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Deep-Sea Research II ▮ (▮▮▮▮) ▮▮▮–▮▮▮

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Stress hormones suggest opposite trends of food availability for planktivorous and piscivorous seabirds in 2 years

Z Morgan Benowitz-Fredericks *, Michael T. Shultz, Alexander S. Kitaysky

Institute of Arctic Biology, University of Alaska Fairbanks, 311 Irving I, Fairbanks, AK 99775, USA

ARTICLE INFO

Article history:

Accepted 5 April 2008

Keywords:
Corticosterone
Food availability
Marine birds
Seasonal variations
Bering Sea
Pribilof Islands

ABSTRACT

Apex predators can provide valuable information about effects of climate variability on trophodynamics in the Bering Sea. We used corticosterone (the primary avian stress hormone, "CORT") as a proxy of changes in prey availability for planktivorous and piscivorous seabirds. CORT secretion reflects energy balance in breeding individuals and can be used to monitor changes in the marine environment that alter food availability. We tested whether CORT in planktivorous least auklets (*Aethia pusilla*) and piscivorous thick-billed murres (*Uria lomvia*) on two Pribilof Islands differed spatially or temporally in 2003 and 2004. During June–September of each year, we sampled birds breeding on St. Paul and St. George Islands. We found that seasonal dynamics of CORT varied between years. Although the seasonal dynamics were similar between islands in a year, in 2004 there were inter-island differences in CORT levels for both species. In 2003, CORT in murres was low throughout the season, suggesting that their prey availability (primarily forage fishes) was consistently good. In 2004, CORT levels suggested that overall food availability was poor for murres and declined as the season progressed. For auklets, inter-annual variability was associated with contrasting intra-seasonal patterns in the availability of zooplankton prey (primarily *Neocalanus* spp.). In 2003, high early-season (June) CORT indicated that auklets were food-limited, but CORT decreased in July, suggesting that the availability of zooplankton improved as the season progressed. In 2004, CORT was low early in the season (June), but an abrupt increase late in the season (July) suggests that food became scarce. Our data indicate that environmental differences between 2003 and 2004 affected prey availability for planktivorous and piscivorous alcids in opposite ways. These results suggest that in the shelf regions of the Bering Sea, the populations of apex predators feeding on zooplankton may be affected by environmental fluctuations differently than those feeding on forage fish.

1. Introduction

The Bering Sea shelf ecosystem is sensitive to climate fluctuations on multiple temporal and spatial scales (reviewed in Macklin et al., 2002). The timing and magnitude of changes in physical factors such as temperature, wind patterns, and sea ice evoke strong responses in dynamics of distribution and abundance of organisms at all trophic levels (Springer et al., 1996; Hunt et al., 2002; Baier and Napp, 2003; Bond and Overland, 2005). Prey availability for both planktivorous and piscivorous species fluctuates on decadal scales in response to climate regimes, but also inter- and intra-annually (Roby and Brink, 1986; Springer et al., 1986; Anderson and Piatt, 1999; Napp et al., 2002). For seabirds, environmental fluctuations have been proposed to exert their effects via both top-down and bottom-up processes and two general scenarios have been described. (1) In the shelf systems in both the Sea of Okhotsk and Bering Sea, 2-year studies have found inverse relationships between prey available to planktivorous and piscivorous birds (Springer et al., 1986; Kitaysky and Golubova, 2000). In the Sea of Okhotsk, this relationship was proposed to be driven by bottom-up processes in which climate regimes affect the movement and distribution of water masses, and thereby the availability of zooplankton and forage fish (Kitaysky and Golubova, 2000). In the Bering Sea in the early 1980s, top-down regulation of zooplankton by pollock was suggested (Springer et al., 1986). (2) In contrast, in the waters off of British Columbia, climate regimes affect plantktivorous and piscivorous seabirds the same way—cold water/late spring is better for birds feeding at both trophic levels (Bertram et al., 2001). These studies illustrate the value of using seabirds to identify differences in ecosystem dynamics, although it is not clear whether the different results reflect fundamental differences in ecosystems due the physical oceanography of shelf systems versus upwelling systems, seasonal

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* Corresponding author. Tel.: +1 907 474 5179.
E-mail addresses: zedmorgan@gmail.com (Z.M. Benowitz-Fredericks), ftmts@uaf.edu (M.T. Shultz), ffask@uaf.edu (A.S. Kitaysky).

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doi:10.1016/j.dsr2.2008.04.007

Please cite this article as: Benowitz-Fredericks, Z. M., et al., Stress hormones suggest opposite trends of food availability for planktivorous and piscivorous seabirds in 2 years. Deep-Sea Research II (2008), doi:10.1016/j.dsr2.2008.04.007

dynamics of prey availability, or prevalence of bottom-up versus top-down processes in different oceanographic regions.

In this study, we focus on inter- and intra-annual dynamics of prey availability to piscivorous and planktivorous seabirds breeding in the southeastern Bering Sea shelf region. Although a single measurement of prey availability is often used as a proxy of relative annual prey availability, for predators the timing and seasonal dynamics of prey availability may be as important as the seasonal biomass of prey. Seasonal dynamics of food availability are particularly important to predators breeding in high latitude environments, because they must meet the high energetic demands of reproduction in a limited time window (Cushing, 1995; Anderson and Piatt, 1999; Bertram et al., 2001). Thus, predators may suffer if prey availability is not aligned with their breeding phenology (and therefore energetic demands). This potential for spatial and temporal mismatch between predators and prey exists at all trophic levels (Cushing, 1995; Anderson and Piatt, 1999). Elucidation of intra-annual seasonal dynamics of zooplankton and forage fish availability to top predators may allow us to identify inter-annual variability which is not evident in a single measurement of prey availability.

Seabirds are marine top predators, and their survival, reproductive success, diet and foraging effort have all been used to infer prey availability (Cairns, 1987; Hatch and Sanger, 1992; Montevecchi, 1993; Furness and Camphuysen, 1997; Suryan et al., 2002; Davoren and Montevecchi, 2003). In most cases, researchers demonstrate strong relationships between these parameters and climatic indices, and hypothesize that the relationships are due to the fact that climate affected prey availability (Guinet et al., 1998; Jones et al., 2002; Gjerdrum et al., 2003; Peck et al., 2004; Bertram et al., 2005; Gaston et al., 2005; Grosbois and Thompson, 2005). This is of critical importance in understanding impacts of climate change on marine top predators, but rarely provides information about intra-seasonal dynamics of prey availability, and does not always shed light on the mechanisms of physical forcing and ecosystem processes (Hunt et al., 2002). Even direct measures of prey abundance (via trawling) may not provide an accurate assessment of what is available to the birds because they do not account for the many foraging decisions that seabirds must make (e.g., diet preference, foraging distance, depth, and foraging effort). In addition, some of the parameters often used to infer prey availability during the reproductive season may reflect other environmental parameters instead (reviewed in Ritz et al., 2005). For example, reproductive parameters are important measures in terms of ultimate consequences for seabird population dynamics, but they may not be a reliable measure of prey availability for several reasons: (1) they are subject to the vagaries of intense short-duration perturbations that are unrelated to prey availability, such as weather or predation events (Braun and Hunt, 1983; Regehr and Montevecchi, 1997); (2) they provide little information about seasonal dynamics of prey availability; (3) they vary among species, depending on the extent to which parents are willing to incur costs to buffer their chicks against fluctuations in prey availability (Cairns, 1987; Kitaysky et al., 2000). In contrast, there are physiological measures of energy balance that integrate the energy expenditure associated with self-maintenance and breeding effort over both short and long time scales.

Corticosterone (CORT) is the primary avian glucocorticoid. Although often referred to as a ‘stress’ hormone, it is the primary mediator of allostasis: the integrated physiological response to both predictable (e.g., developmental or seasonal) and unpredictable (e.g., fluctuations in food availability, predation pressure, sickness) changes in energy balance (McEwen and Wingfield, 2003b). It is secreted from the adrenal glands and functions to mobilize energy stores and adjust behavior and physiology in ways appropriate to the conditions at hand (de Kloet et al., 1999; Scheller and Sekeris, 2003; Boonstra, 2005; Dallman, 2005). Corticosterone in both free-living and captive birds strongly reflects food availability (Kitaysky et al., 1999, 2001, 2007; Pravosudov et al., 2001; Clinchy et al., 2004; Schoech et al., 2004; Pravosudov and Kitaysky, 2006). Elevated CORT indicates that birds have a higher ratio of energy expenditure to food intake. In other words, they are (a) consuming less food (b) consuming lower quality food, or (c) working harder to obtain the same quantity/quality of food. Other factors affect CORT; for instance, two major causes of elevated CORT are sickness (Lindstrom et al., 2005; Silverman et al., 2005; Owen-Ashley et al., 2006), and predation pressure (Blanchard et al., 1998; Cockrem and Silverin, 2002a). However, in this study we reduced the potential sources of variation in CORT by sampling birds that were actively breeding (therefore unlikely to be sick, Owen-Ashley et al., 2006), on relatively predation-free colonies. In this context, seasonal and inter-annual changes in CORT are reliable indicators of changes in food availability, and often also reflect reproductive performance (Buck et al., 2007; Kitaysky et al., 2007). Corticosterone has an added advantage in that its collection is non-lethal, easy to obtain in the field (a series of blood samples following a single capture, compared to the extensive monitoring required to obtain reproductive success or foraging trip data), and allows intensive sampling over large spatial and temporal scales.

We compared the spatial and temporal dynamics of prey availability for planktivorous and piscivorous seabirds, using CORT as a proxy for prey availability. We sampled least auklets (*Aethia pusilla*) and thick-billed murres (*Uria lomvia*) breeding on St. George and St. Paul Islands (the Pribilof Islands) in 2 years: 2003 and 2004. Our goals were to determine (1) whether we could detect inter- or intra-annual differences in CORT and (2) whether these patterns differed for top predators feeding at different trophic levels.

2. Methods

2.1. *Species, study sites and bird capture*

Least auklets (LEAU) and thick-billed murres (TBMU) were captured on two islands: St. Paul Island and St. George Island, in the Bering Sea, Alaska. The two islands are situated ca. 88 km apart in the middle shelf domain of the southeastern Bering Sea (Fig. 1A), an area with relatively high production as a result of local structural fronts and proximity to the shelf-edge (Springer et al., 1996; Hunt et al., 2002).

LEAU are small (mass of adults (mean ± S.E.) in this study = 84 ± 7.4 g), planktivorous seabirds in the Alcid family. They are sexually monomorphic (except for bill depth), and share parental duties (Jones, 1993). In both years on St. George Island, LEAU were captured from both of the two distinct colonies on the island: “Ulakaia Ridge”, a large inland talus ridge on the northern side of the island, and “Zapadni Beach”, a boulder beach on the south side of the island (Fig. 1B). On St. Paul Island, birds were captured at “Tolstoi Point” and “Zapadni Point”, auklet colonies on boulder beaches on opposite sides of a bay on the south side of the island (Fig. 1B) Colonies on both islands were non-contiguous and separated by at least 5 km. Our goal was to sample at least 10 breeding birds from each island three times over the reproductive season (June–September). Birds were captured in nesting areas either in flight (using mist nets) or while walking on rocks (using noose carpets). On each island, LEAU were captured during daylight hours in three sampling periods: 1 (3–17 June), 2 (28 Jun–15 July) and 3 (26 July–2 August). These corresponded with incubation, early- and late-chick rearing. Although we did not access nesting burrows to determine presence of eggs or chicks,

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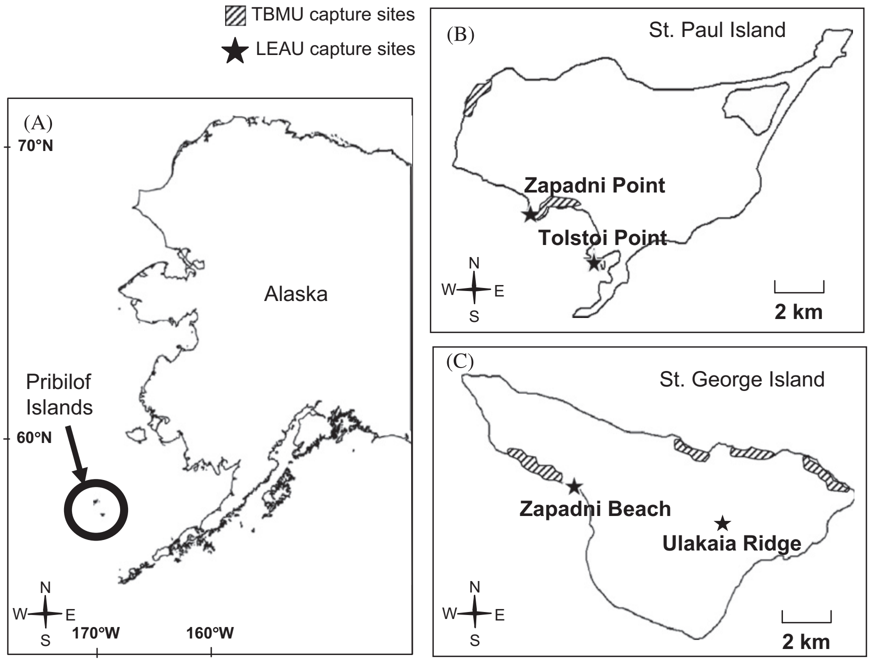

Fig. 1. Study site map showing (A) the location of the Pribilof Islands, and capture locations for thick-billed murres (TBMU; *Uria lomvia*) and least auklets (LEAU; *Aethia pusilla*) on (B) St. Paul Island and (C) St. George Island.

Table 1
Sample sizes for CORT in two seabird species captured at two Pribilof Islands in 2 years

Island	Stage	Species			
		Least auklets		Thick-billed murres	
		2003	2004	2003	2004
St. George	1	10	18[a]	18[a]	10
	2	24[a]	10	26[a]	10
	3	14[a]	10	15[a]	10
St. Paul	1	14[a]	22[a]	8	10
	2	12[a]	20[a]	9	8
	3	–	7	10	7

Stage was determined both by date and by presence of eggs (TBMU), brood patches (both), chicks (TBMU), or chick meals in gular pouches (LEAU). Breeding stages were not synchronous between the two species

[a] Birds were sampled from two physically distinct locations on the same island at that stage—CORT levels did not differ between locations on the same island in any case.

reproductive stages and breeding status of birds were verified by presence of brood patches or plankton in gular pouches (or regurgitation of prey upon capture/handling). In 2003, birds were not sampled on St. Paul during stage 3 (Table 1).

TBMU are large (mean mass of birds in this study $= 1098 \pm 95$ g) alcids, and are generally piscivorous, although they are known to feed on euphausiids and other large invertebrates (Springer et al., 1986; Coyle et al., 1992; Gaston and Hipfner, 2000). They are sexually monomorphic and share parental duties (Gaston and Hipfner, 2000). On the Pribilofs, they do not nest in discrete colonies in the same way that LEAU do, but are distributed non-contiguously on coastal cliffs. In 2003 on St. George Island, 10 TBMU were captured from opposite sides of the island at each sampling period to compare intra-island location effects. In other island-years, birds were taken from multiple locations (Fig. 1C; Table 1). TBMU were captured from nesting ledges using noose poles—9 m telescoping fiberglass poles with monofilament nooses at the end. In each year, TBMU were sampled during daylight hours in three sampling periods: 1 (30 June–10 July), 2 (29 July–13 August) and 3 (17–25 August). These corresponded with incubation, early- and late-chick rearing. Reproductive stages and breeding status of birds were verified by the presence of a brood patch and/or eggs, young chicks, or old chicks at the capture site. Note that TBMU initiate egg laying much later in the season than do LEAU.

2.2. *Blood sampling*

For all birds, initial blood samples were taken within 3 min of capture (contact with net or noose). Catecholamine hormones such as adrenaline are stored and released into circulation almost immediately in response to a stressor like capture. In contrast, elevations in steroid hormones like CORT are not manifest in circulation for several minutes, because they cannot be stored and must first be synthesized in response to the stressor (reviewed in Sapolsky et al., 2000). It has been demonstrated that for birds, blood samples obtained within 3 min of initial capture are a reliable reflection of baseline (pre-capture) levels (reviewed in Romero and Reed, 2005). After the initial sampling, birds were held in breathable mesh bags and additional blood samples were taken at 10, 30 and 50 min post-capture. Use of a $<$3-min sample to obtain baseline CORT concentrations, followed by restraint and serial blood sampling protocol is a standard endocrine technique for assessing CORT production in free-living and captive birds (e.g., Wingfield, 1994; Silverin, 1998; Kitaysky et al., 1999). Because the rate at which CORT levels rise can differ among individuals (Cockrem and Silverin, 2002b; Cockrem, 2004), for each bird we chose the sampling point which yielded the highest levels of CORT. In all cases, this was the 30- or 50-min sample. This parameter (maximum CORT level attained in response to a standardized capture, handling and restraint stressor) reflects the birds' capacity to produce CORT. When animals are exposed to chronic stress and maintain elevated CORT levels for prolonged

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periods of time, their adrenal size and capacity increase and CORT secretion is 'facilitated'. Facilitation results in higher maximum CORT production in response to an acute stressor such as a capture, handling and restraint protocol (Akana et al., 1992; Dallman et al., 2004). Thus, maximum CORT in seabirds provides an integrated measure of stress over a longer time period (weeks) than baseline CORT (days) (Kitaysky et al., 2001, 2002). Because it takes time to effect these changes in adrenal capacity, maximum CORT tends to correspond to baseline CORT measures taken several weeks earlier (Kitaysky et al., 2001, 2002). Three LEAU were released after the baseline sample during the first sampling stage on St. Paul in 2003; therefore sample sizes are smaller for maximum CORT.

All blood was taken from the brachial vein, using sterile single-use 25-gauge (TBMU) or 26-gauge (LEAU) needles (B-D Precision Glide^{TM}). Blood was collected in heparinized microhematocrit tubes, emptied into 0.5-ml microcentrifuge tubes and kept on ice until centrifugation, no more than 8 h after collection. Whole blood was centrifuged for 5 min to separate the plasma from the red blood cells. Plasma was drawn off red blood cells and kept frozen in separate microcentrifuge tubes until assayed for corticosterone. While being held, all birds were banded with metal US Fish and Wildlife bands, which ensured that no individual was sampled twice.

2.3. Hormone assay

Total corticosterone (free and bound fractions) was measured at the University of Alaska Fairbanks, using a radioimmunoassay. For each sample, 20 μl of plasma were equilibrated with 2000 cpm of tritiated corticosterone prior to extraction with 4 ml of distilled dichloromethane. After extraction, percent hormone recovered from each sample was assessed, and used to correct final values. Samples were reconstituted in phosphate buffered saline, split into duplicates and combined with antibody and radiolabel in a radioimmunoassay (Wingfield and Farner, 1975; Wingfield et al., 1991). Dextran-coated charcoal was used to separate antibody-bound hormone from unbound hormone. All samples from one species in an island-year were run in the same assay (four assays per species). Average hormone recovered per sample was 89%. Inter- and intra-assay variations were 7.3% and 2.1%, respectively.

2.4. Data analysis

All analyses were conducted using SAS 9.12 (SAS/STAT, 2003). All CORT data were log-transformed to meet the assumptions of normal distribution and homogeneity of variance required for parametric tests (Zar, 1999).

We tested for intra-island heterogeneity in CORT by conducting ANOVAs for each island-year in stages where we had samples from two locations (Table 1; $n = 7$ for LEAU (both islands, both years), $n = 3$ for TBMU (all three stages on St. George, 2003)). There was no effect of intra-island sampling location on CORT in TBMU ($p > 0.08$ for all comparisons) or for LEAU ($p > 0.1$ for all comparisons), so data from different locations on an island were pooled by stage for subsequent analyses.

Because one of our primary questions was whether planktivorous and piscivorous birds responded differently to inter-annual variation, we first conducted ANOVAs (one with baseline CORT as the dependent variable and one with maximum CORT) that included year, species, and the year × species interaction term. We were not interested in directly comparing CORT levels between species because there are likely to be inherent differences in absolute CORT levels among species that do not reflect relative food availability (Cockrem, 2004). Instead, we wanted to compare inter-annual patterns between species, and thus focused on the year × species interaction term. Specifically, a significant interaction between year and species would suggest that inter-annual food availability changed in different ways for piscivorous and planktivorous species.

In order to assess inter-annual and intra-seasonal patterns of CORT for each species, we used mixed-model ANOVAs (SAS PROC MIXED). Separate models were run for baseline CORT and maximum CORT. For each species, island, year, stage, and year × stage were included as factors in a single model. See Table 1 for sample sizes.

3. Results

3.1. Inverse relationship for planktivorous and piscivorous birds

The significant year × species interaction term showed that the two species responded differently to inter-annual differences (Fig. 2; base CORT year × species term: $F_{1,298} = 31.83$, $p < 0.0001$; maximum CORT year × species term: $F_{1,295} = 21.12$, $p < 0.0001$). There was a significant difference between species (baseline

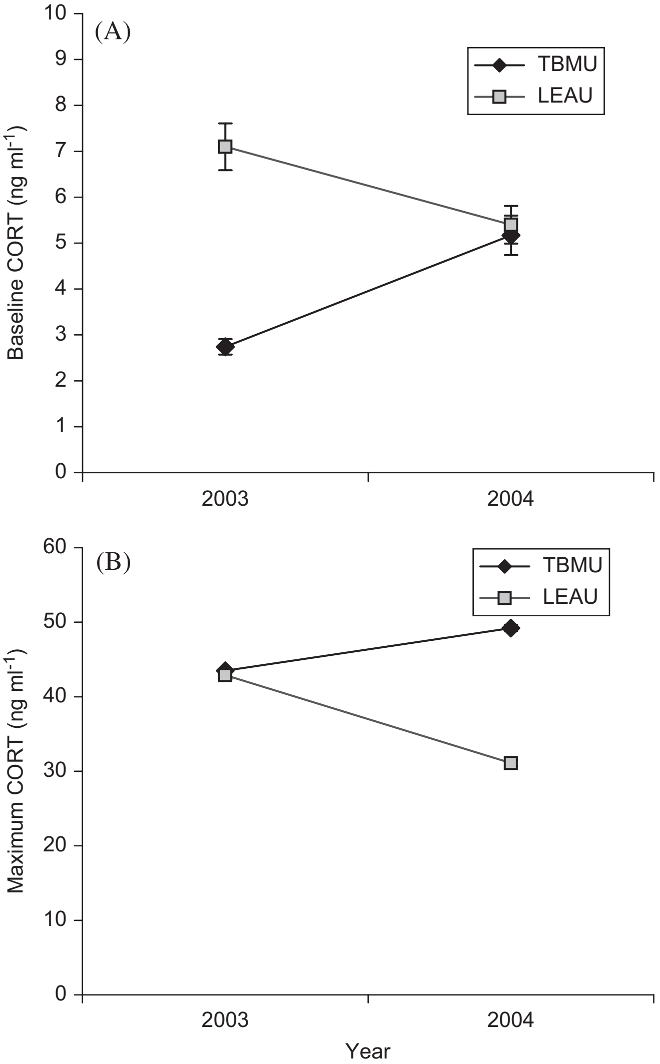

Fig. 2. Mean (±S.E.) annual (A) baseline CORT and (B) maximum CORT in breeding least auklets (LEAU; *Aethia pusilla*) and thick-billed murres (TBMU; *Uria lomvia*) on the Pribilof Islands in 2003 and 2004. S.E. bars are very small for maximum CORT. For auklets, CORT was higher in 2003; the opposite was true for murres.

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CORT: $F_{1,298} = 44.24$, $p < 0.0001$; maximum CORT: $F_{1,295} = 24.59$, $p < 0.0001$) and none between years when both species were pooled (baseline CORT: $F_{1,298} = 2.41$, $p = 0.11$; maximum CORT: $F_{1,295} = 2.97$, $p = 0.08$).

3.2. *Least auklets*

3.2.1. *Baseline CORT*

On average, baseline CORT did not differ between years (Fig. 3A; year effect: $F_{1,154} = 0.46$, $p = 0.50$) or stages (Fig. 3A; stage effect $F_{2,154} = 1.09$, $p = 0.34$). Rather, seasonal dynamics differed in the 2 years (Fig. 3A; year × stage interaction: $F_{2,150} = 13.50$, $p < 0.0001$)—CORT levels declined over the season in 2003, and increased over the season in 2004 (Fig. 3A). Baseline CORT was higher on St. George Island (Fig. 3A; island effect: $F_{1,154} = 5.68$, $p = 0.01$).

3.2.2. *Maximum CORT*

On average, maximum CORT was significantly higher in 2003 (Figs. 2B and 4A; year effect: $F_{1,151} = 9.44$, $p = 0.003$). There were no consistent differences between stages (Fig. 4A; stage effect: $F_{2,151} = 1.23$, $p = 0.30$), but seasonal dynamics were different in the 2 years (Fig. 4A; year × island interaction: $F_{2,151} = 3.6 = 3.60$, $p = 0.04$). There was no difference between islands (island effect: $F_{1,151} = 0.34$, $p = 0.46$).

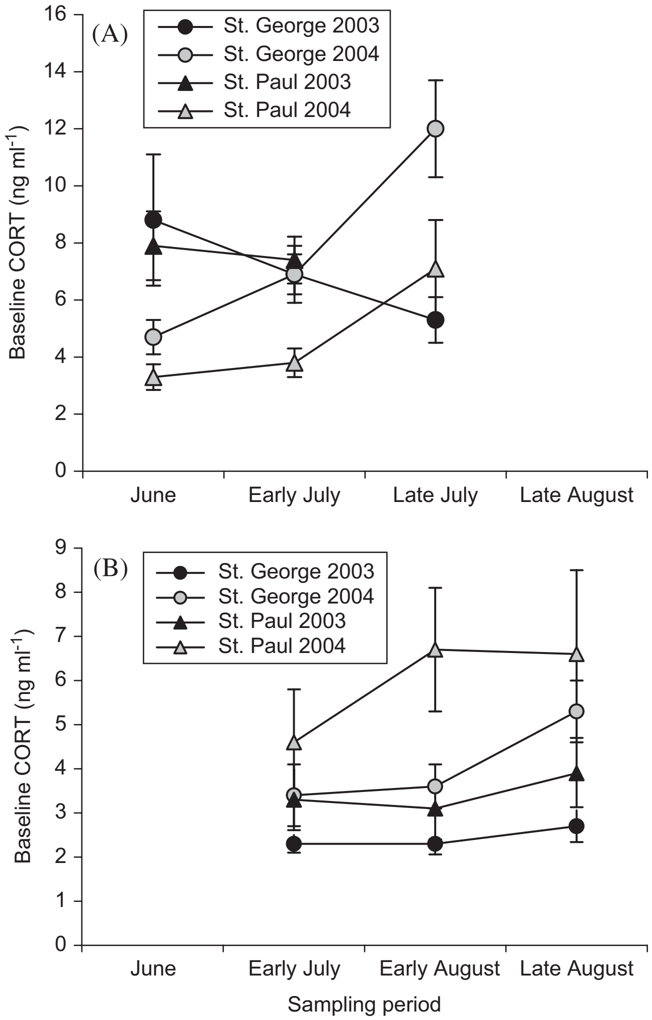

Fig. 3. (A) Seasonal dynamics of baseline CORT (mean±S.E.) in least auklets (LEAU; *Aethia pusilla*) by island and year. 2003 and 2004 showed opposite seasonal dynamics on both islands. (B) Seasonal dynamics of baseline CORT (mean±S.E.) in thick-billed murres (TBMU; *Uria lomvia*) by island and year. St. Paul and St. George showed similar trends, but CORT was generally higher on St. Paul, and rose earlier in the season on St. Paul in 2004.

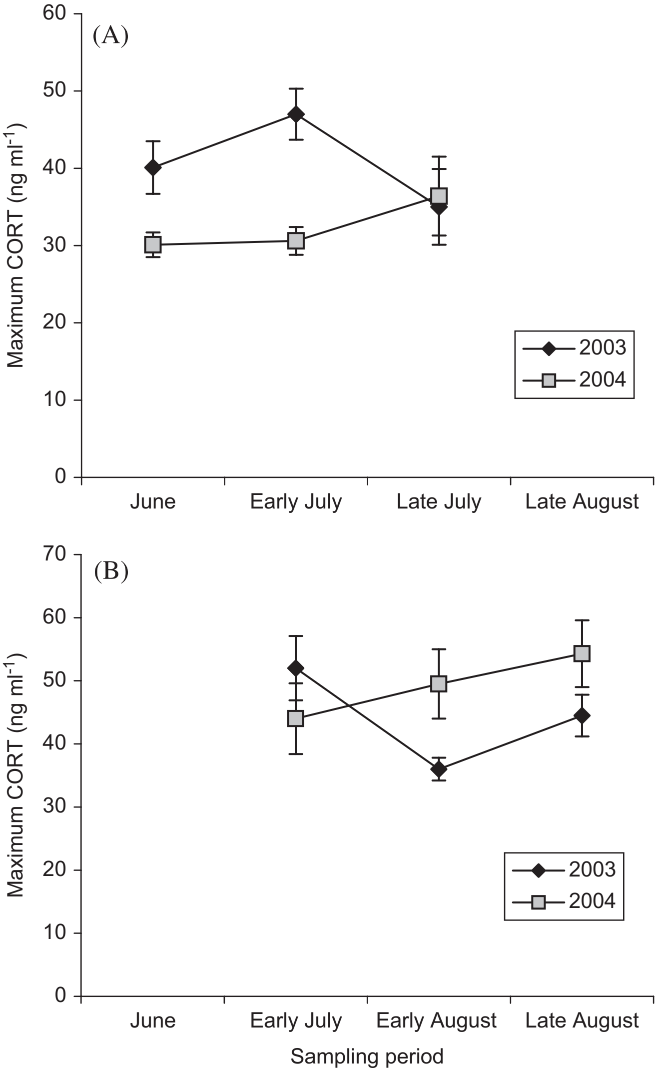

Fig. 4. Seasonal dynamics (mean±S.E.) of maximum CORT in (A) least auklets (LEAU; *Aethia pusilla*) by year and (B) thick-billed murres (TBMU; *Uria lomvia*) by year (both islands pooled). Within years, there were no significant differences in maximum CORT between islands for either species.

3.3. *Thick-billed murres*

3.3.1. *Baseline CORT*

Baseline CORT was significantly higher in 2004 than in 2003 (Fig. 2A; year effect: $F_{1,134} = 26.37$, $p < 0.0001$). Baseline CORT on St. Paul Island was consistently higher than on St. George Island (Fig. 3B; island effect: $F_{1,134} = 7.69$, $p = 0.006$), and increased as the season progressed (Fig. 3B; stage effect: $F_{2,134} = 4.0$, $p < 0.02$). However, seasonal dynamics did not significantly differ by year (Fig. 3B; year × stage interaction: $F_{2,134} = 1.45$, $p = 0.23$).

3.3.2. *Maximum CORT*

There were no significant differences between years (Fig. 2B; year effect: $F_{1,134} = 3.12$, $p = 0.08$), islands (island effect: $F_{1,134} = 0.18$, $p = 0.70$) or stages (Fig. 4B; stage effect: $F_{2,134} = 1.6$, $p = 0.20$). Seasonal dynamics were different in the 2 years (Fig. 4B; year × stage interaction: $F_{2,134} = 3.10$, $p = 0.04$).

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4. Discussion

In 2 years, seabirds breeding on the Pribilof Islands and feeding primarily on large zooplankton (LEAU) or forage fish (TBMU) exhibited different inter- and intra-annual dynamics of CORT. Seabirds have two possible foraging responses to declines in availability of preferred prey (Suryan et al., 2000). (1) Birds could continue feeding on the preferred prey and either work harder to maintain intake or consume less; or alternatively (2) they could switch to less desirable prey that is easier to obtain but less energetically rewarding. Changes in CORT should reflect either of these changes in energy balance (McEwen and Wingfield, 2003a) and therefore, in the context of this study, the availability of bird's preferred prey.

4.1. *Inverse relationship for planktivorous and piscivorous birds*

Our data indicate that planktivorous (LEAU) and piscivorous (TBMU) birds breeding on the Pribilofs respond differently to inter-annual environmental variation. Average annual CORT was higher for planktivorous LEAU in 2003 compared to 2004, but the opposite was true for TBMU (Fig. 2). This pattern in CORT is similar to the inverse patterns of food availability and reproductive success previously observed for planktivorous and piscivorous birds in Bering Sea shelf system (including TBMU and LEAU at the Pribilofs; Springer et al., 1986), and in the Sea of Okhotsk (Kitaysky and Golubova, 2000), and unlike the positive covariation observed in British Columbia (Bertram et al., 2001). Near the Pribilofs, inverse relationships between trophic levels have been attributed to top-down regulation of zooplankton by planktivorous fish (Springer and Roseneau, 1985; Springer et al., 1986; Ciannelli et al., 2002). However, bottom-up processes may also be involved. For example, in Tauyskaya Bay in the Sea of Okhotsk, the distribution and abundance of prey for predators feeding at different trophic levels appeared to be driven by short-term climate regimes that generated different degrees of exchange between warm-water masses in the bay and cold-water masses outside the bay. "Cold" climate regimes resulted in water movement that increased availability of macro-zooplankton and "warm" climate regimes increased availability of meso-zooplankton (and thereby forage fish, who consume meso-zooplankton, Kitaysky and Golubova, 2000).

On the Bering Sea shelf, one physical process proposed to play an important role in determining inter-annual differences in the spring phytoplankton bloom and subsequent dynamics of zooplankton and forage fish is the timing of sea-ice retreat (Hunt et al., 2002; Hunt and Stabeno, 2002; Macklin et al., 2002; Baier and Napp, 2003; Hunt and Megrey, 2005). Specifically, late sea-ice retreat is associated with an early, cold-water phytoplankton bloom, relatively low biomass of small shelf copepods, and poor survival of larval and juvenile forage fish. Early sea-ice retreat is associated with a later, warm-water plankton bloom, a large biomass of small shelf copepods later in the season, and high survival of larval and juvenile forage fish (part of the "Oscillating Control Hypothesis" (OCH), Hunt et al., 2002). The OCH generates a clear prediction for TBMU: availability of their preferred prey should be higher in years of early sea-ice retreat.

A Bering Sea Ice Retreat Index (IRI) is available from the National Oceanic and Atmospheric Administration (NOAA)—it is calculated as the last day of the last week when ice covered more than 10% (by area) of a $2^\circ \times 2^\circ$ grid near NOAA Mooring 2 (56.8°N, 164°W; http://www.beringclimate.noaa.gov/data). The IRI represents the number of days with ice cover remaining after March 15. The larger the value of the IRI, the later the ice retreat (IRI $= 0$ in years when ice was absent in the grid on or before March 15). Although Springer et al.'s (1986) results were consistent with the OCH (more pollock was available and consumed by piscivorous seabirds in 1983 (IRI $= 14$) compared to 1982 (IRI $= 63$)), 2002 and 2003 showed relatively similar timing of ice retreat (IRI 2003 $= 22$, IRI 2004 $= 27$). TBMU CORT levels were consistent with OCH predictions (higher in 2004 when ice retreat was slightly later) despite the small difference in timing of sea-ice retreat. Thus, if bottom-up processes driven by sea-ice retreat are involved, our data speak to the responsiveness of the system to the timing of sea-ice retreat and our ability to detect small signals using CORT in seabirds. We would expect to even find more striking differences in prey availability for piscivorous birds in years with larger differences in timing of ice retreat.

4.2. *Seasonal dynamics of CORT*

We compared CORT dynamics intra-annually as well as inter-annually. For LEAU, seasonal dynamics of CORT varied between years; it was highest during incubation in 2003 and highest during late-chick rearing in 2004 (Fig. 3A). For TBMU, seasonal dynamics of baseline CORT showed no significant differences in the 2 years (CORT tended to be higher during late-chick rearing in both; Fig. 3B). However, CORT data from Pribilof TBMUs in the 1990s clearly demonstrate that there is not a consistent effect of reproductive stage; in some years CORT is higher during incubation, or early-chick rearing (Kitaysky et al., 2002). This suggests that the lack of difference between the 2 years of this study is due to similar seasonal dynamics of TBMU prey. The inter-annual variation in seasonal dynamics of CORT that has been observed in both species indicates that CORT is not a species- or population-specific reflection of the energetic demands of a particular reproductive stage (incubation or chick rearing), but is responsive to seasonal dynamics of prey availability in a given year (see also Kitaysky et al., 2007).

4.3. *Inter-island differences*

St. George Island and St. Paul Island are 88 km apart, in the middle shelf domain of the southeastern Bering Sea. St. George Island is closer to the shelf-edge, thus providing birds with more ready access to these productive foraging areas (Springer et al., 1996; Flint et al., 2002). In general, birds from the two islands exhibited similar seasonal dynamics of CORT (Fig. 3), suggesting that the ecosystem changes responsible for the seasonal dynamics were operating on a scale that affected relative prey availability for birds at both islands similarly. However, oceanographic conditions around the islands can generate different levels and dynamics of productivity and presumably prey availability on smaller scales (Kowalik and Stabeno, 1999; Flint et al., 2002). Indeed, we did observe inter-island differences in 2004: despite similar dynamics on both islands, CORT in LEAU was consistently higher on St. George (Fig. 2A), while for TBMU it was higher on St. Paul (Fig. 2B).

Although TBMU CORT did not show much seasonal variability, in 2004 CORT on St. Paul Island increased earlier in the season than on St. George Island (Fig. 2B). This suggests that St. Paul Island birds had to work harder to obtain prey sooner in the season than birds on St. George Island. Birds from the two islands likely utilize different foraging areas (Kitaysky et al., 2000) and diets of St. George Island birds are more variable than those of St. Paul Island birds (Decker et al., 1995). This presumably reflects access to oceanic prey from the shelf-edge. Such access may buffer them from changes that reduce food availability on the shelf and explain the temporal lag in elevated CORT.

Please cite this article as: Benowitz-Fredericks, Z. M., et al., Stress hormones suggest opposite trends of food availability for planktivorous and piscivorous seabirds in 2 years. Deep-Sea Research II (2008), doi:10.1016/j.dsr2.2008.04.007

In contrast, it is not clear why LEAU on St. George Island in 2004 had more difficulty obtaining prey than those on St. Paul Island (Fig. 2A). We would expect that St. George Island. LEAU, similar to TBMU, would fare consistently better than those on St. Paul Island given their proximity to the shelf-edge. One possibility is that advection of oceanic water onto the shelf can generate localized patches of high prey density around one island or another (Kowalik and Stabeno, 1999). The fact that there are inter-island differences in CORT for both species clearly indicates that smaller scale processes are likely to be determining prey availability around each island, despite the similar seasonal trends.

4.4. *CORT dynamics in least auklets*

CORT data indicate that availability of LEAU prey varied both between and within years.

It is not clear what drives patterns of availability of the large calanoid copepods preferred by LEAU. *Neocalanus plumchrus* or *N. cristatus* tend to dominate LEAU. These species are primarily oceanic (Cooney and Coyle, 1982), but are often advected onto the shelf and found in auklet diets (A. Springer, unpublished; Roby, 1991; Jones, 1993; Hunt et al., 1996, 1998; Hunt, 1997; Flint and Golovkin, 2002). Although the middle domain species *Calanus marshallae* is the primary prey species in some years (e.g., Springer et al., 1986; Hunt et al., 1996), it did not appear to be a significant part of LEAU diets during this study (A. Springer, unpublished).

Average prey availability in 2003 appeared worse than in 2004 (Fig. 2). Our data do not allow us to distinguish between at least two, non-exclusive potential causes for lower LEAU prey availability in 2003: (1) inter-annual variability affected physical processes that altered either abundance or distribution of preferred prey for LEAU on the Pribilof Island. (2) A larger cohort of forage fish consumed and thereby directly reduced abundance and availability of LEAU prey. In terms of bottom-up regulation, relatively little is known about the physical factors affecting the distribution and abundance of *Neocalanus* spp. around the Pribilofs (Napp et al., 2002). However, the movement of large water masses can alter distribution (see discussion of drifter data below; Stabeno et al., 2008, this volume; Kitaysky and Golubova, 2000). In addition, in 2004, abundance of *Neocalanus* spp. was correlated with indices of water column stability and salinity, which suggests a role for climate-driven nutrient availability (Coyle et al., 2008). The fact that TBMU CORT was consistently lower in 2003 (Fig. 2) does suggest that forage fish (TBMU prey) were more abundant in 2003, and implicates top-down regulation as a potential mechanism, but this is contradicted by LEAU CORT data.

CORT dynamics suggest that LEAU prey availability may not be driven by top-down regulation. If a large cohort of juvenile forage fish was directly competing with LEAU for zooplankton prey in 2003, we would expect LEAU CORT to increase as the season progressed and zooplankton stocks became depleted. Instead, LEAU CORT decreased as the season progressed (Fig. 3A), suggesting that either the availability of the prey they were consuming early in the season increased, or new prey items became available. At least on St. Paul Island in 2003, the decrease in CORT appears to have been associated with a diet shift (A. Springer, unpublished).

In 2004, elevated CORT in late July suggests that LEAU had to work harder to obtain prey as the season progressed (Fig. 3A). In this case, preferred prey appears to have disappeared from the system late in the season. LEAU chick diets on St. Paul Island show that *Neocalanus* spp. comprised approximately 80% of regurgitations in early July when CORT was low (Fig. 3A), but literally disappeared (0%) by late July when CORT was high, replaced by euphausiids and crab juveniles (A. Springer, unpublished). This is corroborated by zooplankton sampling data, which indicate that *Neocalanus* spp. were virtually absent from the areas around the Pribilofs in late July and early August 2004 (Coyle et al., 2008). A combination of drifter data and late-season trawls offer a potential explanation for this change in LEAU prey availability.

Currents typically bring nutrient-rich water from the Gulf of Alaska up along the 50 or 100 m isobath and past the Pribilof Islands (Stabeno et al., 2001, 2008). Data from satellite-tracked drifters indicate that in 2004, oceanic water masses originating in the Gulf of Alaska occupied the area around the Pribilof Island from May until mid-July (Stabeno et al., 2008). However, in late July 2004 this oceanic water mass moved away from the Pribilofs. Although we do not know the origin of the water mass that replaced it, Coyle et al. (2008) sampled near the Pribilofs in late July/mid-August and found warm, highly stratified water (presumably of Middle Domain origin) which contained almost no oceanic zooplankton and few forage fishes. Increased CORT may have coincided with the displacement of prey-laden oceanic water by depauperate middle domain water. Thus, prey availability for LEAU may be affected by the proximity, dynamics and prey content of oceanic water masses on the shelf, but this possibility requires further investigation.

4.5. *CORT dynamics in thick-billed murres*

In general, apparent prey availability for TBMU showed less intra-seasonal variability than for LEAU. Forage fish availability may have fluctuated less than zooplankton availability, or TBMU may be buffered by their flexible foraging behavior. Compared to auklets they have access to prey over a wider depth range, due to their diving proficiency (Takahashi et al., 2008), and can forage at other trophic levels (Springer et al., 1986; Coyle et al., 1992; Gaston and Hipfner, 2000). These aspects of their foraging ecology may confer greater resilience to fluctuations in the distribution and density of their preferred prey.

Consistently low CORT in TBMU in 2003 suggests that availability of their prey was relatively good throughout their breeding season (Fig. 3B). 2004 was worse for TBMU, which appeared to have more difficulty obtaining prey overall compared to 2003 (Fig. 2B). In 2004, CORT increased as the season progressed (Figs. 3B and 4B), suggesting that forage fishes became scarce later in the season. Coyle et al. (2008) show that abundance of juvenile pollock, one of their primary prey items (Hunt et al., 1996), was low in the vicinity of the Pribilofs in late July and early August. CORT data are in agreement, but also indicate that the low availability of forage fish late in the season likely reflects a change from earlier in the season, when lower CORT suggests that prey availability was higher (Figs. 3B and 4B). Our data do not offer explanations for the apparent seasonal changes in TBMU prey availability, but scarcity of their own prey is a possibility. If large zooplankton were not abundant late in the season in 2004 (Coyle et al., 2008), forage fish (which consume zooplankton but are not constrained to remain near the islands like breeding seabirds) may have moved elsewhere in search of prey.

4.6. *CORT, population dynamics and reproductive success*

Measures of LEAU population parameters or reproductive success at the Pribilofs are not available. However, TBMU population size and annual reproductive success have been monitored on the Pribilofs (Byrd et al., 2008a, b). Concordance with our data suggests that differences in CORT levels reflect differences in prey availability that have consequences for breeding biology and survival. For example, we found that CORT is consistently higher where populations are declining (St. Paul Island). In terms of reproductive success, CORT was highest on St. Paul Island in 2004, when TBMU had lower reproductive success than St. Paul Island 2003, or St. George Island 2004 (Fig. 3B; Byrd et al., 2008a) Reproductive success is not expected to always reflect food availability (and therefore CORT) during the breeding season (see Section 1). However, these data suggest that food limitation may be involved in both reduced reproductive success and population decline for seabirds breeding at the Pribilofs.

4.7. Conclusions

Stress hormones (CORT) in seabirds reflect spatially and temporally integrated sampling of prey, and the ability to quantify CORT frequently allowed us to identify the presence of changes in the Bering Sea ecosystem with relatively high resolution. In this study, rapid (within weeks) changes in CORT in seabirds suggest seasonal changes in the distribution and abundance of zooplankton and forage fishes that, at least for planktivorous LEAU, differed in 2 years. Differences between the islands in apparent food availability highlight the importance of small-scale differences, potentially driven by factors such as proximity to the shelf and the movement of water masses.

Two successive years yielded nearly opposite prey availability, as inferred from CORT, for seabirds foraging at different trophic levels. In addition, our data suggest that on the Bering Sea shelf, seasonal dynamics of food availability are different for planktivorous and piscivorous birds. Although this study spanned only 2 years, it suggests that climate variability may have inverse effects on prey of planktivorous and piscivorous marine predators in the shelf ecosystems of the North Pacific. Our data do not allow us to determine whether prey availability is regulated by top-down or bottom-up processes, but the two are clearly not exclusive (e.g., Munch et al., 2005). It will be important to determine whether this inverse relationship between trophic levels is upheld in different predator species, and over longer time scales, especially in light of the hypothesis that the regulation of North Pacific ecosystems changes fundamentally in response to regime shifts (Hunt et al., 2002).

Acknowledgments

We thank the following people: C. Hovnanian, J. Klima, T. Dempsey, A. Banks and S. Baker for excellent work in the field, and Z. Kitaiskaia for her meticulous hormone analyses. The Alaska National Maritime Wildlife Refuge, in particular G.V. Byrd and A. Sowls, provided generous logistical support and assistance; K. Sundseth and K. Holser were extremely helpful with on-island logistics. A. Springer shared his unpublished diet data. We are grateful to G. Hunt, A. Macklin, S. Moore, T. Morgan and an anonymous reviewer for comments which substantially improved this manuscript. F. Huettman and C. Williams provided assistance with Fig. 1. This research was supported by NPRB Grant #RO320 to A.S. Kitaysky. Z.M. Benowitz-Fredericks, M.T. Shultz and A.S. Kitaysky were supported by Alaska EPSCoR (NSF #EPS-0346770). Z.M. Benowitz-Fredericks also received support from an NSF predoctoral fellowship.

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