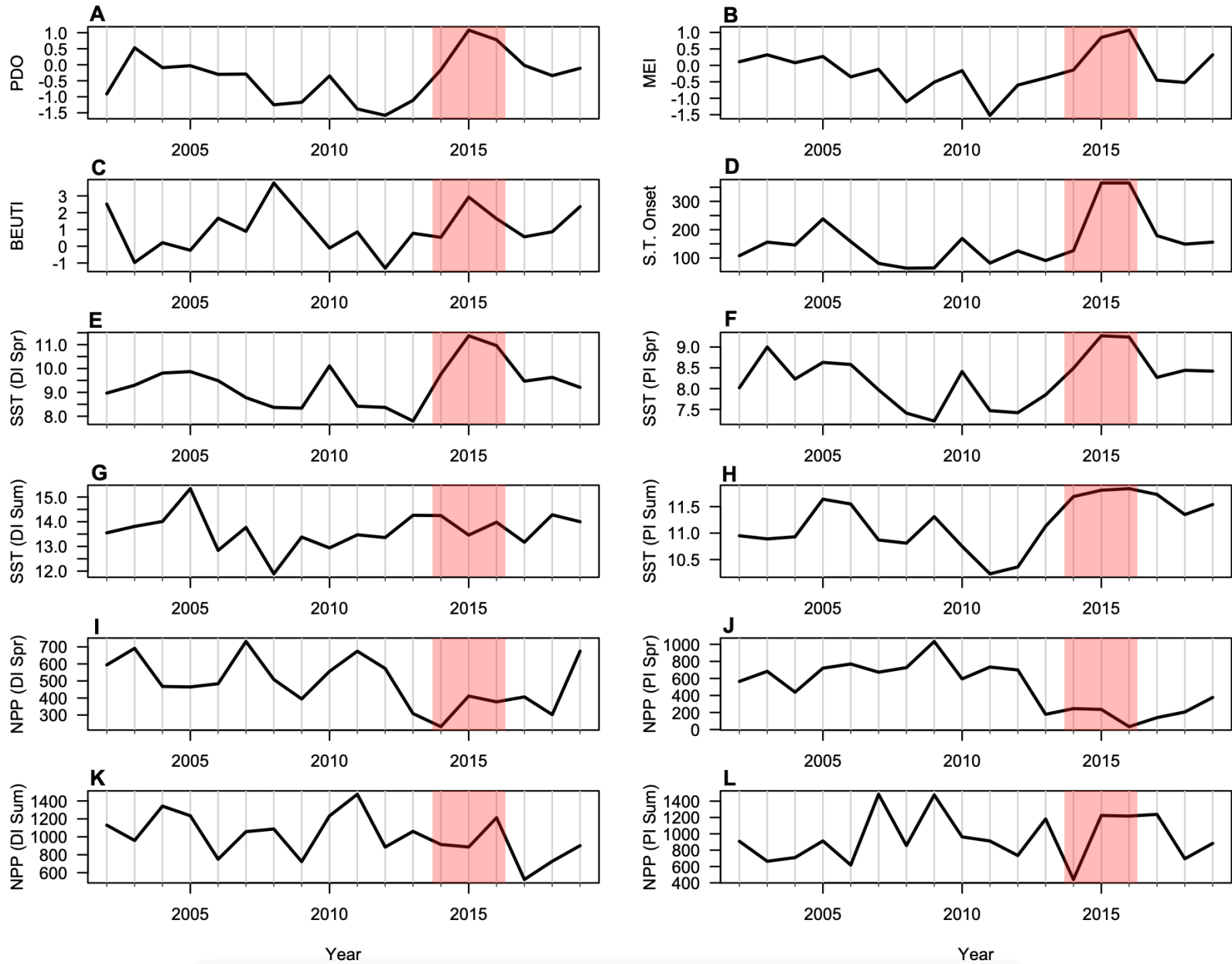
Figure 2. Environmental predictors included in principal components analysis (PCA). Graph shows all years used to build the PCA, starting in 2002; the study years were 2010 – 2019. The red bar in each graph brackets the years affected by the NE Pacific marine heatwave (2014 – 2016). Predictor and data source: A) Pacific Decadal Oscillation (PDO), from NOAA Extended Reconstructed Sea Surface Temperature v. 3b. B) Multivariate El Niño Index (MEI), from XX. C) Biologically Effective Upwelling Transport Index (BEUTI), from Michael Jacox. D) The onset of the Spring Transition (S.T. Onset), from the Northwest Fisheries Science Center Ocean Ecosystem Indicators. E – H) Island-specific sea surface temperature from February through April (DI / PI Spr) and May through August (DI / PI Sum) from the MODIS-Aqua satellite from NASA. I – L) Island-specific values from Carbon-based Productivity Model of Net Primary Production (NPP) with the same seasonal ranges as SST, from the Oregon State University Ocean Productivity Group. See Methods for fuller description of how predictors were tabulated.
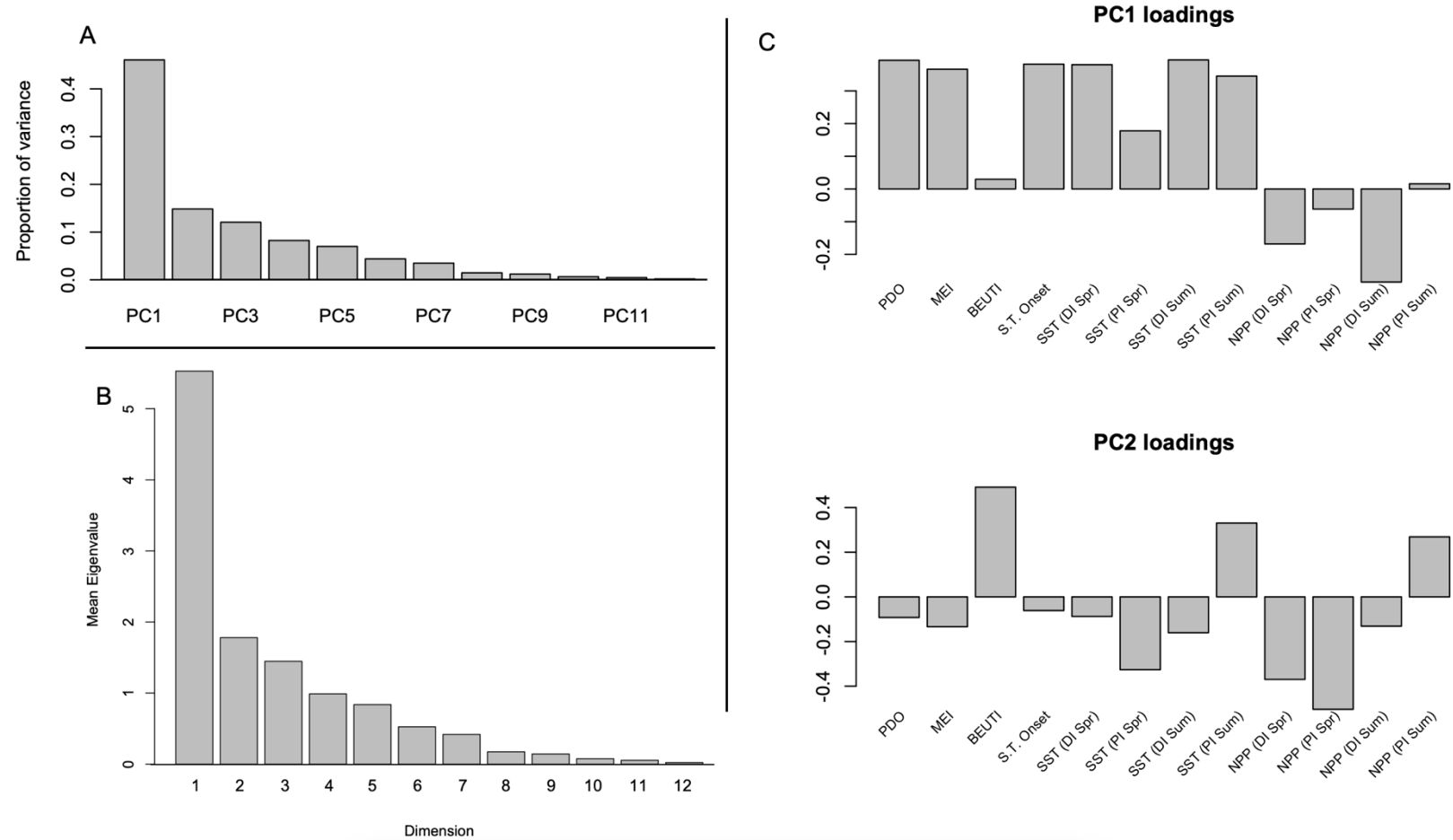
Figure 3. Principal Component Scores and Loadings of environmental predictors. See Methods for more detailed descriptions of the environmental predictors. A) Proportion of variance explained by each principal component. B) Mean eigenvalues. C) Loadings for the first two principal components. Abbreviations are the same as in Figure 2. The first principal component, PC_1, accounts for 45% of the variance and depicts the conditions found during the NE Pacific marine heatwave: positive PDO and MEI, higher sea surface temperatures, a delayed spring transition onset (or not transition at all), etc. The second principal component, PC_2, accounts for 16% of the variance and captures more generally moderate marine conditions.

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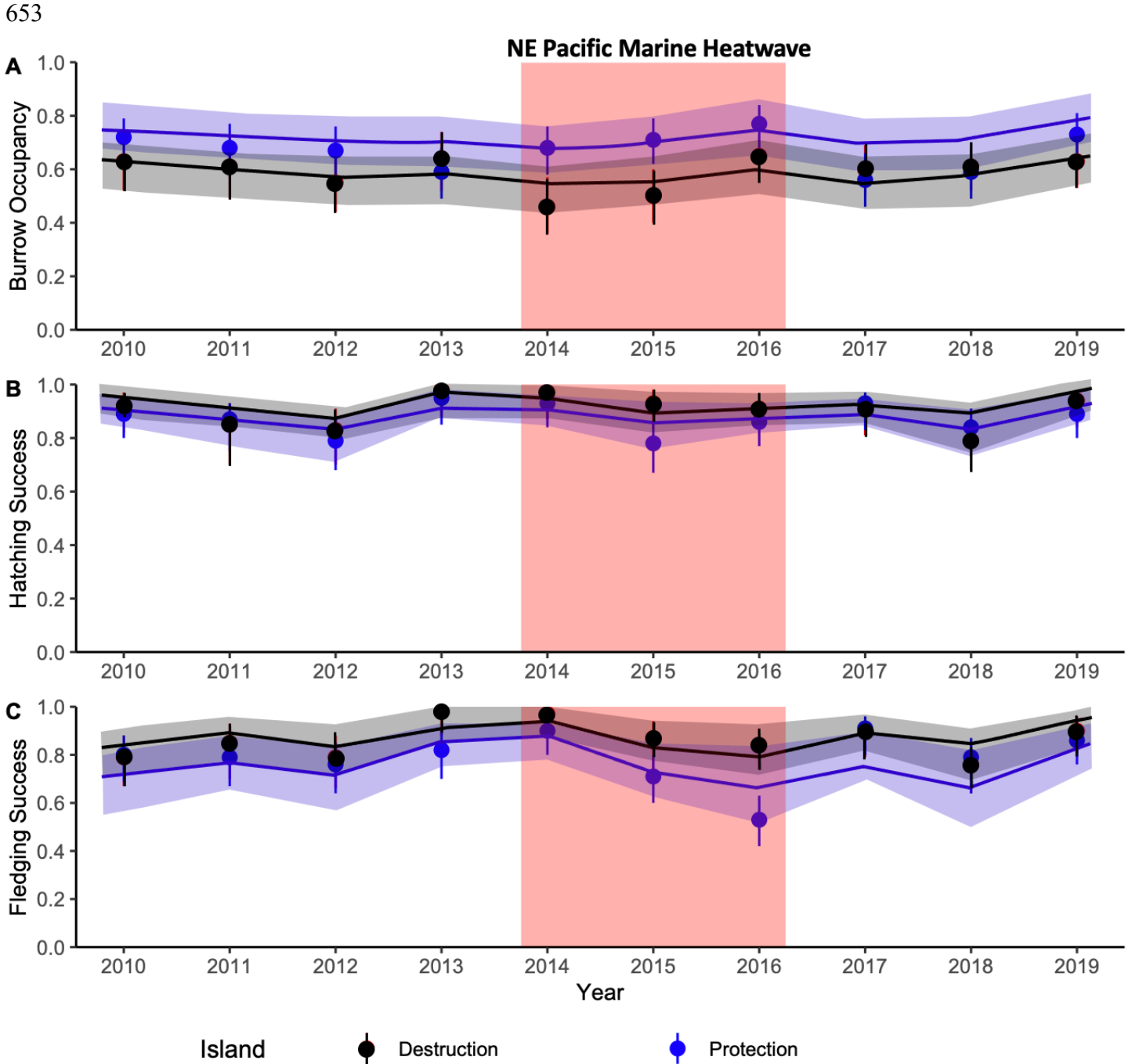
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655 Figure 4. Times series plots for rhinoceros auklet breeding metrics at Protection Island (Salish
656 Sea) and Destruction Island (California Current). A) Burrow occupancy; B) Hatching success; C)
657 Fledging success. Points are the annual observed proportions of burrow occupancy, hatching
658 success, and fledging success rates, with error bars showing sample binomial 95% confidence
659 intervals. The solid line is the posterior median of the fitted values and the shaded ribbon is the
660 95% credible interval. In each panel, a shaded red column shows the three seasons (2014 – 2016)
661 of the NE Pacific marine heat wave.
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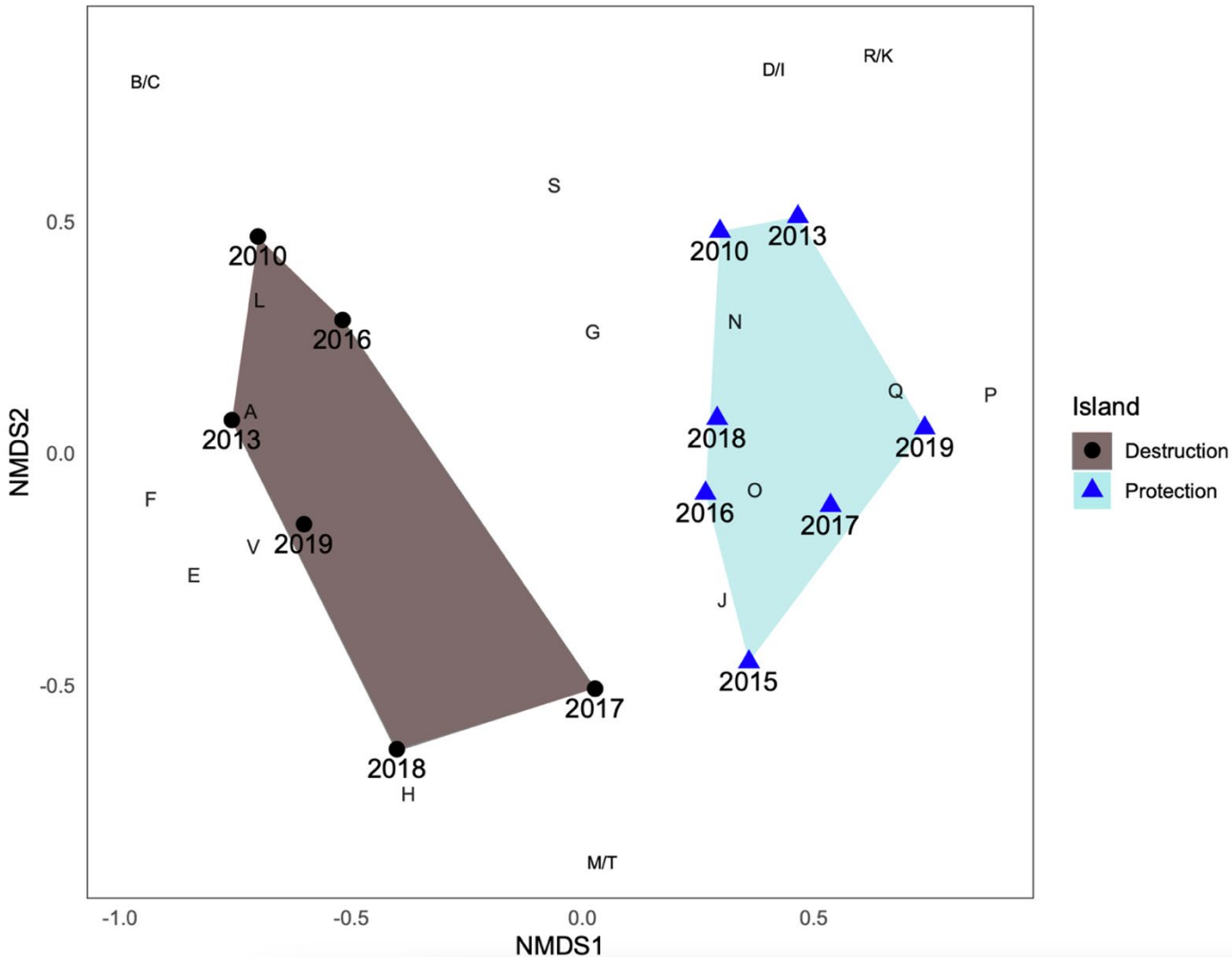
Figure 5. A hull plot showing nonmetric multidimensional scaling (NMDS) ordinations for annual differences in prey species composition for rhinoceros auklets at Destruction Island (California Current) and Protection Island (Salish Sea). Convex hulls show items in a class (here, the islands' distinct compositions). For the purposes of clarity, letters denote species' names to lowest identifiable taxonomic level: A) Northern Anchovy *(Engraulis mordax)*; B); Slender Barricuda (*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 (*Stenobrachius leucopsarus*); I) Market Squid (*Doryteuthis opalescens*); J) Pacific Herring (*Clupea pallasii*); K) Snake Prickleback (*Lumpenus sagitta*); L) Unknown Rockfish Juveniles (Family: Sebastinae); M) Search (*Bathymaster signatus*); N) Unknown Salmonid (Family: Salmonidae) ; O) Pacific Sand Lance (*Ammodytes hexapterus*); P) Shiner Perch (*Cymatogaster 24ggregate*); Q) Unknown Squid (Order: Teuthida); R) Three-spine Stickleback (*Gasterosteus aculeatus*); S) Surf Smelt (*Hypomesus pretiosus*); T) Unknown Hexagrammid (Family: Hexagrammidae); U) Whitebait Smelt (*Allosmerus elongatus*); V) Other. Letters separated by a slash (/) would otherwise occupy the same space.

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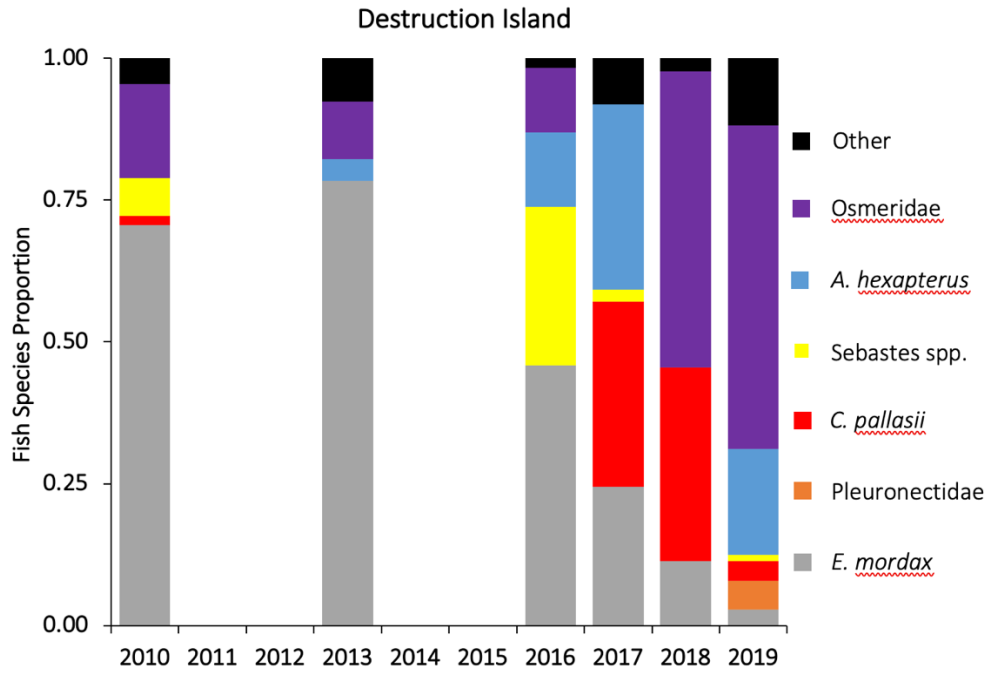
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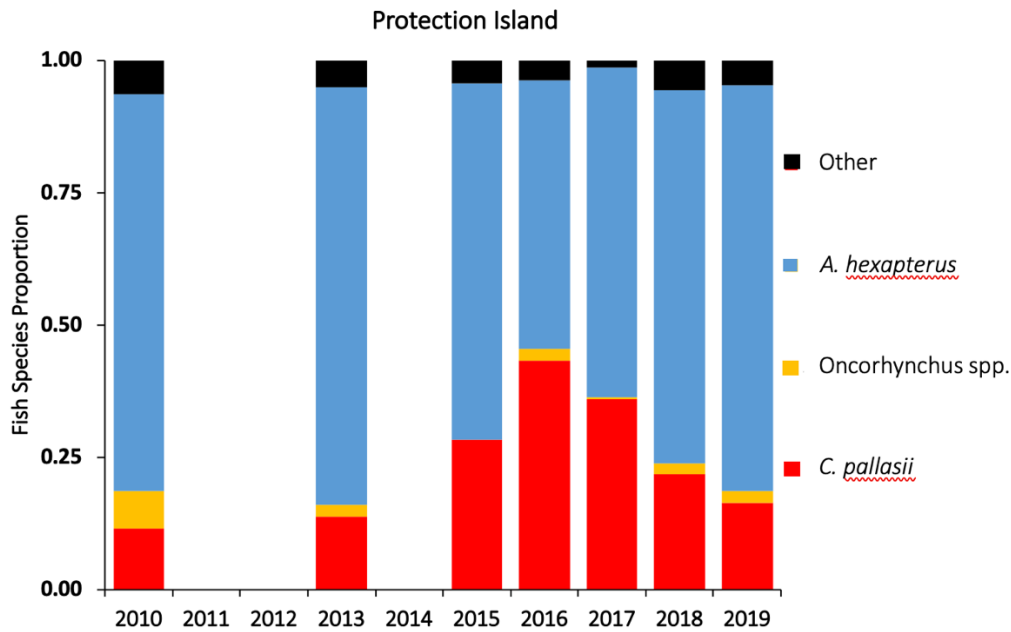
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685 Figure 6. Stacked bar plots of major prey species in rhinoceros auklet bill loads from Destruction
686 Island (California Current, top) and Protection Island (Salish Sea, bottom). Major prey species
687 were defined as those present in >5% of bill loads for at least one year of the sample period.
688 Osmeridae are smelt species, Sebastes are rockfish species, and Pleuronectidae are flatfish
689 species. Error bars are standard error. See Table S1 for full list of species found in auklet bill
690 loads.

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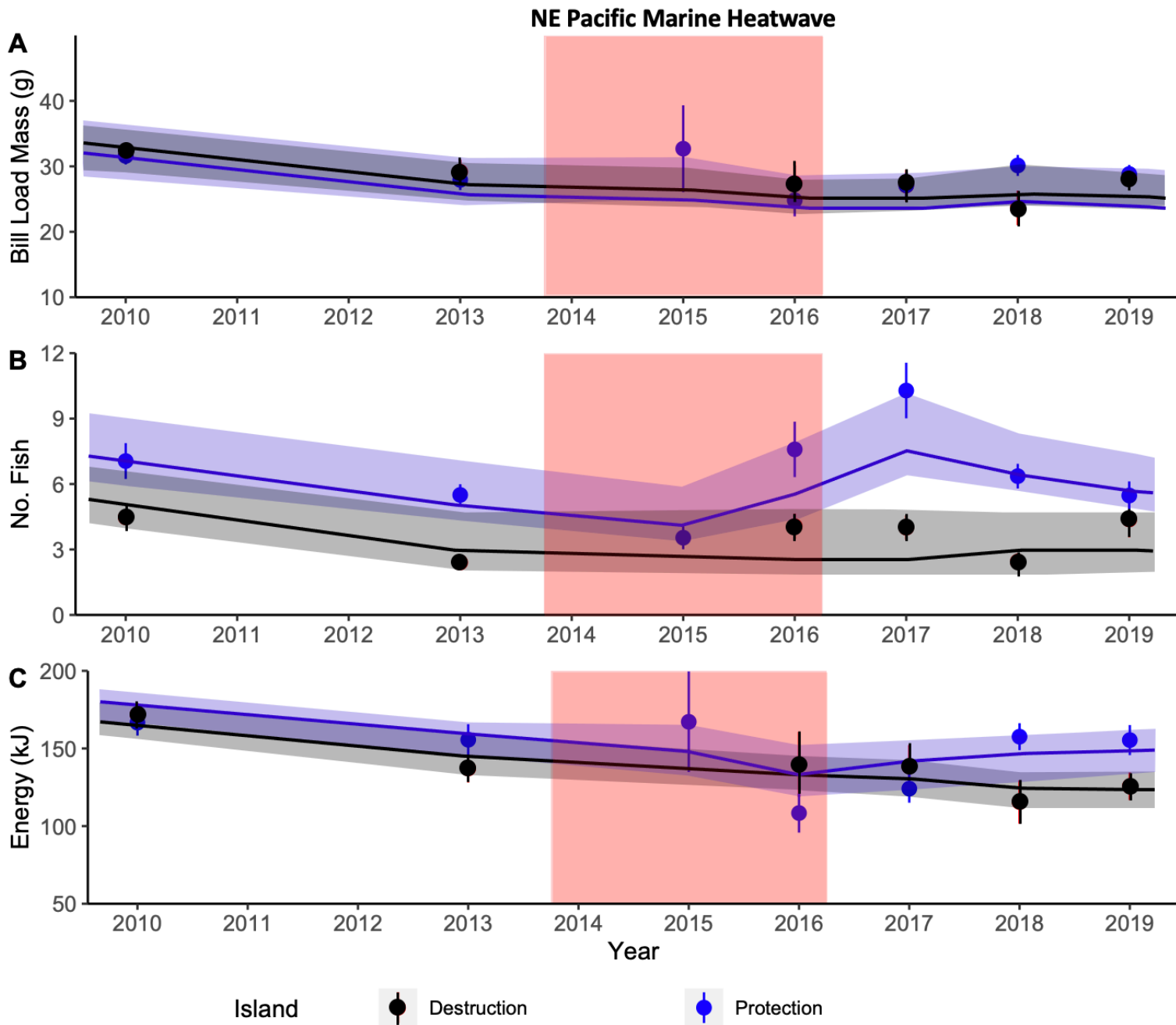
Figure 7. Time series plots of diet metrics for rhinoceros auklet colonies on Protection Island (Salish Sea) and Destruction Island (California Current). A) Average bill load mass (g); B) average number of prey items per bill load; C) average bill load energy content (kJ). Points are annual means and 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. In each panel, the shaded red column shows the three seasons (2014 – 2016) affected by the NE Pacific marine heat wave.

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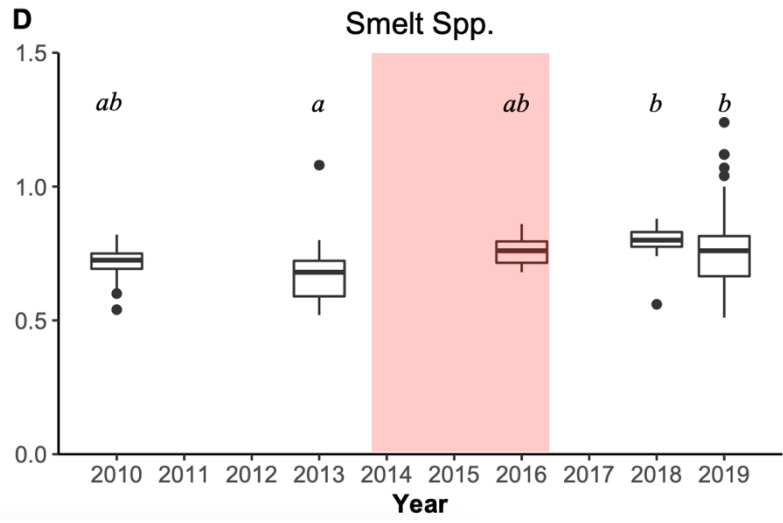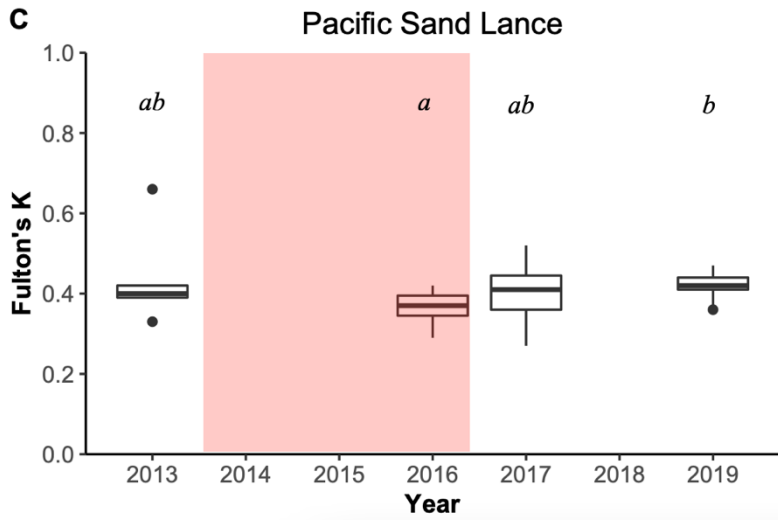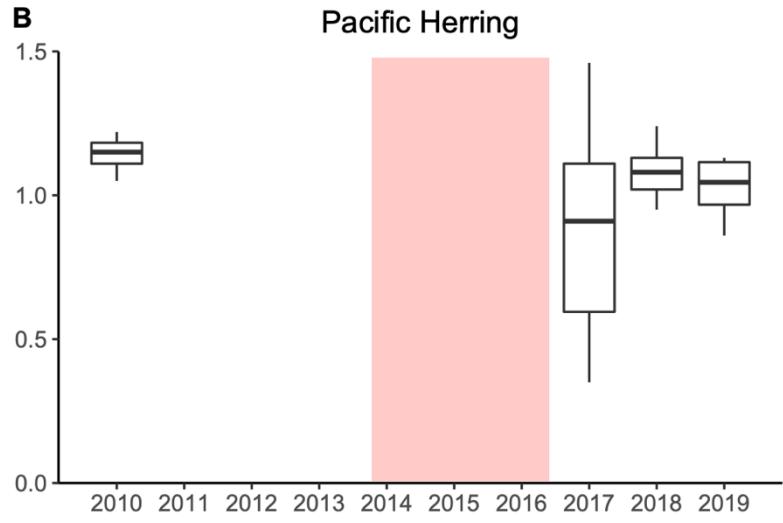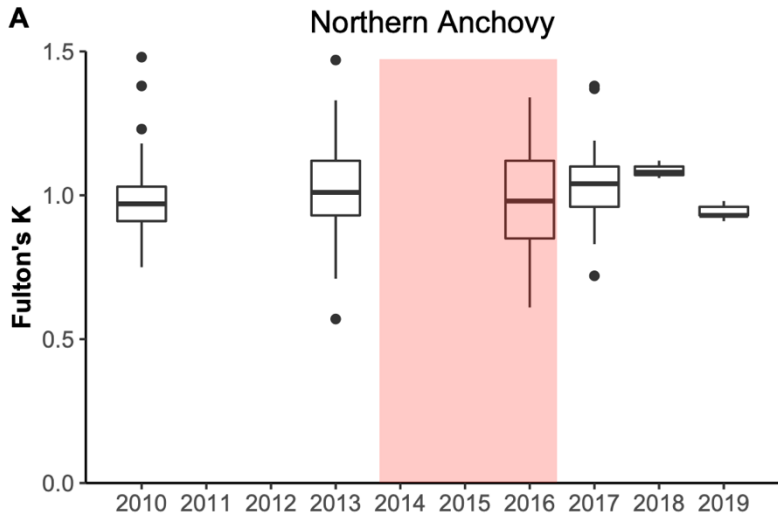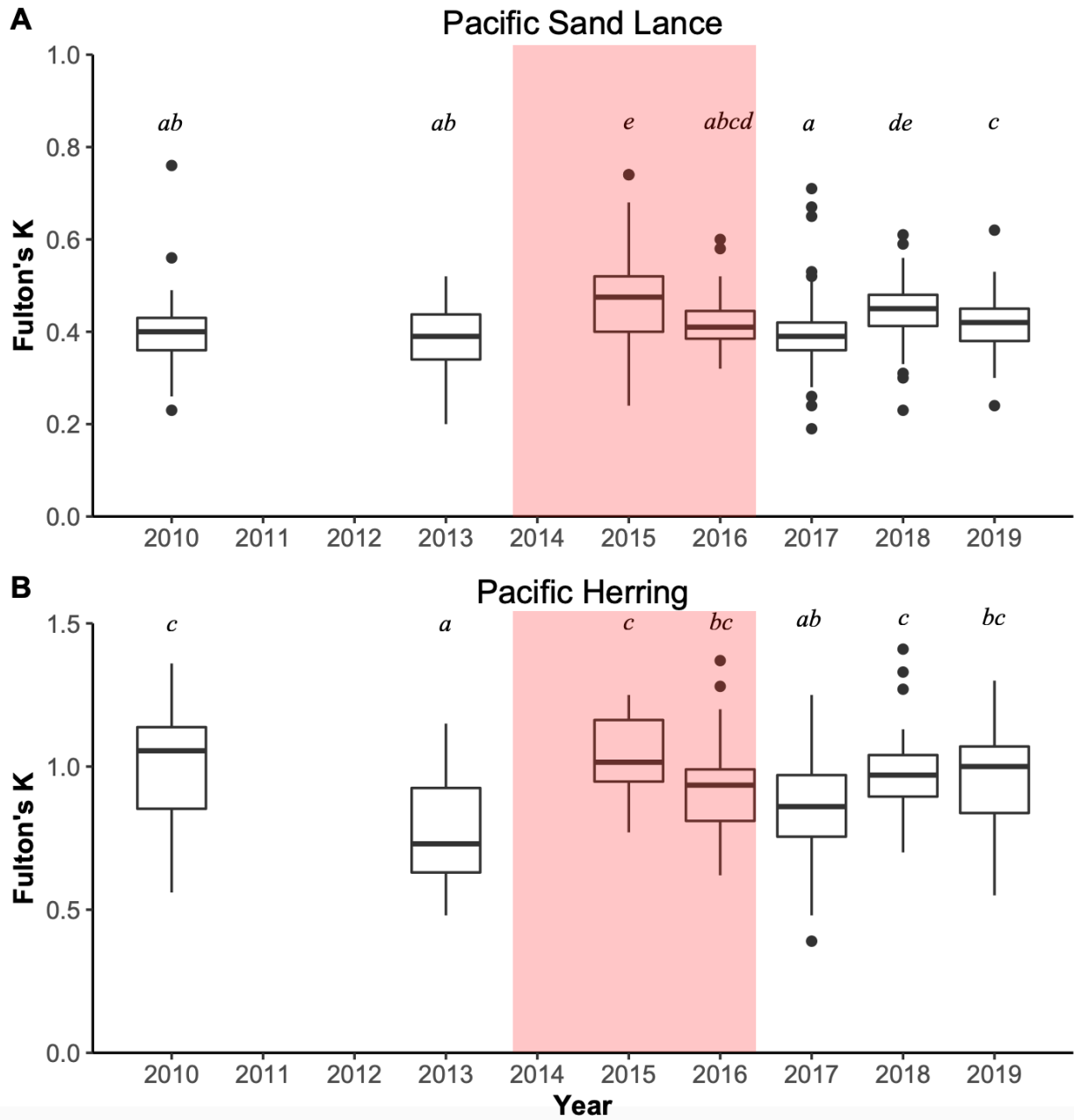
Figure 9. The same scheme as Figure 8, but for Protection Island. A) Pacific sand lance. B) Pacific herring.

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1055 Wagner et al. Supplemental Information
1056 Table S1
1057 See Attached Excel Workbook
1058   List of prey to the lowest taxon identifiable and their energy contents as determined by
1059 bomb calorimetry in 2009. With northern lampfish (*Stenobrachius leucopsarus*) and Pacific
1060 lamprey (*Lampetra tridentatus*), the dried fishmeal was too oily for pellet formation and reliable
1061 energy densities were not obtained, so we used the value of 8050 J/g wet-mass from Van Pelt et
1062 al. (1997). For species for which we did not have whole samples collected by the end of the 2009
1063 season, we used an average of all energy densities from all fish. For partial fish that were only
1064 identifiable to higher taxonomic categories (i.e. genus or family), we estimated energy density by
1065 averaging the values for all species in that category represented in the auklet diet.
1066   If a significant linear regression between length and energy density (defined by $R^2 > 0.5$
1067 and $P < 0.05$) existed for any of the prey identifiable to species, we used the regression
1068 parameters to calculate length-specific energy densities for each individual of that species. In all
1069 other cases, we averaged the energy densities to obtain a representative value for each species.
1070 Both Pacific herring (*Clupea pallasii*) and northern anchovy (*Engraulis mordax*) showed step-
1071 wise length vs. energy density patterns, with the step at lengths corresponding to the age-0 to
1072 age-1 transition described in the literature (herring: 120 mm SL, Foy & Paul 1999; anchovy: 95
1073 mm SL, Hart 1973, Litz et al. 2008). Above the transition, both species had a higher and more
1074 variable energy density that was not related to length (herring: $R^2 < 0.0001$, $P = 0.907$; anchovy:
1075 $R^2 < 0.0001$, $P = 0.988$). Below the transition, the relationship between length and energy density
1076 was linear and significant for herring ($R^2 = 0.88$, $P < 0.001$), but noisier for anchovy ($R^2 = 0.30$, P
1077 $= 0.158$), probably due to low sample size ($N = 8$). Tirelli et al. (2006) found a similar
1078 relationship between length and energy density for European anchovy (*E. encrasicolus*), with a
1079 similar step-wise increase in variability. We therefore used the age-class transitions from the
1080 literature to separate herring and anchovy into age-0 and age-1+ categories to estimate energy
1081 density and applied the same decision rules ($R^2 > 0.5$; $P < 0.05$) to determine whether to use
1082 regression parameters or energy density averages.
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Table S1.

Species (Common)	Species (Scientific)	Length (mm) [mean]	W-Weight (g) [mean]	W-Weight [SE]	W-Weight n	L-W R^2	L-W a	L-W b	L-W n	Energy (J/g ww) [mean]	Energy [SE]	Energy n	L-E R^2	L-E β_0	L-E β_1	L-E n
bay pipefish	*Syngnathus griseolineatus*	149.0	1.3		1					5706.2		1				
cabezon	*Scorpaenichthys marmoratus*	41.0	2.1		1					4719.4		1				
pacific sandfish	*Trichodon trichodon*	77.0	6.9	0.9	4	0.925	1.47E-04	2.471	4	3889.3	41.9	3	1.000	3084.8	16.3	3
pacific sandlance	*Ammodytes hexapterus*	85.4	2.9	0.0	2898	0.970	8.73E-07	3.335	2891	5231.9	233.0	32	0.667	1792.6	63.6	32
pacifc saury	*Cololabis saira*	122.5	7.5	0.6	17	0.967	7.71E-06	2.857	17	5813.3	138.0	11	0.124	8712.4	7.8	11
sablefish	*Anoplopoma fimbria*	62.0	4.1	2.1	9	0.957	2.27E-05	2.829	9	3357.5	325.1	5	0.155	2623.5	9.7	5
slender barracudina	*Lestidium ringens*	94.0	0.9		1											
snake prickleback	*Lumpenus sagitta*	194.0	18.5		1					5713.4		1				
three-spine stickleback	*Gasterosteus aculeatus*	67.0	3.1	0.4	2					3875.0	492.6	2				
tube-snout	*Aulorhynchus flavidus*	120.5	2.6	0.3	2					4152.3	201.4	2				
northern lampfish	*Stenobrachius leucopsarus*	59.3	2.3	0.7	4	0.990	1.49E-06	3.458	4							
all clupeoids	Family: Clupeidae	94.0	10.5	0.3	977		3.69E-06	3.213		5157.6						
CLUP age-0	Family: Clupeidae									4196.1						
CLUP age-0-1	Family: Clupeidae									5077.2						
CLUP age-1	Family: Clupeidae									6199.5						
northern anchovy	*Engraulis mordax*	100.2	11.2	0.3	472	0.955	4.04E-06	3.189	471	5714.2	294.2	26				
northern anchovy, age-0	*Engraulis mordax*									4494.2	115.1	8	0.302	2647.8	22.1	8
northern anchovy, age-1	*Engraulis mordax*									6256.5	353.8	18	0.000	6215.7	0.3	18
pacific herring	*Clupea pallasii*	88.2	9.9	0.5	505	0.979	3.34E-06	3.237	499	4558.1	216.2	34				
pacific herring, age-0	*Clupea pallasii*									3897.9	100.6	24	0.881	2266.9	19.7	24
pacific herring, age-1	*Clupea pallasii*									6142.6	354.3	10	0.002	5515.9	4.4	10
all cod	Family: Gadidae	61.7	2.4	0.5	33		1.40E-06	3.447		3561.9						
pacific cod	*Gadus macrocephalus*	85.0	7.1	4.1	3	0.985	7.18E-07	3.573	3	3604.3	230.3	3	0.098	3166.4	5.2	3
walleye pollock	*Theragra chalcogramma*	60.8	2.1	0.2	26	0.970	2.08E-06	3.322	25	3519.6	164.5	7	0.008	3255.1	3.9	7

all hexagrammids	Family: Hexagrammidae	57.4	2.2	0.1	72		4.06E-05	2.748		3991.6						
greenling	*Hexagrammos* spp.	55.5	2.3	0.1	61	0.736	9.15E-06	3.084	61	3952.7	174.0	8	0.003	3367.6	9.8	8
lingcod	*Ophiodon elongatus*	68.4	2.0	0.2	11	0.548	7.21E-05	2.412	11	4030.5	344.7	8	0.054	1199.8	40.3	8
all salmon	*Oncorhynchus* spp.	88.0	8.6	0.4	213		1.00E-05	3.041		4023.5						
chinook (king) salmon	*Oncorhynchus tshawytscha*	92.7	11.6	1.1	36	0.956	1.16E-05	3.022	36	3875.4	108.5	21	0.007	4032.8	-1.5	21
chum salmon	*Oncorhynchus keta*	90.7	9.1	0.8	83	0.953	7.75E-06	3.072	83	3886.3	76.6	14	0.403	3261.4	5.5	14
coho salmon	*Oncorhynchus kisutch*				0					4150.6	70.0	9	0.334	3383.8	5.7	9
pink salmon	*Oncorhynchus gorbuscha*	83.8	6.8	0.5	77	0.948	6.08E-06	3.120	77	3996.3	77.1	29	0.250	2934.0	9.8	29
sockeye salmon	*Oncorhynchus nerka*	76.7	6.8	3.4	3	1.000	9.49E-06	3.055	3	4209.1		1				
all smelt	Family: Osmeridae	72.9	4.0	0.3	348		1.68E-06	3.360		5672.5						
surf smelt	*Hypomesus pretiosus*	109.0	15.2	1.6	46	0.977	1.11E-06	3.456	46	4901.6	251.7	19	0.620	1337.7	35.2	19
whitebait smelt	*Allosmerus elongatus*	87.1	5.1	0.2	78	0.896	2.25E-06	3.265	77	4767.0	179.2	11	0.275	1983.9	29.4	11
eulachon	*Thaleichthys pacificus*	92.0	6.5		1					9083.3		1				
larval smelt	Family: Osmeridae									3938.1	43.3	6	0.456	3065.8	13.8	6
all rockfish	*Sebastes* sp.	54.8	2.7	0.1	232	0.870	2.15E-05	2.920	231	5139.2	130.1	8	0.762	1730.3	62.7	8
all fish	Class: Actinopterygii	84.4	4.7	0.1	4818		2.18E-05	3.078		4611.2						
all squid	Order: Teuthida	44.7	5.0	2.2	7									-		
clawed armhook squid	*Gonatus onyx*	38.0	3.1	0.7	5	0.738	4.43E-04	2.390	4	1984.5	232.8	4	0.877	2011.6	92.9	4
fiery armhook squid	*Gonatus pyros*	30.0	1.6		1											
market squid	*Doryteuthis opalescens*	93.0	17.7		1											
lamprey	*Lampetra tridentatus*	261.0	37.1		1											

1101

1102 Table S2
1103 Principal component scores used in PCA regression analysis for breeding and diet metrics. PC_1,
1104 which accounted for 46% of variation, described conditions similar to the NE Pacific MHW,
1105 with elevated SSTs, decreased primary productivity and upwelling, and so on. PC_2, which
1106 accounted for 17% of observed variation, described more moderate conditions for the NE
1107 Pacific. The three years of the NE Pacific MHW are bold.
1108

Year	PC_1	PC_2
2010	-0.1	-0.9
2011	-1.62	-1.09
2012	-1.25	-0.73
2013	-0.44	0.55
2014	**0.58**	**0.21**
2015	**1.96**	**0.77**
2016	**1.98**	**-0.094**
2017	0.44	1.52
2018	0.37	0.54
2019	0.33	0.11

1109

1110 Table S3. Results of pairwise least-square means test on individual condition for major prey
1111 species at Destruction Island and Protection Island whose initial linear mixed-models had
1112 significant results. Pair-wise comparisons that differ significantly are shown in **bold.**

1113

1114 **Destruction Island**
1115 Pacific Sand Lance

Year	2013	2016	2017
2016	0.13	-	-
2017	0.1	0.24	-
2019	0.99	**0.04**	0.67

1116

1117 Smelt Spp.

Year	2010	2013	2016	2018
2013	0.80	-	-	-
2016	0.89	0.52	-	-
2018	0.16	**0.03**	0.97	-
2019	0.32	**0.04**	0.99	0.83

1118

1119 **Protection Island**
1120 Pacific Sand Lance

Year	2010	2013	2015	2016	2017	2018
2013	0.56	-	-	-	-	-
2015	**0.00002**	**0.00001**	-	-	-	-
2016	0.17	0.06	**0.002**	-	-	-
2017	0.99	0.96	**<0.00001**	0.05	-	-
2018	**<0.00001**	**<0.00001**	0.06	0.11	**<0.00001**	-
2019	**0.02**	**0.00008**	**0.00004**	0.99	**0.02**	**0.0008**

1121

1122 Pacific Herring

Year	2010	2013	2015	2016	2017	2018
2013	**0.000006**	-	-	-	-	-
2015	0.99	**0.001**	-	-	-	-
2016	0.23	**0.008**	0.66	-	-	-
2017	**0.00001**	0.41	**0.04**	0.87	-	-
2018	0.96	**0.0001**	0.99	0.99	**0.02**	-
2019	0.78	**0.001**	0.35	0.99	0.09	0.99

1123
1124