Across the North Pacific, dietary-induced stress of breeding rhinoceros auklets increases with high summer Pacific Decadal Oscillation index

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ABSTRACT: Multi-colony studies of breeding seabirds may provide insights into the mechanistic links between large-scale climate variability and local changes in prey availability. In the North Pacific, the Pacific Decadal Oscillation (PDO) is a dominant climate index characterized by contrasting patterns in sea surface temperature between the western and eastern North Pacific. To examine how inter-annual variability in the PDO affects rhinoceros auklets *Cerorhinca monocerata* across the North Pacific, we measured inter-annual changes in nutritional stress (as reflected in plasma levels of corticosterone) of adults breeding on 5 colonies (2 and 3 colonies from the western and eastern Pacific, respectively). We also examined concurrent changes in mass and energy content of food loads delivered to chicks. We found that higher summer PDO values were associated with increased corticosterone levels and lower mass and energy contents of the food loads in both the western and eastern North Pacific colonies. Results indicated that oceanographic conditions during higher PDO values induced local changes in forage fish communities, leading to reduced prey availability, which, in turn, increased the nutritional stress of breeding birds. We conclude that the higher summer PDO index in recent years was associated with food-poor conditions for breeding rhinoceros auklets across their reproductive range, and prolonged periods of high summer PDO may be detrimental to the populations of this seabird species. Our results highlight the complexity of the mechanisms of how large-scale climate variability affects seabirds with a large geographical distribution.

KEY WORDS: Climate variability · Oceanographic drivers · Bioindicator · Ecological response · Marine predator · *Cerorhinca monocerata* · Corticosterone hormone · Food availability

1. INTRODUCTION

Understanding the mechanistic link between global climate variability and local marine ecosystems is es- sential to predict the impacts of climate change on top marine predators (Sydeman et al. 2015, Kitaysky & Hunt 2018). Climatic factors such as ocean tempera- ture drive changes in the composition of pelagic fish

communities around the world (Kitaysky & Golubova 2000, Chavez et al. 2003, Drinkwater et al. 2010, Yati et al. 2020). These changes in food resources affect the population dynamics of marine top predators such as seabirds and marine mammals. In particular, seabirds are known as sensitive ecological indicators (Cairns 1987, Piatt et al. 2007). However, even within a single species, the effect of climate variability may vary among regional populations of seabirds. For example, a previous study showed a negative relationship between winter sea surface temperature (SST) and breeding productivity of black-legged kittiwakes *Rissa tridactyla* both within and across regions of the British Isles (Frederiksen et al. 2007). In contrast, the southern and northern colonies of black-legged kittiwakes in the Bering Sea showed opposite nutritional stress responses to variability in climate indices such as the Pacific Decadal Oscillation (PDO) and winter sea-ice cover (Satterthwaite et al. 2012). Therefore, scaling up the impact of climate variability on seabirds at a single colony to populations across the range of a species may provide misleading results.

Studying seabirds at multiple colonies across a wide spatial range may provide better insights into how large-scale climate variability affects a seabird species (e.g. Wolf et al. 2009). To understand such bottom-up effects of climate variability on the ecology of a seabird species with a large geographical distribution, it is crucial to use a comparable set of measurements across regions. Reproductive success is commonly associated with climate-driven variability in food abundance (Cury et al. 2011). However, reproductive success often responds non-linearly to food availability (Cury et al. 2011), and it is also affected by other factors such as severe weather (e.g. Price et al. 2020), predation, and human disturbance (Piatt et al. 1990, Schreiber 2002), and by colony-specific reproductive responses to food-related stress (e.g. Schultner et al. 2013). Thus, reproductive success may not always be a pertinent indicator of bottom-up effects induced by climate variability. Instead, the physiological condition of seabirds may respond more sensitively and consistently to such food-related effects (Kokubun et al. 2018). Accordingly, in this study, we focused on measuring baseline plasma corticosterone (CORT) concentrations as a unified index across populations to examine the effects of changes in food resources on the physiological stress level of adult breeding seabirds.

CORT is the primary avian glucocorticoid hormone secreted to regulate metabolic pathways when food stress occurs (Kitaysky et al. 2001, 2010). Observational and experimental studies indicate a log-linear negative relationship between food availability and baseline CORT levels in seabirds (Kitaysky et al. 2010 and references therein). Furthermore, high baseline CORT levels during breeding periods have been associated with low re-sighting or survival rates in subsequent breeding periods in common murres *Uria aalge* and black-legged kittiwakes (Kitaysky et al. 2007, Goutte et al. 2010, Satterthwaite et al. 2010). A decline in survival rates strongly affects the population dynamics of long-lived seabirds (Croxall & Rothery 1991). Accordingly, we considered baseline CORT values as an indicator of nutritional stress levels of adult seabirds that might influence their population dynamics.

Rhinoceros auklets *Cerorhinca monocerata* are long-lived seabirds breeding across the North Pacific. They are monitored with comparable methods across their range and provide an opportunity to investigate the relationship between climate and regional populations at a broad geographic scale. Rhinoceros auklets nest in earthen burrows and show bi-parental care of their single chick; each parent delivers a single 'bill-load' containing multiple whole prey items to feed its chick once per night (Watanuki et al. 2009, 2022). Auklets breeding in the western Pacific mainly feed on Japanese anchovy *Engraulis japonicus*, sardine *Sardinops* spp., and juvenile salmon *Oncorhynchus* spp. (Watanuki & Ito 2012, Okado et al. 2020, Watanuki et al. 2022). In the western Pacific, the availability of Japanese anchovy is higher under warmer oceanographic conditions, as reflected in higher SSTs, and the proportional mass of Japanese anchovy in the diet positively relates to chick growth rates and fledging success (Takahashi et al. 2001, Watanuki et al. 2009). Further, in colder conditions, auklets in the western Pacific mainly forage on cold-water prey species such as sardine (Watanuki et al. 2022). Auklets breeding in the eastern Pacific mainly feed on sandlance *Ammodytes* spp., capelin *Mallotus* spp., and juvenile rockfish *Sebastes* spp. (Burger et al. 1993, Thayer et al. 2008, Cunningham et al. 2018). These forage fish appear to be more readily available when water temperatures are lower (Thayer et al. 2008). When sandlance and capelin decline in the food load, auklets forage on other prey species, such as sablefish *Anoplopoma* spp. and greenling *Hexagrammos* spp. (Thayer et al. 2008). Thus, auklets use a variety of forage fish species with different water temperature preferences in both the western and eastern Pacific.

In the North Pacific, the PDO index shows ecologically relevant decadal climate variability, characterized by contrasting SST trends between the western and eastern regions (Mantua et al. 1997, Chavez et

al. 2003, but see also Kuroda et al. 2020, Litzow et al. 2020). High PDO values generally indicate warm conditions in the eastern but cool conditions in the western North Pacific. At a decadal scale, the PDO index coincides with climatic shifts between warm and cold states which are associated with changes in fish communities across the North Pacific ('regime shifts'; Mantua et al. 1997, Chavez et al. 2003, Tian et al. 2006). These shifts also correspond with changes in seabird chick production and diet (e.g. black-legged kittiwakes; Hatch 2013). The inter-annual variability of the PDO index during breeding periods, which consists of a similar contrasting SST pattern, is also relevant for seabirds. Changes in the PDO have previously been shown to correlate with the annual survival of Nazca boobies *Sula granti* in the Galápagos Islands (Champagnon et al. 2018) and nutritional stress levels in red-legged kittiwakes *R. brevirostris* in the southeastern Bering Sea during summer (Will et al. 2018). However, it is unknown how the contrasting effects of the PDO on temperature patterns may affect prey availability and nutritional stress levels in seabirds such as the rhinoceros auklet.

The main objective of this study was to better understand how inter-annual climate variability reflected in the PDO might affect the nutritional stress levels of rhinoceros auklets breeding in the North Pacific. We predicted that (1) a high summer PDO index is associated with local changes in forage fish communities, leading to reduced availability of prey for auklets because their main prey species respond to warming temperatures contrastingly between the western and eastern Pacific. Such reductions in prey availability would increase the nutritional stress of breeding birds in both regions. An alternative prediction is that (2) inter-annual variability in the PDO does not affect the nutritional stress of breeding birds due to their foraging flexibility and prey-switching. To test these contrasting predictions, we measured inter-annual changes in the nutritional stress of breeding adults and the mass and energy content of chick diet collected at 5 colonies spread across the western and eastern Pacific.

2. MATERIALS AND METHODS

2.1. Study sites

Fieldwork was conducted at auklet colonies on 2 and 3 islands in the western and eastern Pacific, respectively (Fig. 1). Western Pacific study sites included Teuri Island (44° 25′ N, 141° 18′ E), located in the Sea of Japan off the west coast of Hokkaido, and Daikoku Island (42° 57′ N, 144° 52′ E), located in the Pacific off the east coast of Hokkaido. Eastern Pacific study sites included Middleton Island (59° 26′ N, 146° 19′ W), located in the northern Gulf of Alaska, St. Lazaria Island (56° 59′ N, 135° 42′ W), located in the eastern Gulf of Alaska, and Triangle Island (50° 52′ N, 129° 05′ W), in the Eastern Coastal Transition Zone, northwest of Vancouver Island in British Columbia. Fieldwork occurred during May–August 2015–2019 at Teuri Island, 2015–2017 at Daikoku Island, 2004 at Middleton Island, 2003–2004 at Triangle Island, and 2013–2015 at St. Lazaria Island.

2.2. Climate variability

As an indicator of climate variability during breeding periods of rhinoceros auklets, we averaged the monthly PDO values from May, June, and July for each study year (https://oceanview.pfeg.noaa.gov/erddap/tabledap/cciea_OC_PDO.htmlTable?time, PDO). Inter-annual variability in the PDO index is relevant for the distribution and availability of prey fishes in seabirds (Hatch 2013). The summer PDO index is correlated with the annual PDO index during our study years (slope coefficient ± SE of annual PDO = 1.07 ± 0.12, adjusted r^2 = 0.912, p < 0.001, n = 9 yr).

2.3. Nutritional stress

Adults were captured by hand in or near their nest burrows during the chick-rearing period, except on Daikoku Island, where the field study was
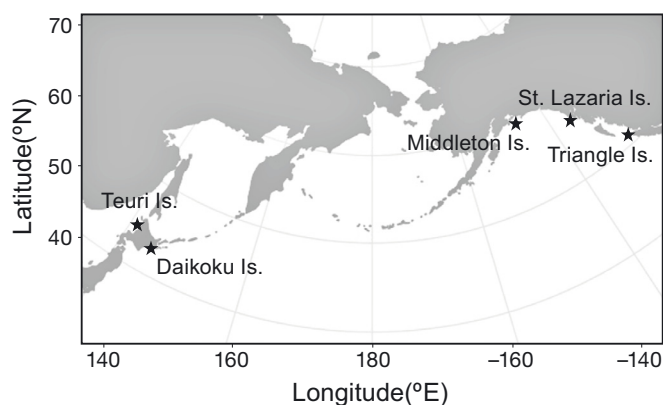

Fig. 1. Field study sites. Stars: location of each focal colony of rhinoceros auklets

conducted from the end of the incubation to the early chick-rearing period. Blood samples were taken within 3 min of capture from 251 birds (see Table 1). The hormone titers in samples collected within 3 min of capture provide a measure of baseline CORT levels and do not reflect the adrenocortical response induced by capture (Kitaysky et al. 2007). Blood samples were kept on ice until centrifugation to separate plasma from red blood cells. Plasma samples were stored frozen until assayed for CORT. Plasma CORT concentrations were measured by radioimmunoassay following Kitaysky et al. (2007). To control for the hormone extraction efficiency, 20 µl of tritiated CORT (2000 cpm) was added to each plasma sample before extraction with 4 ml HPLC-grade dichloromethane. After extraction, recovery values of the labeled hormone from each sample were used to correct final values (average hormone recovery was 93.5%). We reconstituted extracted samples in phosphate-buffered saline buffer with gelatin and combined them with an antibody (Esoterix B3-163) and radio-labelled CORT (PerkinElmer) in a radioimmunoassay. Antibody-bound and unbound fractions of hormones were separated by using dextran-coated charcoal. Inter- and intra-assay variations were 7.9 and 1.8%, respectively.

2.4. Diet

We captured adult auklets (different from birds captured for blood sampling) at their breeding colonies when the birds were delivering food loads to feed their chicks. We collected 967 full bill-loads and identified each prey item they contained to the lowest taxonomic level possible (see Table 1). We measured wet mass of each item in the field and calculated the mass percent of prey species for each colony in each year. Sandlances were categorized into 1 of 2 age classes: age-0+ (<110 mm total length, hereafter 'age-0') and age-1≤ (≥110 mm, hereafter 'age-1') in the western colonies (Takahashi et al. 2001); age-0 (<100 mm total length) and age-1 (≥100 mm) in the eastern colonies (Will et al. 2015). We estimated the energy content of each food load from the total mass and energy density of the prey species it contained (Table S1 in the Supplement at www.int-res.com/articles/suppl/m708p177_supp.pdf). Then, we calculated the energy density of each food load by dividing the energy content by the mass of each food load.

2.5. Statistical analysis

First, inter-annual differences in CORT levels, food load mass, food load energy content, and food load energy density were tested by 1-way ANOVA with Scheffé's post hoc test, after testing for normality of the data (Shapiro-Wilk test). CORT levels were $\log_{10}$ transformed to meet normality assumptions prior to analyses. Second, we used a generalized linear mixed model (GLMM) to test the relationships among the PDO value, CORT level, food load mass, food load energy content, food load energy density, and fish mass proportion. The region (western or eastern Pacific) of each colony was included as a fixed factor. Colony and year nested within a colony were included as random factors. We could not include the sex of the birds in the models because we did not have relevant measurements to determine the sex of 62 out of 251 birds. For those birds with information on sex, we found no difference in plasma CORT levels between the sexes (GLMM: mean ± SE sex effects on males = −0.01 ± 0.05, p = 0.997, n = 189). Slope coefficients (mean ± SE) and p-values were calculated by post hoc comparisons on each factor in the model. Marginal and conditional r^2 (r^2_m and r^2_c, respectively) were also calculated; r^2_m was calculated from the fixed factors, and r^2_c was calculated from both fixed and random factors (Nakagawa & Schielzeth 2013). We used the 'lme4', 'multcomp', and 'MuMIn' packages in R v.4.1.0 (R Development Core Team 2021). Statistical significance was set at α = 0.05.

3. RESULTS

3.1. Inter-annual differences in CORT levels and food loads

In the western Pacific, on Teuri Island, we found inter-annual differences in CORT levels (ANOVA, $F_{4,94}$ = 5.2, p = 0.001), food load mass ($F_{4,418}$ = 4.1, p = 0.003), energy content ($F_{4,418}$ = 3.7, p = 0.006), and energy density ($F_{4,418}$ = 2.9, p = 0.022). CORT levels in 2016 were higher than those in the other 4 years (Table 1, Table S2; Scheffé, p < 0.05 for all comparisons). The food load mass and energy content in 2016 were lower than in 2019, and the food load energy density in 2016 was lower than in 2017 (Table 1, Table S2; p < 0.05 for both comparisons). On Daikoku Island, we found inter-annual differences in CORT levels ($F_{2,40}$ = 10.4, p < 0.001), food load mass ($F_{2,106}$ = 11.5, p < 0.001), energy content ($F_{2,106}$ = 7.9, p = 0.001), and energy density ($F_{2,106}$ = 8.3, p < 0.001).

Table 1. Plasma corticosterone (CORT) concentrations of adult rhinoceros auklets, along with food load mass, food load energy content, and food load energy density delivered by adults to chicks across 5 colonies in the North Pacific. Reported values are means ± SE for each colony and each year, with sample size for plasma (N_{cort}) and food load (N_{food}). Data on food load mass are cited from literature given in the footnotes, except for St. Lazaria

Colony	Year	CORT ($\log_{10}$, ng ml^{-1})	N_{cort}	Food load mass (g load^{-1})	Food load energy content (kJ load^{-1})	Food load energy density (kJ [load mass]$^{-1}$)	N_{food}
Northwest Pacific							
Teuri[a]	2015	0.89 ± 0.06	39	17.7 ± 1.5	83.0 ± 8.0	4.50 ± 0.08	53
	2016	1.26 ± 0.10	12	16.6 ± 1.1	74.3 ± 5.4	4.37 ± 0.07	63
	2017	0.85 ± 0.07	22	20.5 ± 1.0	97.1 ± 4.9	4.69 ± 0.03	111
	2018	0.71 ± 0.09	12	20.9 ± 1.1	96.5 ± 6.1	4.49 ± 0.09	100
	2019	0.68 ± 0.11	14	22.4 ± 0.9	103.5 ± 4.7	4.55 ± 0.07	96
Daikoku[b,c]	2015	1.16 ± 0.09	18	21.1 ± 1.7	106.2 ± 8.8	5.01 ± 0.10	36
	2016	1.60 ± 0.07	15	18.7 ± 1.7	92.4 ± 9.0	4.85 ± 0.07	27
	2017	1.13 ± 0.06	10	29.6 ± 1.7	138.6 ± 7.8	4.67 ± 0.01	46
Northeast Pacific							
Middleton[d]	2004	0.68 ± 0.11	8	27.0 ± 1.0	160.7 ± 5.2	6.23 ± 0.16	107
Triangle[d]	2003	0.92 ± 0.07	29	27.7 ± 1.1	126.1 ± 5.4	4.64 ± 0.12	85
	2004	0.65 ± 0.10	20	30.8 ± 1.6	128.6 ± 8.5	4.24 ± 0.23	41
St. Lazaria	2013	0.64 ± 0.06	32	31.0 ± 1.2	118.3 ± 6.8	3.87 ± 0.17	97
	2014	0.86 ± 0.09	11	27.6 ± 1.6	110.4 ± 8.4	4.23 ± 0.24	51
	2015	0.89 ± 0.12	9	19.7 ± 3.1	83.0 ± 15.7	3.92 ± 0.29	54

[a]Updated from Watanuki et al. (2022); [b]Okado et al. (2020); [c]Okado et al. (2021); [d]Thayer et al. (2008)

CORT levels in 2016 were higher than in the other 2 years (Table 1, Table S2; p < 0.01 for both comparisons). The food load mass and energy content in 2017 were higher than in 2015 and 2016, and the food load energy density in 2017 was lower than in 2015 (Table 1, Table S2; p < 0.05 for all comparisons).

In the eastern Pacific, on Triangle Island, we found inter-annual differences in CORT levels ($F_{1,47} = 5.2$, p = 0.027), which were higher in 2003 than in 2004 (Table 1, Table S2; p < 0.05). The inter-annual difference in food load mass, energy content, and energy density was not significant (mass: $F_{1,124} = 2.5$, p = 0.119; energy content: $F_{1,124} = 0.1$, p = 0.802; energy density: $F_{1,124} = 3.0$, p = 0.085), but the energy density in 2004 tended to be lower than in 2003 (Table 1, Table S2; p = 0.085). On St. Lazaria Island, we found inter-annual differences in CORT levels ($F_{2,49} = 3.3$, p = 0.045). However, using multiple comparisons with Scheffé's post hoc test, we found no statistically significant differences in CORT levels in any of the year pair-wise comparisons (Table S2; p > 0.1). We found inter-annual differences in food load mass ($F_{2,199} = 9.4$, p < 0.001) and energy content ($F_{2,199} = 3.5$, p = 0.033). The food load mass in 2015 was lower than in 2013 and 2014, and the food load energy content in 2015 was lower than in 2013 (Table 1, Table S2; p < 0.05 for all comparisons). The food load energy density did not differ between years ($F_{2,199} = 0.68$, p = 0.506).

3.2. Diets

The prey species composition of rhinoceros auklets' bill-loads varied among the 5 study years on Teuri Island (Fig. 2a). The main prey species by mass were juvenile Japan Sea greenling *Pleurogrammus azonus* in 2015 (comprising 34% in food loads), 2017 (71%), and 2019 (33%), squid in 2016 (26%), and age-0 sandlance in 2018 (51%). On Daikoku Island, juvenile salmon appeared as the main prey species in all 3 years (40% in 2015, 54% in 2016, and 72% in 2017). At both western colonies, the proportions of Japanese anchovy delivered were relatively small (<16%), and no anchovy appeared in the food loads collected in 2016 and 2017.

The prey species compositions were also different among the eastern Pacific colonies and varied inter-annually (Fig. 2b). The main prey species on Middleton Island was sandlance (44% of age-0 sandlance and 21% of age-1 sandlance). On Triangle Island, Pacific saury *Cololabis saira* was the main prey in 2003 (53%), followed by age-1 sandlance (26%), which was the dominant item in 2004 (35%). Herring *Clupea* spp. (23–32%) and capelin (28–37%) dominated the diet at St. Lazaria Island in all years. The diet composition on St. Lazaria Island was similar in 2013 and 2014, whereas in 2015, juvenile sablefish appeared in the diets as the second most important item (27%).
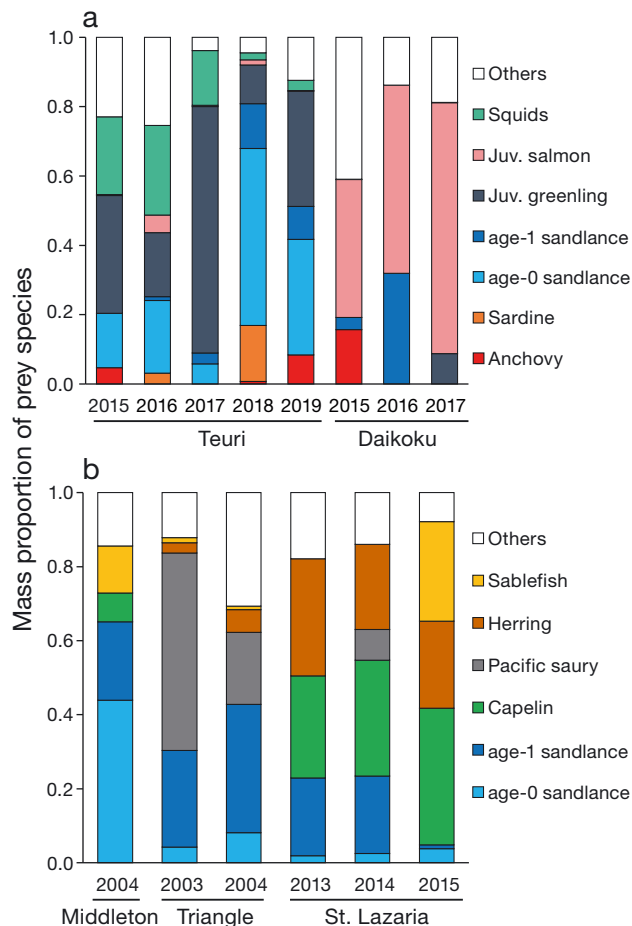
Fig. 2. Changes in the mass proportion of prey species in bill-loads of rhinoceros auklets breeding on the (a) western and (b) eastern Pacific colonies

3.3. Effects of PDO and food load changes on baseline CORT

The PDO indices varied from −0.65 to 1.88 during our study years, with most study years (except 2013) having positive values. Plasma CORT concentrations were positively associated with the PDO index (Table 2, Fig. 3a). The relationship was also statistically significant when each region was analyzed separately (Table 2).

The plasma CORT concentrations were negatively related to food load mass and energy content (Table 2, Fig. 3b,c) but not to food load energy density (Table 2, Fig. 3d).

3.4. PDO and food loads

There was a negative relationship between the summer PDO index and the food load mass collected

at all colonies (Table 2, Fig. 3e). This negative trend persisted when the western and eastern Pacific colonies were analyzed separately (Table 2). A similar trend was also found between the summer PDO index and the energy content of food loads (all colonies: p = 0.002; western: p = 0.014; eastern: p = 0.082; Table 2, Fig. 3f).

3.5. Fish composition and food load mass

In the western Pacific, there was a negative relationship between the mass proportion of squid and the food load mass collected at Teuri Island (Table 2, Fig. 4a). On Daikoku Island, the food load mass was highest in 2017, with the largest mass proportion of juvenile salmon. However, the relationship between the mass proportion of salmon and the food load mass collected at Daikoku Island was not statistically significant (Table 2, Fig. 4b). In the eastern Pacific, there was a positive relationship between the mass proportion of age-1 sandlance and the food load mass collected at Middleton, Triangle, and St. Lazaria islands (Table 2, Fig. 4c).

4. DISCUSSION

The main objective of this study was to better understand how inter-annual variability in the PDO might affect breeding rhinoceros auklets across the North Pacific. In agreement with our first prediction that the inter-annual variability in the PDO is associated with nutritional stress of breeding birds, high summer PDO related positively to baseline CORT levels and negatively to food load mass and energy content of rhinoceros auklets breeding in both the western and eastern North Pacific regions. Below, we first discuss how dietary changes might affect stress levels of breeding rhinoceros auklets, and then consider how inter-annual variability in PDO might associate with dietary changes. Finally, we briefly examine the importance of measuring the nutritional stress levels of adult seabirds to understand the effects of inter-annual environmental change on seabird populations.

4.1. Diet and nutritional stress levels

We found a negative relationship between the food load mass and energy content for chicks and baseline plasma CORT levels of adult birds (Table 2, Fig. 3b,c).

Table 2. Results from generalized linear mixed models examining the relationships among Pacific Decadal Oscillation (PDO), plasma corticosterone (CORT) concentration of adult rhinoceros auklets, food load mass, food load energy content, food load energy density, mass proportion of prey, and colony location. ***p < 0.001; **p < 0.01; *p < 0.05; NS: not significant

| Colony	Model	Intercept	Slope coefficient	SE of slope coefficient	Region effects (on West)	SE of region effects	p Slope coefficient	p Region effects	Marginal r^2	Conditional r^2	Interaction term
All											
	CORT ~ PDO + Region + (1|Colony) + (1|Colony:Year)	0.83	0.20	0.07	−0.18	0.16	0.006**	0.52	0.23	0.40	NS
	CORT ~ Food load mass + Region + (1|Colony) + (1|Colony:Year)	1.80	−0.03	0.01	−0.10	0.24	0.017*	0.93	0.20	0.48	NS
	CORT ~ Food load energy content + Region + (1|Colony) + (1|Colony:Year)	1.92	−0.01	0.003	−0.09	0.28	0.014*	0.96	0.16	0.52	NS
	CORT ~ Food load energy density + Region + (1|Colony) + (1|Colony:Year)	1.04	0.01	0.15	−0.31	0.21	1.000	0.27	0.11	0.43	NS
	Food load mass ~ PDO + Region + (1|Colony) + (1|Colony:Year)	25.83	−3.92	1.04	3.87	2.47	<0.001***	0.26	0.10	0.15	NS
	Food load energy content ~ PDO + Region + (1|Colony) + (1|Colony:Year)	119.30	−14.58	4.22	19.09	22.55	0.002**	0.72	0.06	0.20	NS
Northwest Pacific											
	CORT ~ PDO + (1|Colony) + (1|Colony:Year)	0.77	0.26	0.11			0.024*		0.10	0.44	
	Food load mass ~ PDO + (1|Colony) + (1|Colony:Year)	25.85	−3.83	1.51			0.021*		0.05	0.17	
	Food load energy content ~ PDO + (1|Colony) + (1|Colony:Year)	121.79	−17.13	1.36			0.014*		0.03	0.17	
Teuri	Food load mass ~ mass proportion of squid + (1|Year)	22.34	−0.19	0.06			0.002**		0.03	0.03	
Daikoku	Food load mass ~ mass proportion of juv. salmon + (1|Year)	7.91	0.28	0.21			0.231		0.11	0.25	
Northeast Pacific											
	CORT ~ PDO + (1|Colony) + (1|Colony:Year)	0.70	0.14	0.06			0.042*		0.07	0.10	
	Food load mass ~ PDO + (1|Colony) + (1|Colony:Year)	29.74	−4.12	1.59			0.017*		0.05	0.07	
	Food load energy content ~ PDO + (1|Colony) + (1|Colony:Year)	137.32	−12.44	6.12			0.082		0.01	0.15	
	Food load mass ~ mass proportion of 1≤sandlance + (1|Colony) + (1|Colony:Year)	19.02	0.40	0.10			<0.001***		0.06	0.08	
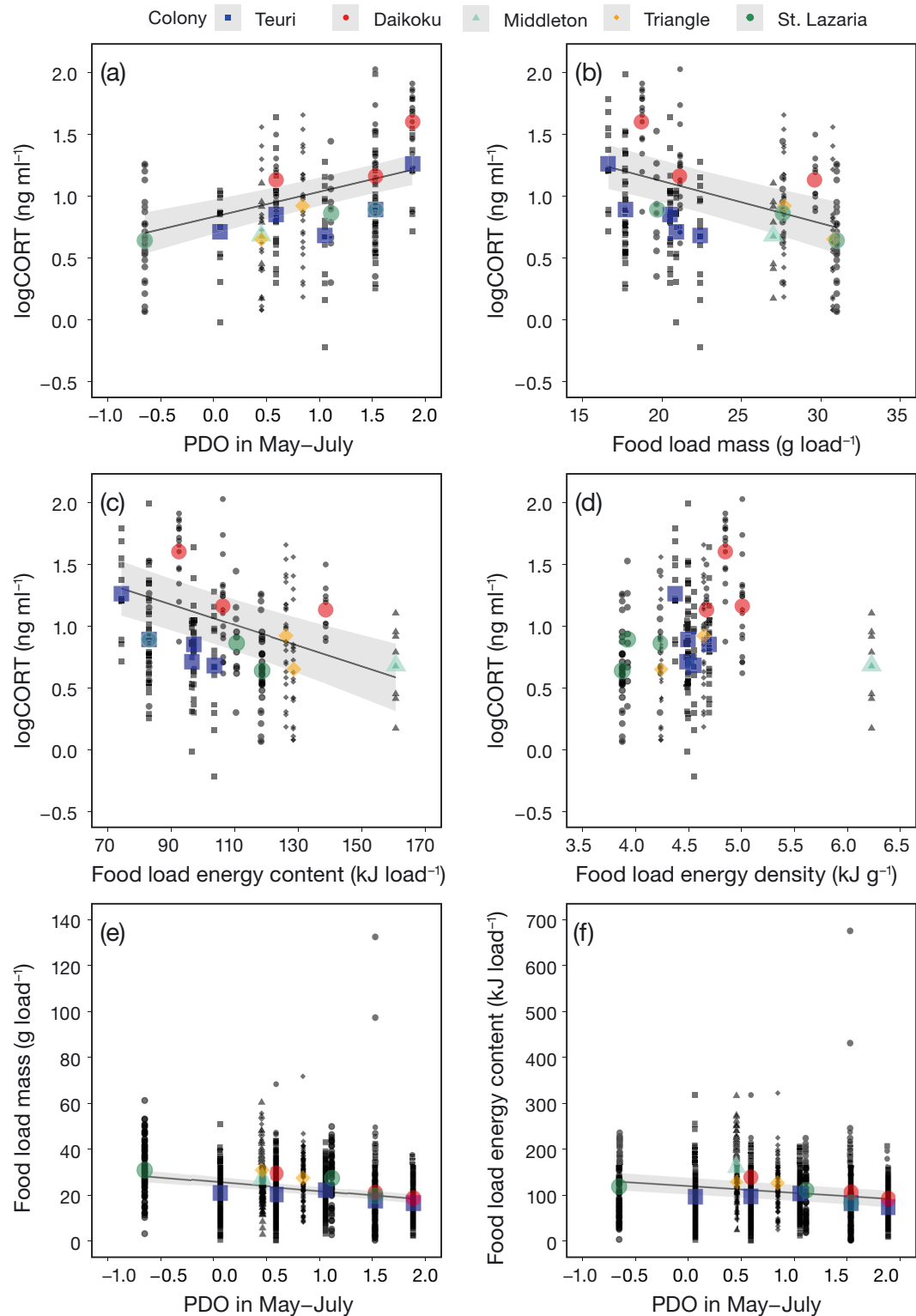
Fig. 3. Relationships between (a) summer Pacific Decadal Oscillation (PDO) index and plasma corticosterone (CORT) concentration; food load (b) mass, (c) energy content, and (d) energy density and plasma CORT concentration; and summer PDO index and food load (e) mass and (f) energy content for rhinoceros auklets from 5 colonies in the western and eastern North Pacific. Solid lines: slopes of the statistically significant relationships as determined by generalized linear mixed models; shaded area: SE of estimates; black points: individual values; colored points: mean values of each colony–year
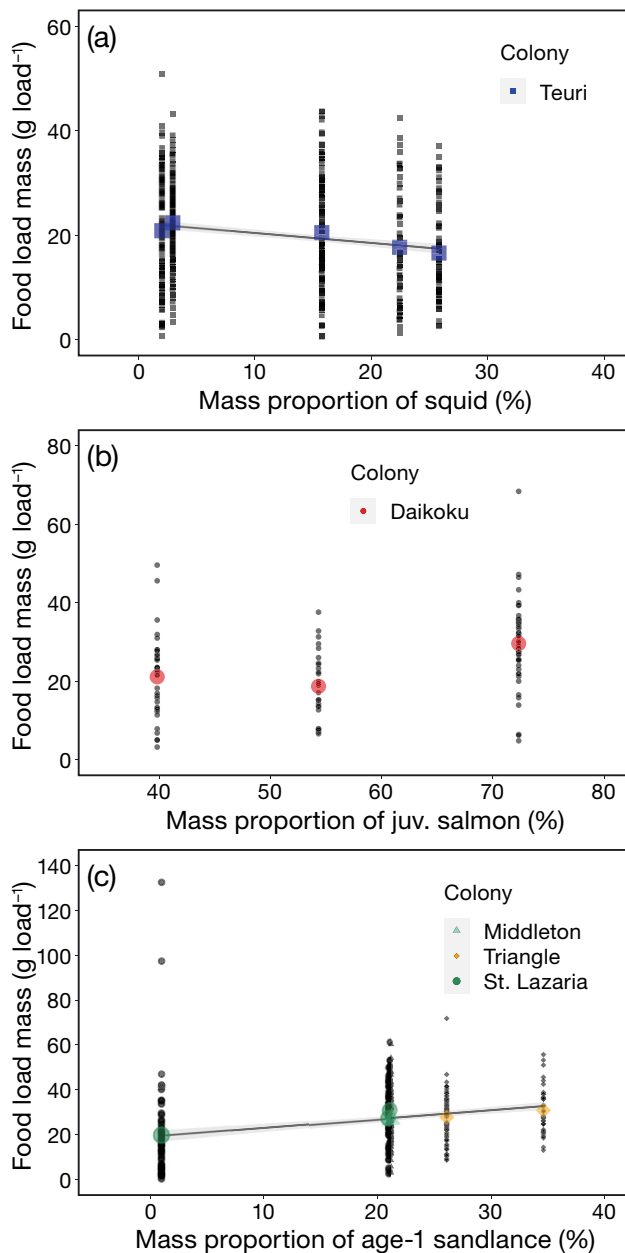
Fig. 4. Relationship between mass proportion of (a) squid and food load mass in diets on Teuri Island, (b) juvenile salmon and food load mass in diets on Daikoku Island, and (c) age-1 sandlance and food load mass in diets on 3 rhinoceros auklet colonies in the eastern North Pacific. Solid lines: slopes of the statistically significant relationships as determined by generalized linear mixed models; shaded area: SE of estimates; black points: individual values; colored points: mean values of each colony–year as in Fig. 3

Even though a direct causal relationship between chick diets and adult nutritional stress levels is not always expected, previous studies showed that the physiological state of adult seabirds was affected by

dietary changes when their chicks' energy intake was reduced (Will et al. 2015, Kokubun et al. 2018). Previous studies of rhinoceros auklets also showed that isotopic signatures of body tissues did not differ between adults and chicks, indicating that adults often feed on prey similar to what they capture to feed their chicks (Ito et al. 2009, Hipfner et al. 2013, Carle et al. 2015, but see Davoren & Burger 1999). Results of our study imply that changes in the food load composition and mass/energy content of prey delivered to chicks are not independent of the nutritional stress incurred by adult birds and that both reflect environmentally induced changes in the availability of prey they consume.

Prey quality, such as energy density, can affect nutritional stress levels in adult birds (Will et al. 2015). However, we did not find a relationship between the food load energy density and baseline plasma CORT levels of adult auklets (Table 2, Fig. 3d). Moreover, the average energy density of food load fluctuated little between years (e.g. 4.37–4.69 kJ g^{-1} at Teuri Island). A previous study also showed that the food load mass is more important for auklets' productivity than the food load energy density (Watanuki et al. 2022). Thus, auklets appear to be able to adapt to changes in the species composition of the fish community, but not to the changes in abundance and/or availability of food.

Plasma CORT levels of birds breeding on Daikoku Island were higher than those on Teuri Island (Table 1). We collected birds' blood samples at Daikoku Island at the end of the incubation period and the early chick-rearing period, but only during the chick-rearing period on other islands. So relatively high stress levels of adults on Daikoku Island compared to Teuri Island may also reflect the difference in breeding stages (Shultz & Kitaysky 2008, but see Kitaysky et al. 2010).

4.2. Climate variability and food composition

We found that a large-scale climate variability index, the summer PDO, was positively correlated with adult baseline plasma CORT levels (Table 2, Fig. 3a) and negatively correlated with the mass and energy content of auklets' food loads (Table 2, Fig. 3e,f). Generally, the PDO index indicates opposite SST trends between the western and eastern North Pacific (Chavez et al. 2003, but see also Litzow et al. 2020). During our study years, the summer PDO indices varied from −0.65 to +1.88 (recorded range: −3.6, 3.51), and the PDO transitioned from a negative to a positive

state between 2013 and 2014 (Zeng et al. 2021). This climate variability likely affected the abundance, distribution, and/or size of prey species across the range of rhinoceros auklets.

In the western Pacific, the abundance of warm-water anchovy decreased and cold-water sardines increased around the PDO transition in 2013–2014 (Yatsu 2019, Kuroda et al. 2020). This may explain why anchovies were less available to auklets on Teuri and Daikoku islands during our study period compared to the earlier period before the PDO transition (Watanuki et al. 2009, 2022, this study). Instead, other prey species, such as sardine, greenling, sandlance, and squid, were observed in relatively high proportions in the diet. Most of these species are smaller and less energy-rich than anchovy (Takahashi et al. 2001, Okado et al. 2021), and sardine, the only species with a similar energy density as anchovy (sardine: 6.26 kJ g^{-1}, Okado et al. 2021; anchovy: 6.29 kJ g^{-1}, Takahashi et al. 2001), was observed in only limited numbers throughout our study period (Fig. 2a). Correspondingly, we observed relatively lower food load mass and energy content at Teuri Island in 2015–2016 compared with before 2013 and after 2017 (16.6–17.7 vs. 20.5–35.9 g) (Watanuki et al. 2022, this study). Specifically, the food load mass and food load energy content were the lowest at both colonies in the western Pacific in 2016. The estimated abundance of greenling around northern Hokkaido was also the lowest in 2016 in the time series started in 1985 (Japan Fisheries Research and Education Agency 2020). The lower food load mass and increased squid contribution to the diet (Table 2, Fig. 4a) indicate that auklets in Teuri Island switched to foraging on squid when the availability of fish was low in their foraging areas in 2016. Additionally, although the food load mass increased after 2017, these values were approximately 10 g lower than before 2013, when auklets mainly foraged on anchovy (Watanuki et al. 2022), suggesting that foraging conditions have not completely recovered to the favorable conditions observed prior to 2013.

In the eastern Pacific, we found that age-1 sandlance was a major prey item in food loads during our study years (as in a previous study by Thayer et al. 2008). We also found a positive relationship between the proportion of age-1 sandlance in the diet and food load mass. Previously, the length and body condition of age-1 sandlance were found to be negatively related to the PDO index on Middleton and St. Lazaria islands in the Gulf of Alaska (Thompson et al. 2019). Moreover, the abundances and whole-body energy content of larval fishes such as sandlance were recorded as being relatively low in 2015–2016, the years of high PDO (von Biela et al. 2019, Nielsen et al. 2021). Thus, our results suggest that increased food load mass and energy content in the eastern Pacific were associated with decreased PDO index (close to zero) via a high availability of age-1 sandlance (Figs. 2b & 3e,f). Large (age-1) sandlance was also observed in food loads in 1998, corresponding with the beginning of a negative PDO phase in the Gulf of Alaska (Thayer et al. 2008). We observed that the proportion of large sandlance substantially decreased in 2015, corresponding with the beginning of a positive PDO phase. Contrastingly, the proportion of sablefish increased from zero in 2013–2014 to 27% in 2015 on St. Lazaria Island. Although the energy density of sablefish and age-1 sandlance are similar (Vermeer & Devito 1986, Will et al. 2015) and the mean mass of sablefish was larger than age-1 sandlance, the mean food load mass and energy content declined in 2015 due to fewer prey items per load in 2015 than in 2013 and 2014. On Middleton Island, sandlance was the main prey species for auklets in 1978–2003 (Thayer et al. 2008) and in our 2004 results. However, a recent study showed that the proportion of capelin, which has a similar energy density to age-1 sandlance, was higher than that of sandlance in 2008–2013, when the PDO index was negative (Cunningham et al. 2018). These results suggest that changes in species composition of food load might be related to the PDO transition, which is associated with changes in the availability of prey (and with changes in baseline plasma CORT) for rhinoceros auklets in the eastern Pacific.

In summary, PDO variability might reflect climate-related changes in forage fish communities in the western and eastern Pacific. The changes in forage fish communities might affect the mass and energy content of prey available to rhinoceros auklets breeding in both the western and the eastern Pacific, where the relationship between the change in PDO and that in water temperature is opposite.

4.3. Ecological implications

Many previous studies have investigated the effects of climate variability, especially ocean warming, on various seabirds (e.g. Sydeman et al. 2012). It is often considered that warming conditions consistently affect seabirds negatively in terms of foraging success (Divoky et al. 2021), reproductive success (Frederiksen et al. 2007), survival (Sandvik et al.

2005, Gibson et al. 2023), and regional abundance (Veit et al. 1996). However, our study suggests that it is difficult to generalize the results from a single location to the entire species' range due to region-specific mechanisms linking climate variability and local marine ecosystems. Warmer temperature conditions are associated with better foraging conditions for rhinoceros auklets in the western Pacific (Watanuki et al. 2009), whereas the opposite is true for the eastern North Pacific (Thayer et al. 2008), which resulted in a consistent PDO–CORT positive relationship across both regions (this study). Such regional variations in seabird responses are partly due to the contrasting regional responses of forage fish, for example, as shown in the complexity of life-history responses to climate variability in Pacific sardine populations between the western and eastern North Pacific (Sakamoto et al. 2022). Our results emphasize the need to recognize the complexity of the mechanisms that link climate variability and local marine ecosystems to fully assess the impact of ocean warming on seabirds across the globe.

Our results reinforce that baseline plasma CORT can be used as a sensitive indicator of environmentally induced nutritional stress in breeding seabirds. In general, seabirds have relatively high mortality rates during the non-breeding period compared to the breeding period, which may be related to harsh oceanographic conditions and food scarcity (Harris & Wanless 1996, Sandvik et al. 2005, Jones et al. 2019). However, stress levels incurred during the breeding period can increase the mortality rate of post-breeding adult seabirds (Kitaysky et al. 2007, 2010). For example, birds with high CORT levels during a breeding period were observed less frequently during the following breeding period, and this trend was stronger in a declining population (Kitaysky et al. 2007, 2010). We found that the CORT levels of adult birds increased incrementally with the high PDO index, at least during the positive PDO phase. Therefore, continued positive PDO phases in recent years may be detrimental to rhinoceros auklet populations across the North Pacific via the decreased survival rates of adult birds associated with high nutritional stress. Future studies should further assess how baseline CORT levels relate to survival rates after breeding to examine the physiological mechanisms of stress-related mortality. In addition, a longer-term study is needed to evaluate the full range of climatic impacts because our study occurred almost exclusively in the positive PDO phase, except for 2013. Longer time-series would also enable us to examine potential lagged effects of the PDO on the availabil-

ity of forage fish and nutritional stress levels in rhinoceros auklets. Indeed, a previous study showed that the effect of climate variability on seabirds in the eastern Bering Sea can be delayed up to 2 yr (Zador et al. 2013). As these lagged effects may be colony-specific, longer time-series of stress metrics would be needed for each colony; our study, with a limited number of colony-years, may not be adequate to formally address this point here. A retrospective analysis of seabird nutritional stress levels is now possible using historical records as reflected through CORT levels in feather samples from museum specimens (e.g. Will et al. 2018), which would help us understand the effects of large-scale–long-term climate variability on seabirds.

4.4. Conclusions

We found that the PDO, a large-scale climate variability index in the North Pacific, is positively associated with baseline plasma CORT of breeding rhinoceros auklets across both western and eastern Pacific colonies via changes in forage fish communities. These results highlight the complexity of the mechanisms of how large-scale climate variability affects seabirds that have a large geographical distribution and high diversity of prey species. Our results also provide further support that baseline plasma CORT can be used as a sensitive indicator of the impacts of climate variability on seabirds, as increased stress levels in adult auklets were closely related to climate-induced reductions in the availability of prey. We suggest that prolonged periods of high summer PDO may be detrimental to this species of seabird.

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