

RESEARCH ARTICLE

Long-term assessment of relationships between changing environmental conditions and the physiology of southern Beaufort Sea polar bears (*Ursus maritimus*)

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Abstract

Climate change is influencing polar bear (*Ursus maritimus*) habitat, diet, and behavior but the effects of these changes on their physiology is not well understood. Blood-based biomarkers are used to assess the physiologic health of individuals but their usefulness for evaluating population health, especially as it relates to changing environmental conditions, has rarely been explored. We describe links between environmental conditions and physiologic functions of southern Beaufort Sea polar bears using data from blood samples collected from 1984 to 2018, a period marked by extensive environmental change. We evaluated associations between 13 physiologic biomarkers and circumpolar (Arctic oscillation index) and regional (wind patterns and ice-free days) environmental metrics and seasonal and demographic co-variables (age, sex, season, and year) known to affect polar bear ecology. We observed signs of dysregulation of water balance in polar bears following years with a lower annual Arctic oscillation index. In addition, liver enzyme values increased over time, which is suggestive of potential hepatocyte damage as the Arctic has warmed. Biomarkers of immune function increased with regional-scale wind patterns and the number of ice-free days over the Beaufort Sea continental shelf and were lower in years with a lower winter Arctic oscillation index, suggesting an increased allocation of energetic resources for immune processes under these conditions. We propose that the variation in polar bear immune and metabolic function is likely indicative of physiologic plasticity, a response that allows polar bears to remain in homeostasis even as they experience changes in nutrition and habitat in response to changing environments.

KEYWORDS

Arctic oscillation, biomarker, climate change, clinical pathology, physiologic plasticity, physiology, polar bear, population health, *Ursus maritimus*, wildlife

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1 | INTRODUCTION

Biomarkers of physiologic function can be powerful in contributing to the understanding of population health because physiology mechanistically connects an individual to its environment (Cooke et al., 2014; Madliger et al., 2018). Blood-based physiologic biomarkers provide dynamic measures of metabolic function including organ system function, electrolyte balance, protein quantity, and nutrition, as well as immune function (Friedrichs et al., 2012). These biomarkers of physiologic function can be used to infer pathologic states in individuals (Cooke et al., 2020; Gånheim et al., 2007; Madliger et al., 2021). Linking individual physiologic changes with abiotic factors is key to understanding the effects of rapid environmental change on population health (Cooke et al., 2020; Madliger & Love, 2015; Moore, 2008). Thus far, most eco-physiological investigations have associated environmental changes with stress hormones in wildlife (see Boonstra et al., 2020; Busch & Hayward, 2009; Möstl & Palme, 2002; Narayan et al., 2019; Sheriff et al., 2011). Studies of other physiological measures, including those referencing immune and metabolic function, are less common, but may result in complementary tools for assessing population health (Cosgrove et al., 2017; Wilson et al., 2021).

The Arctic is warming substantially faster than the rest of the planet (Cohen et al., 2014; DeRepenigny et al., 2020; IPCC, 2018). Environmental changes to Arctic ecosystems include loss of sea ice, increased air and sea temperatures, altered precipitation patterns, and the thawing of permafrost (Box et al., 2019; Frey et al., 2014; Serreze & Meier, 2019; Stroeve & Notz, 2018). Climate-induced environmental changes have resulted in measurable effects on the habitat use, fitness, or health of many Arctic species, including polar bears (*Ursus maritimus*) (Derocher, 2005), sea birds (Irons et al., 2008), reindeer (*Rangifer tarandus platyrhynchus*) (Descamps et al., 2017), ringed-seals (*Pusa hispida*) (Ferguson et al., 2017), and beluga whales (*Delphinapterus leucas*) (Hauser et al., 2016). For polar bears, the loss of sea ice habitat is considered the ultimate threat to their long-term persistence (Atwood, Marcot, et al., 2016; Hamilton & Derocher, 2018; Laidre et al., 2020; Moore & Huntington, 2008).

Polar bears exist throughout ice-covered areas of the circumpolar Arctic in 19 subpopulations (Obbard et al., 2010). Research suggests that climate change may redistribute polar bears (Wiig et al., 2008), alter predator-prey dynamics (Hamilton et al., 2017), and change diet and energetics (Blanchet et al., 2020; Molnár et al., 2009; Pagano & Williams, 2021; Whiteman, 2018). While these effects may ultimately influence subpopulation vital rates (Bromaghin et al., 2021; Hamilton & Derocher, 2018), identifying the mechanistic links between environmental change and population dynamics remains challenging. A key step in addressing that challenge is identifying associations between environmental and population-level changes over time, which requires comprehensive longitudinal data on species experiencing the effects of a changing environment.

The southern Beaufort Sea (SB) subpopulation of polar bears provides an opportunity to investigate the connections between environmental processes and physiologic function. Research on

the SB spans over 40 years and has documented changes in habitat use (Atwood, Peacock, et al., 2016; Rode et al., 2010, 2012), diet (McKinney et al., 2017), aspects of health (Atwood et al., 2015, 2017; Kirk et al., 2010a, 2010b; Routti et al., 2019; Whiteman et al., 2018), and population dynamics, including declines in survival and abundance (Bromaghin et al., 2015, 2021; Regehr et al., 2010), all concomitant with the loss of sea ice habitat. In this study, we sought to identify relationships between environmental processes, abiotic conditions, and polar bear physiology. We used a longitudinal dataset of blood-based measurements that spans several decades to examine associations between environmental change and biomarkers of physiologic function. Our first objective (i) was to investigate relationships between regional-scale (i.e., sea ice phenology and wind speed) and circumpolar-scale (i.e. Arctic Oscillation) environmental processes and a suite of blood-based biomarkers that index metabolic and immune functions. Using models developed for the first objective (i), we then (ii) considered if behaviors including habitat selection, short-term fasting, and reproductive status (for adult females) further influenced variation in analyte values. Our research addresses how biomarkers of polar bear physiologic function are affected by a changing climate and contributes to our understanding of the usefulness of blood-based biomarkers as a tool for assessing the health of wildlife populations experiencing environmental changes (Ames et al., 2020; Burek et al., 2008; Cooke et al., 2014; Madliger et al., 2021).

2 | METHODS

2.1 | Field and diagnostic

We used blood samples from polar bears captured on land and on the sea ice of Alaska's southern Beaufort Sea (USA) from 1983 to 2018. Spring captures (March–May) occurred on sea ice, whereas fall captures (October and November) occurred on either the sea ice or land (Figure 1). Polar bears were located by helicopter and immobilized with a rapid injection dart (Palmer Cap-Chur Equipment) containing Sernylan or M-99 prior to 1987 and, thereafter, zolazepam-tiletamine (Telazol® or Zoletil®, Stirling et al., 1989). These pharmaceuticals should not have an effect on blood biochemistry (Bush & Custer, 1980). Immobilized bears were examined, weighed (kg), marked with a unique ear tag number and tattoo on the upper lip and age was assessed. Bears observed with obvious injuries were excluded from the study. From 2012, bears were implanted with an AVID® subcutaneous microchip. The age was determined by direct observation (cubs of the year and yearlings), by the extraction of a vestigial premolar and an analysis of cementum annuli on initial capture for bears >1 year old, or was based on prior capture history (Atwood, Peacock, et al., 2016; Ramsay & Stirling, 1988). We classified polar bears >4 years old as adults and bears that were 1–4 years old as young. Capture and handling of polar bears were conducted under appropriate research permits and animal care and used approvals, including the

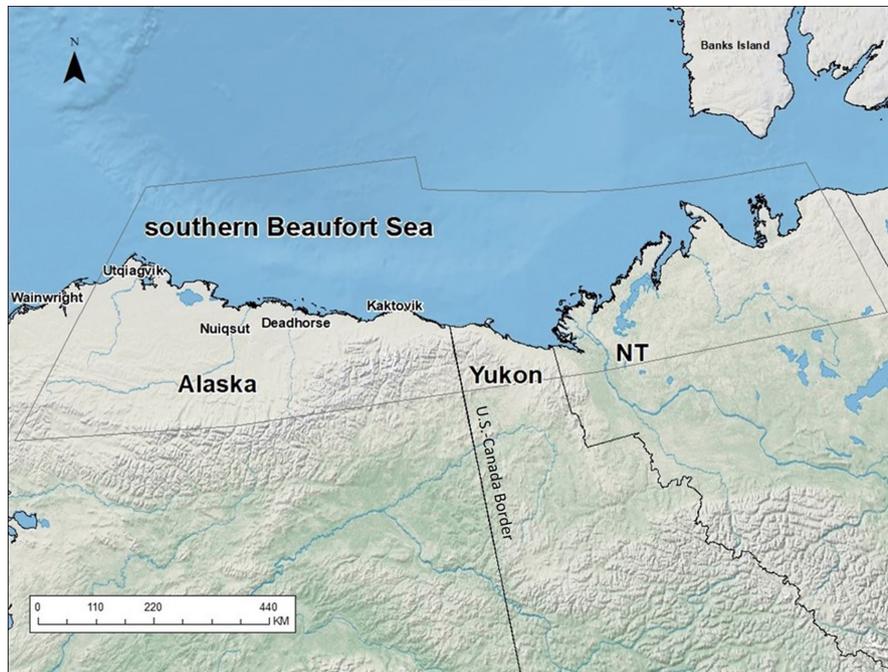


FIGURE 1 Between 1983 and 2018, polar bears were captured within the IUCN defined boundary (thin line) for the southern Beaufort Sea subpopulation between Utqiagvik, Alaska, and the United States–Canada border. Map lines delineated in study areas do not necessarily depict accepted national boundaries.

most recently Marine Mammal Research Permit MA690038-17 and USGS IACUC approval 2017-03.

Blood was collected into evacuated plain tubes (Vacutainer; BD Biosciences) by venipuncture of the femoral vein and was stored in a cooler with chemical heat packs to prevent freezing. Upon returning from the field each day, the serum was separated from blood by centrifugation at 1500g for 5 min (TRIAC, Clay Adams) and frozen at -20°C . Frozen sera were transported to the laboratory and stored at -70°C until analyzed. All serum samples were analyzed on the same VetScan VS2 biochemistry analyzer (Abaxis, Union City, California) using a comprehensive diagnostic panel commonly used to assess general physiologic health in animals (Fry et al., 2019; Thrall et al., 2012). The panel included measurements of the following analytes: alanine aminotransferase (ALT), alkaline phosphatase (ALP), albumin (ALB), blood urea nitrogen (BUN), calcium (Ca), creatinine (CREA), phosphorus, sodium, and total protein (TP). Globulin (GLOB) was calculated by subtracting ALB from TP. For some samples, only a subset of these analytes was available. The functional and interpretive characteristics of the biomarkers evaluated are summarized in Table 1 (recreated from Fry et al., 2019). The long-term stability of stored blood samples can be a concern in retrospective studies. Based on the literature (Cray et al., 2009; Reynolds et al., 2006), analyte stability is optimized when blood-based samples are curated immediately after collection and stored at -70°C for the long-term, as was the case with our samples. We verified sample stability by comparing analyte panel values from a subset of individuals whose samples were stored for different lengths of time (i.e., 2–8 years) and run on the same VetScan VS2 unit (see Appendix S1). Because we observed significant differences in serum protein (ALB, GLOB, $p < .01$) values relative to storage time, we exercised caution in interpreting those analyte results.

Between 2005 and 2018, a complete blood count (CBC) was performed on whole blood samples on the day of capture. Blood for CBC analysis was collected into vacutainers containing potassium EDTA (Vacutainer; BD Biosciences) and transported as described above. CBC included total white blood cell count (WBC), differential blood cell counts, and packed cell volume (PCV) and was conducted manually as described by Kirk et al. (2010a) for captures before 2008 and using a diagnostic analyzer (HM5, Abaxis) from 2008. Differential blood cell counts included counts of neutrophils and lymphocytes, which enabled us to evaluate an increased ratio as a measure of acute stress (see Table 1).

2.2 | Statistical analysis

Our analysis was designed to evaluate the influence of environmental processes occurring at different temporal and spatial scales on biomarkers of physiology (Table 1) and was not designed to predict relationships. We evaluated how biomarker values correlate with variation in circumpolar- and/or regional-scale atmospheric circulation and weather, which are known to influence sea ice phenology, habitat quality, and access to and condition of prey (Atwood et al., 2021; McKinney et al., 2017; Pilfold et al., 2015; Rigor et al., 2002; Rode, Regehr, et al., 2021; Stroeve et al., 2011). We evaluated the effects of these processes using the Arctic oscillation (AO) index, the number of ice-free days over the continental shelf, and wind speed. We further explored the extent to which differences in summer habitat selection (i.e., use of land versus sea ice), breeding status of females, and short-term fasting status influenced physiologic biomarkers. Because demographic characteristics of polar bears and season affect physiology (Atwood, Peacock, et al., 2016; Derocher et al., 1990; Fry et al., 2019;

TABLE 1 Summary of blood-based analytes; physiologic function.

	Analyte (dependent variable)	Brief interpretive use	Metabolic function	Immune function
Liver enzymes	Alanine transferase (ALT)	Increases with some hepatic and severe muscle disorders	X	
	Alkaline phosphatase (ALP)	Increases in some liver and bone disorders; increases during active bone growth (juveniles)	X	
Proteins	Albumin (ALB)	Synthesized by liver; source of amino acids; acts as carrier protein; increases with dehydration; a negative acute phase protein; decreases in inflammatory responses; as globulin increases. Chronic inflammation should lead to decreased albumin; decreases with some liver and renal disorders	X	X
	Globulin (GLOB)	A positive phase protein that when increased indicates an immune response of significant duration (several days or more); individual globulins can be measured for specific information		X
	Total protein (TP)	Changes in TP are reflected by changes in albumin, globulins, or both	X	X
Kidney function	Blood urea nitrogen (BUN)	Product of protein catabolism; source of nitrogen for protein synthesis; eliminated primarily by kidney; decreases with low protein intake and liver failure; increases with high protein meals and with decreased renal elimination (↓ Glomerular filtration rate (GFR))	X	
	Creatinine (CREA)	Catabolic product of muscle; eliminated through kidney; low muscle mass results in lower basal concentrations; increases with decreased renal elimination (↓GFR).	X	
	Phosphorous	Structural component of bone; important anion for energy generation (ATP); increases with decreased renal elimination (↓GFR)	X	
Electrolytes	Sodium	Important cation for osmoregulation; strictly regulated by renal and hormonal function	X	
	Calcium	Structural component of bone; hormonally regulated	X	
	White blood cell count (WBC)	Generally, a measure of immune function including acute infection resulting from injury, infection, inflammation, or general pathology		X
Complete blood count	Neutrophil:lymphocyte ratio (N:L ratio)	Increased ratio suggests acute stress		X
	Packed cell volume (PCV)	Decreased PCV indicates anemia associated with hemorrhage or inflammation; increases suggest dehydration	X	

Kirk et al., 2010a; Rode et al., 2017; Rode, Regehr, et al., 2021; Whiteman et al., 2015, 2018), we included sex, age, and denning status, as well as season of capture and year as co-variates in our analysis.

The AO index is a measure of the variability in sea-level atmospheric pressure, surface air temperature, and surface winds over the Arctic (Ogi et al., 2016; Rigor et al., 2002; Thompson & Wallace, 1998) and has been shown to affect polar bear diet (McKinney et al., 2017), body condition and behavior (Pilfold et al., 2015; Rode et al., 2018), and ringed seal (*Pusa hispida*) condition and vital rates (Ferguson et al., 2017, 2020; Harwood et al., 2020). A lower AO is associated with sea ice persisting longer during spring, a higher proportion of multi-year ice present, and fall freeze-up occurring earlier across the Arctic basin (i.e., the annual ice-free season is shorter) (Rigor et al., 2002). In years with higher AO, the opposite effects prevail, including delayed sea ice formation in the fall, which extends the number of ice-free days during late summer and early fall (Rigor et al., 2002; Stroeve et al., 2011). We included two measures of the AO index in our model, the average annual AO (AAO) and the winter AO (WAO) to evaluate the influence of circumpolar-scale environmental processes on polar bear physiology. AAO was calculated by averaging monthly AO in the calendar year prior to capture. This metric, which ranges from -2 to 2, captures annual atmospheric circulation patterns that may affect sea ice conditions experienced by SB polar bears prior to capture. The winter AO is a more proximate measure of the AO index as it relates to spring sea ice conditions. The WAO was calculated as the mean AO for the months of January–March in the year of capture. We expected that during years with a higher WAO sea ice would be thinner and break up more easily, resulting in increased lead formation, which provides hunting habitat for polar bears (Rigor et al., 2002). We calculated AAO and WAO using data reported by

the Climate Prediction Center, National Weather Service, National Oceanic and Atmospheric Administration (<https://www.cpc.ncep.noaa.gov/products/precip/CWlink/>).

We used indices of sea ice phenology (ice-free days) and sea surface windspeed (mean and standard deviation in the 14 days prior to capture) to assess relationships between regional-scale environmental conditions and physiologic function. Sea ice data were obtained from the National Snow and Ice Data Center (NSIDC) and processed as described in Atwood et al. (2021). We considered the number of ice-free days over the continental shelf in the SB based on sea ice concentrations of $\leq 50\%$ [50] and $\leq 15\%$ [15]. Polar bears generally prefer sea ice concentrations $>50\%$, although SB polar bears have been shown to tolerate lower sea ice concentrations (Durner et al., 2009; Pagano & Williams, 2021). Further, 15% sea ice is the minimum concentration reliably detected from imagery (Stern & Laidre, 2016). Sea ice concentration data were obtained using 25×25 km resolution raster of passive microwave satellite imagery (Cavalieri et al., 2006).

Wind speeds influence sea ice movement, affecting the formation and closure of leads and, subsequently, the distribution of sea ice foraging habitat (Carlens et al., 2006; Pilfold et al., 2015; Rode et al., 2017). We extracted offshore wind speed from the North American Regional Reanalysis (NARR) at 11 NARR grid points distributed longitudinally from Utqiagvik, Alaska, USA, to the MacKenzie River Delta, Northwest Territories, Canada. NARR wind estimates were disseminated as u, v vector components with 3-h periodicity. Briefly, we derived wind speeds (m/s) from the u, v components, averaged them daily, and then for each capture date, we calculated the 14-day average and standard deviation from daily means (Atwood et al., 2021). Table 2 summarizes the climate variables and co-variates used to model changes in blood-based biomarkers.

TABLE 2 Description of model parameters.

	Variable	Description
Environmental processes	Mean wind speed ¹	Mean wind speed in SB 14 days prior to capture
	Variability of wind speed ¹	Standard deviation of wind speed in SB 14 days prior to capture
	Ice-free days 15% ²	Number of ice-free days over the continental shelf in the SB in year prior to capture as determined by 15% sea ice concentration (Cavalieri et al., 2006)
	Ice-free days 50% ²	Number of ice-free days over the continental shelf in the SB (two concentrations) as determined by 50% sea ice concentration (Cavalieri et al., 2006)
	Arctic oscillation (AO) ³	Mean of monthly Arctic oscillation index in the year prior to capture
	Winter Arctic oscillation (WAO) ³	Mean monthly AO for January–March of year of capture
Co-variates	Capture year	Calendar year of capture
	Season	Spring (March–May)/Fall (October–November)
	Denning status	Captured with cubs of the year
	Age class	Young (1–4 years old)/adult >4 years old
Behavior	On/off-shore status	Polar bears with $>5\%$ bowhead in diet were considered onshore bears
	Fasting status	Polar bears with a blood urea nitrogen:creatinine ratio ≤ 12.7 were considered to be fasting for the 10 days prior to capture
	Breeding status	Females captured without cubs were considered to be breeding

Note: ^{a,b}Variables were not included in the same models, ^cindex ranges from -2 to 2.

We analyzed data for male and female polar bears separately using linear model selection procedure for all possible models, with each biomarker as the dependent variable using the leaps package (v3.1; Miller & Lumley, 2020) in R 3.5.0 (R Core Team, 2018). Visual inspection of covariates were examined and there were no trends that suggested interaction effects between co-variables. We report significant dependent variables of all models within $\Delta 2\text{BIC}$ (Bayesian Information Criterion) of the model with the lowest BIC (Burnham & Anderson, 2004; Tredennick et al., 2021). We calculated 85% confidence intervals to identify potentially uninformative parameters in models (Arnold, 2010) and checked for multicollinearity of variables in the top models using variance inflation factors. We used the natural log transformation of ALP, BUN and WBC to standardize their distributions and calculated z-scores to standardize the ice-free days and wind variables.

We successively added each of three behavior variables (summer onshore habitat-use, recent fasting condition, and breeding status), individually, to each model with the lowest BIC to evaluate the influence of the behavior on the biomarker. Bowhead whales (*Balaena mysticetus*) are available to SB bears in summer and fall through scavenging whale remains left on land by subsistence hunters (Herreman & Peacock, 2013; Rogers et al., 2015). To evaluate the influence of on-shore/off-shore habitat use we used dietary data from a subset of polar bears sampled between 2005 and 2016 as part of another study (Bourque et al., 2020; McKinney et al., 2017) to assign bears to summer habitat use categories (onshore or sea ice). Bears with >5% bowhead whale in their diet were considered to have used on-shore habitat during the summer prior to capture (see Atwood, Marcot, et al., 2016). To ascertain fasting status, we calculated the BUN:CREA ratio ((BUN \times 0.466)/CREA) and considered individuals with serum BUN:CREA ≤ 12.7 to have been fasting during the 10 days prior to capture (Cherry et al., 2009; Nelson et al., 1984; Rode et al., 2017). We considered all adult females without cubs to be capable of breeding in the spring of capture, while females captured in spring with cubs-of-the-year and yearlings were not in breeding condition. We compared the log likelihood ratio for the nested models, the model with the lowest BIC with the behavior added as a parameter, and the same model without the behavior, using a chi-squared test.

The data that support the findings of this study are openly available in USGS Alaska Science Center data repository at

<https://www.usgs.gov/centers/alaska-science-center/data>;
<https://doi.org/10.5066/P9OXCJR6>.

3 | RESULTS

We analyzed blood samples from 1258 polar bear captures between 1983 and 2018. Individual polar bears were included in the sample population only once per calendar year. Of these samples, only a small fraction of bears in our sample population was captured more than once (<18%) and with a mean of more than 5 years between those captures. We evaluated whether repeated captures of bears affected analyte values using a general linear mixed model with individual as the random effect and found no difference in results with and without the random term. Sample sizes for biomarkers varied by demographic class and sampling season (Table 3) with subsets of this population to evaluate each of the behaviors (Table 4). The two measures of ice-free days (ice-free [50] and ice-free [15]) and the wind variables (mean wind speed and variability of wind speed) were correlated, and thus not included in the same models ($R_{\text{corr}}=0.89$, $R_{\text{corr}}=0.79$, respectively, $p>.05$). No other predictor variables were correlated. We report the coefficients of significant variables ($p\leq.05$) and coefficients of determination of all models within $\Delta\text{BIC}\leq 2$ for females (Table 5) and males (Table 6). Figures of environmental processes that significantly influenced blood-based biomarkers of physiologic function are shown in Appendix S2.

3.1 | Model selection: Female SB polar bears

Demographic and seasonal covariates were included in top models for all analytes, whereas associations between analytes and environmental parameters varied (Table 5). BUN declined in years with a positive WAO for denning females, and with capture year, and increased with the number of ice-free days based on 15% sea ice concentration. CREA levels were lower for individuals captured during spring, declined with mean wind speed and age, and increased for denning females. Sodium levels were lower for bears captured during spring and significantly higher in years with a lower AAO in the year prior to capture. Calcium and phosphorous levels were higher

TABLE 3 Maximum (minimum) sample sizes for model analysis of blood-based biomarkers.

	Females						Males			
	Spring			Fall			Spring		Fall	
	Adults	Adults with cubs of the year	Young	Adults	Adults with cubs of the year	Young	Adult	Young	Adult	Young
Serum based analytes	368 (354)	100 (92)	69 (65)	110 (108)	9 (9)	41 (41)	252 (546)	64 (63)	21 (20)	17 (17)
Complete blood counts	154 (141)	31 (19)	32 (32)	17 (9)	7 (5)	5 (5)	150 (149)	34 (34)	No data	No data

TABLE 4 Number of polar bear samples available to assess the influence of summer behavior, fasting, and breeding on blood biomarkers.

	Sample size ^a			
	Females		Males	
	On-ice	On-shore	On-ice	On-shore
Summer habitat use	94	123	60	145
Fasting status	Fasting: 552	Not fasting: 153	Fasting: 312	Not fasting: 42
Breeding status	Not breeding: 219		Breeding: 586	NA NA

^aMaximum sample size varied by analyte.

in young females and had opposite responses to season and capture year, with calcium levels lower in spring and increasing with year, and phosphorus levels higher in spring and decreasing with year.

The liver enzymes ALT and ALP were not associated with any of the environmental parameters; however, activity of these enzymes increased annually and was lower in females with cubs of the year. ALT activity in female polar bears was lower in spring than in fall. ALP activity was higher in young individuals.

Associations between environmental processes and markers of immune function varied considerably among models. GLOB increased with the number of ice-free days (15% sea ice concentration) and in years with a lower WAO. ALB decreased during years with a higher WAO, while WBC increased when wind speeds were more variable. GLOB, ALB, TP, WBC, and N:L ratio varied with capture season and demographic co-variables (age class and denning status). GLOB and TP concentrations and N:L ratios were lower during spring and in young bears. Markers of immune function (WBC, TP, ALB) declined over time in females with cubs of the year.

The addition of behavior parameters improved model fit for ALP, phosphorous, calcium, and WBC. ALP activity increased in female bears that used onshore habitat, were breeding, and that had eaten within the 10 days prior to capture. Phosphorus levels were significantly higher in bears that appeared to have recently eaten (i.e., BUN:CREA > 12.7). Calcium and WBC concentrations were significantly higher in mating females (Table 7).

3.2 | Model selection: Male SB polar bears

For male polar bears, environmental parameters were more often associated with biomarkers than for female bears (Table 6). BUN increased with variation in wind speed and was significantly lower during spring than during fall. CREA levels increased with capture year and declined as ice-free days and mean wind speed increased. Sodium increased with lower AAO and was lower for bears captured during the spring, following the same patterns as female polar bears.

The top model for phosphorous included a negative relationship with ice-free days. Influence of the AAO on ALB levels was mitigated by the WAO during the year of capture. ALB and GLOB showed opposite responses to ice-free days, with ALB levels declining and GLOB increasing. These opposing trends resulted in TP levels remaining unchanged.

ALT activity was not associated with environmental variables but increased significantly with capture year and was lower in young bears. ALP activity increased as the number of ice-free days increased and declined with WAO. PCV increased with a declining AAO. WBC and the N:L ratio were lower in younger individuals and WBC count declined with WAO.

The addition of behavior parameters in the top models significantly improved model fit for six analytes. Males that had been fasting prior to capture showed increased liver enzyme activity (ALT and ALP) and phosphorous levels, whereas use of onshore habitat resulted in declines in ALB, CREA, and calcium levels (Table 6).

4 | DISCUSSION

We show that measures of atmospheric conditions, sea ice availability, and wind are associated with biomarkers of metabolic and immune function of SB polar bears. Responses of some analytes (sodium, phosphorous, and PCV) varied with circumpolar-scale parameters; whereas others (WBC, BUN, ALB, GLOB, CREA) varied with regional-scale parameters (i.e., wind speed and ice-free days). Biomarkers of acute and chronic immune function (e.g., WBC and ALB, and GLOB, respectively) varied with the time-lagged effects of the AAO and sea ice conditions. Collectively, these results provide evidence of associations between polar bear physiology and climate-driven changes to the Arctic ecosystem (Atwood, Peacock, et al., 2016; McKinney et al., 2013, 2017; Pagano et al., 2021).

Several of the biomarkers we evaluated (e.g., sodium, CREA, BUN, proteins, and PCV) are used, in part, to assess water balance, which is linked to diet in polar bears (Table 1). Polar bears showed increases in sodium (males and females) and PCV (males only) in the spring following a year when the AAO was in a negative phase. Sodium is an important and narrowly regulated cation of osmoregulation that is hormonally maintained through intake and excretion. Such fluctuations in sodium suggest hemoconcentration, a response that may be driven by changes in diet. We hypothesized that the significant changes observed in sodium, BUN, and PCV may be correlated with the ability of polar bears to maintain consistent access to a fat-rich diet. We did not analyze polar bear nutrition in our study, but our hypothesis regarding hemoconcentration is supported by recent diet and nutrition analyses in the SB (Pagano et al., 2018; Rode, Robbins, et al., 2021). Polar bears primarily obtain water by catabolizing fat from marine mammal prey (Nelson, 1987). Ringed seals, the primary prey of polar bears, showed declines in blubber thickness in years with a lower WAO (Harwood et al., 2020) and reduced reproductive rates with a lower AAO (Nguyen et al., 2017). Changes in the abundance and/or condition of prey could result in decreased

TABLE 5 Summary of the significant coefficients (standard error, *p*-value) in the top models (within 2.0 Δ BIC from the top model) describing the influence of climate and demography on blood-based biomarkers in female SB polar bears.

Analyte	Climate and weather parameters				Demographic parameters				Model fit			
	AAO ¹	WAO	Number ice-free days ^{2a,b}	Mean wind speed ³	Standard deviation wind speed ³	Year	Season ⁴	Age class ⁶	Denning ⁵	Adjusted R ²	BIC	Δ BIC
ALT						0.64 (.04)**	-3.17 (.83)**		-6.81 (.94)**	0.32	-243.70	0
				0.92 (.38)**		0.63 (.04)**	-2.43 (.88)**		-6.95 (.93)**	0.33	-242.83	0.89
			1.27 (.35)**			0.6 (.04)**			-7.31 (.93)**	0.32	-241.90	1.79
ALP						0.01 (.01)**		0.65 (.09)**	-0.37 (.09)**	0.12	-62.14	na ⁷
			0.11 (.03) ^{2a***}					0.63 (.09)**	-0.36 (.09)**	0.12	-61.57	0.57
ALB	0.06 (.02)**								-0.19 (.05)**	0.03	-4.18	na
GLOB	-0.05 (.02)**		0.09 (.02) ^{2a***}				-0.58 (.04)**	-0.19 (.05)**		0.22	-144.91	0
			0.10 (.02) ^{2a***}				-0.57 (.04)**	-0.18 (.05)**		0.22	-143.60	1.31
TP						0.01 (0)		-0.20 (.07)**	-0.28 (.07)	0.16	-89.49	0
							-0.6 (.06)**	-0.2 (.07)**		0.15	-88.40	1.09
BUN	-0.07 (.03)**		0.14 (.05) ^{2a**}			-0.02 (0)			-0.22 (.08)**	0.04	3.11	0.00
			0.14 (.05) ^{2a**}			-0.02 (0)			-0.23 (.08)**	0.03	3.44	0.33
			0.14 (.05) ^{2a**}						-0.24 (.08)**	0.01	3.73	0.62
	-0.07 (.03)**								-0.23 (.08)**	0.02	4.04	0.93
	-0.08 (.03)**		0.14 (.05) ^{2a**}			-0.02 (0)				0.03	4.56	1.45
	-0.06 (.03)**		0.12 (.06) ^{2b**}			-0.02 (0)				0.03	5.11	2.01
CREA				-0.03 (.01)**			-0.09 (.03)**	-0.09 (.03)**	0.09 (.03)**	0.04	-2.46	na

(Continues)

TABLE 5 (Continued)

Analyte	Climate and weather parameters				Demographic parameters				Model fit			
	AAO ¹	WAO	Number ice-free days ^{2a,b}	Mean wind speed ³	Standard deviation wind speed ³	Year	Season ⁴	Age class ⁶	Denning ⁵	Adjusted R ²	BIC	ΔBIC
Sodium	-2.39 (.69)***					0.02 (0)***	-4.52 (.64)***			0.09	-51.4	na
Calcium						0.02 (0)***	-0.37 (.09)**	0.32 (.1)**		0.07	-24.34	na
Phosphorous						-0.02 (.01)**	0.40 (.13)**	0.40 (.15)**		0.03	1.34	0.00
						-0.02 (.01)**	0.37 (.13)**			0.02	2.03	0.69
	0.38 (.14)**					-0.02 (.01)**	0.44 (.13)**	0.42 (.15)**		0.02	2.15	0.81
		0.11 (.05)*				-0.02 (.01)**				0.04	2.72	1.38
	0.31 (.14)*					-0.02 (.01)**	0.35 (.13)**	0.4 (.15)**		0.01	2.75	1.41
	0.37 (.14)**					-0.02 (.01)**	0.35 (.15)*			0.04	2.94	1.60
	0.38 (.13)*			-0.13 (.06)*		-0.02 (.01)**				0.03	3.14	1.81
WBC					0.14 (.04)***			0.15 (.06)**	-0.25 (.06)***	0.15	-21.61	0
										0.13	-19.89	1.72
N:L ratio							-3.26 (.77)***	-2.50 (.7)***		0.11	-12.2	na
PCV							-8.47 (1.19)***	2.44 (.9)**	-2.80 (1.05)**	0.22	-33.88	0
			0.74 (.36) ^{2a*}				-7.93 (1.21)***	2.38 (.89)**	-2.84 (1.04)**	0.23	-32.69	1.19
							-7.72 (1.17)***	2.85 (0.9)**		0.2	-32.1	1.78

Note: ¹Year prior to capture, ²sea ice concentration in year prior to capture, ^{2a}15% cover, ^{2b}50% cover, ³14 days prior to capture, reference is ⁴Fall, ⁵not denning, ⁶adult, ⁷na = no model within 2 ΔBIC of the presented model.

p* < .05; *p* < .01; ****p* < .001.

TABLE 6 Summary of the coefficients (standard error) in the top modes (within 2.0 Δ BIC from the top model) describing the influence of climate and demography on blood-based biomarkers in male SB polar bears.

Analyte	Climate and weather parameters				Demographic parameters				Model fit		
	AAO ¹	WAO	Number ice-free days ^{2a,b}	Mean wind speed ³	Standard deviation wind speed ³	Year	Season ⁴	Age class ⁵	Adjusted R ²	BIC	Δ BIC
ALT						1.04 (.15)***		-13.41 (.3)*	0.18	-54.68	na ⁶
ALP		0.15 (.04)***	0.21 (.04) ^{2b} ***				-0.50 (.13)***	0.45 (.09)***	0.16	-35.16	0
		0.1 (.04)*	0.22 (.04) ^{2a} ***				-0.44 (.13)***	0.45 (.09)***	0.16	-34.07	1.09
			0.22 (.04) ^{2a} ***				-0.42 (.13)**	0.45 (.09)***	0.15	-33.98	1.18
ALB	-0.16 (.06)**	0.1 (.02)***	-0.1 (.02) ^{2a} ***						0.09	-14.68	0
	-0.16 (.06)*	0.09 (.02)***	-0.1 (.02) ^{2a} ***		0.05 (.02)*				0.11	-14.51	0.17
		0.08 (.02)***	-0.11 (.02) ^{2a} ***						0.08	-13.84	0.84
		0.08 (.02)***	-0.11 (.02) ^{2a} ***		0.05 (.02)**				0.09	-13.73	0.95
GLOB			0.13 (.03) ^{2a} ***			-0.27 (.08)**		-0.32 (.06)***	0.13	-26.85	0
	0.16 (.07)*		0.12 (.03) ^{2a} ***			-0.28 (.08)**		-0.31 (.06)**	0.14	-26.22	0.63
	0.2 (.07)***	-0.06 (.03)*	0.12 (.03) ^{2a} ***			-0.27 (.08)**		-0.31 (.06)***	0.15	-26.2	0.65
TP						-0.25 (.09)**		-0.23 (.06)**	0.05	-0.99	0
					0.06 (.02)**			-0.22 (.06)***	0.04	0.56	1.55
BUN					0.1 (.04)*		-0.41 (.15)**		0.05	-1.05	0
							-0.51 (.14)***		0.03	-1	-1
				0.1 (.05)*			-0.39 (.15)*		0.04	-0.18	0.87
				0.15 (.04)***					0.03	0.48	1.53
CREA			-0.13 (.04) ^{2a} ***			0.01 (0)***		-0.31 (.04)***	0.28	-88.63	0
Sodium	-1.99 (.77)**						-3.37 (.89)***		0.06	-4.45	0
	-2.02 (.76)**						-4.12 (.95)***		0.07	-3.63	0.82
							-3.55 (.9)***		0.04	-3.58	0.87
Calcium								0.43 (.09)***	0.06	-9.97	0.00
					0.07 (.04)*			0.41 (.09)***	0.07	-8.52	1.46
					0.01 (0)*			0.45 (.09)***	0.06	-8.35	1.62
					0.01 (0)**			0.42 (.09)***	0.08	-8.02	1.96
					0.01 (0)*			0.43 (.09)***	0.08	-7.99	1.99

(Continues)

TABLE 6 (Continued)

Analyte	Climate and weather parameters				Demographic parameters			Model fit			
	AAO ¹	WAO	Number ice-free days ^{2a,b}	Mean wind speed ³	Standard deviation wind speed ³	Year	Season ⁴	Age class ⁵	Adjusted R ²	BIC	ΔBIC
Phosphorous			-0.17 (.07) ^{2a*}						0.01	6.5	0
WBC		0.07 (.03) [*]						-0.25 (.07) ^{***}	0.08	-1.07	0
N:L ratio								-0.23 (.07) ^{**}	0.05	0.27	1.34
PCV	-2.53 (.90) ^{**}							-2.36 (.81) [*]	0.04	2.03	na
									0.04	-2.69	na

Note: ¹Year prior to capture, ²sea ice concentration in year prior to capture, ^{2a}15% cover, ^{2b}50% cover, ³14 days prior to capture, reference is ⁴Fall, ⁵adult, ⁶na=no model within 2 ΔBIC of the presented model.

* $p < .05$; ** $p < .01$; *** $p < .001$.

fat consumption and increased protein consumption (Cherry et al., 2009; Ferguson et al., 2017; Nelson, 1987; Pagano et al., 2018; Rode, Robbins, et al., 2021), resulting in the dysregulation of water balance. If polar bears increase the proportion of protein in their diet, the need for external sources of water would increase and fat accumulation could decrease, requiring muscle catabolism for gluconeogenesis potentially amplifying this effect (Nelson, 1987). In addition, we found that in years with lower WAO, female polar bears had higher BUN levels, a response that occurs when dietary protein exceeds anabolic requirements. Such changes in the nutritional makeup of diet are likely to result in synergistic effects on polar bear physiology (Ferguson et al., 2017).

We also observed annual changes in biomarkers linked to liver function. In clinical veterinary medicine, small increases in liver enzyme activity are often masked by wide reference intervals (Fry et al., 2019) with pathologic concerns indicated by at least a twofold or greater change in enzyme activity. Although we did not see multifold increases in ALT, it significantly increased with capture year in both male and female bears (Appendix S2, Figure 6). Increases in ALT activity can indicate hepatocyte injury caused by liver disease. We cannot confirm pathophysiology associated with this increasing ALT activity, but several hypotheses warrant further investigation, including whether increases in ALT could indicate liver damage caused by pathogens, pollutants, or diet.

Biomarkers of immune function varied with circumpolar and regional-scale environmental indices for male and female polar bears. Monitoring changes in WBC allow for immediate evaluation of immune system activity, whereas changes in serum proteins, ALB and GLOB, reflect adaptive immune response. WBC increased in females when winds were more variable in the 2 weeks prior to capture and with higher WAO in males. In previous studies, greater wind speed and the higher WAO resulted in reduced polar bear movement and foraging (Rode et al., 2017; Togunov et al., 2017), but also may create the formation of leads that polar bears prefer to hunt. Such conditions may trigger increased opportunities for injuries from contact with conspecifics or interactions with prey that could potentially increase WBC (Ovsyanikov, 1995). To determine whether these WBC changes were suggestive of acute versus chronic inflammatory responses, we evaluated the ratio of neutrophils to lymphocytes. We expected that acute inflammation would exhibit higher neutrophils relative to lymphocytes, whereas chronic infection would have higher lymphocytes relative to neutrophils (Thrall et al., 2012). However, we were unable to differentiate acute versus chronic inflammatory responses using the N:L ratio. We did see that breeding females showed increased WBC; however, the lack of seasonal effect on WBC suggests that this increase could be a response to insults acquired through interactions with males including injury and infection (Delehanty & Boonstra, 2009; Derocher et al., 2010; Ramsay & Stirling, 1986; Whiteman et al., 2018). Identifying the cause of elevated WBC in breeding females will likely require additional data, including behavioral interactions with conspecifics and prey, as well as exposure to pathogens.

TABLE 7 Directional influence of behavior parameters that significantly impact blood-based analytes ($p \leq .05$).

	On shore	Fasting	Breeding
Analyte			
		Females	
ALP	+	-	+
Phosphorous		-	
Calcium			+
WBC			+
		Males	
ALT		-	
ALP		-	
ALB	-		
CREA	-		
Calcium	-		
Phos		-	

The association between environmental conditions and ALB and GLOB (which collectively reflect TP) are further evidence of an effect on immune function, specifically the inflammatory response (Thrall et al., 2012). Individually, both ALB and GLOB were significantly associated with environmental covariates. For both males and females, ALB increased with higher WAO and in males declined with the AAO and ice-free days. GLOB increased with ice-free days and in years with a lower WAO, whereas TP remained unchanged across all environmental conditions. The unchanged TP (i.e., sum of ALB and GLOB) is not unexpected because the inflammatory response is characterized by the increased synthesis of immunoglobulins, fibrinogens, or both (positive, delayed phase and acute proteins), concurrent with a decrease in albumin (negative acute phase protein) (Scott & Stockham, 2013). The changes in serum proteins, paired with increases in WBC under the same conditions, suggest an increased energetic allocation for immune activity in years with a lower WAO. These results may be indicative of the cumulative effects of changing environmental processes on polar bear physiology; however, determining if these environmental parameters cause disease would require extensive diagnostics to ascertain the source of the inflammatory response.

Previous studies have shown differences in pathogen exposure and immune system function based on habitat use for SB polar bears. For example, Whiteman et al. (2018) reported bears that used on-shore habitat had higher WBC counts and GLOB levels than bears that used sea ice year-round. Declines in persistent organic pollutants (Atwood et al., 2017) and methyl mercury exposure (McKinney et al., 2017) were observed in on-shore bears, a response that was attributed to an increase in bears feeding on lower trophic position foods while on land. Atwood et al. (2017), using antibody seroprevalence, demonstrated that the diversity of pathogen exposure varied based on summer habitat use. However, we found limited evidence that on-shore habitat use influenced metabolic and immune function, with significant differences between on-shore and on-ice bears observed in only a few analytes (Table 6). It is important to note

that the previously mentioned studies differed from ours relative to objectives, hypotheses, and study designs (including types of samples collected) and are not directly comparable. The majority of SB polar bears still use sea ice year-round (Atwood, Marcot, et al., 2016; Atwood, Peacock, et al., 2016), which may explain the limited effect of summer habitat use on the blood-based biomarkers used in this study.

Extrapolating clinical pathologic data intended to answer questions about individual animal health to population health is complex and is generally limited to animal husbandry in agricultural settings (Cook et al., 2006; Gånheim et al., 2007; Huzzey et al., 2014). A key challenge in evaluating physiologic function relative to environmental conditions is accounting for processes that occur at different temporal and spatial scales. For example, biochemical analytes represent cellular-level activity days and weeks prior to sampling, whereas the environmental conditions reflect processes occurring over time scales ranging from several days to years. Further, the effects on sea ice characteristics of the climate processes (e.g., WAO, AO) used to describe Arctic-wide conditions can vary relative to spatial scale. For example, a lower WAO is expected to result in increased sea ice volume and delayed melt of sea ice in the greater Beaufort Sea. However, in the eastern Beaufort Sea (i.e., a finer spatial scale), a lower WAO has been found to enhance sea ice divergence, resulting in the early formation of leads (Rigor et al., 2002) that bears use to hunt seals. Inference is further complicated because physiologic profiles of individuals at a single point in time provides a "snapshot" of an individual's physiologic function, which may be muted at the population level, making it difficult to assess whether changes represent physiologic plasticity or pathology. Nevertheless, we found significant relationships between select physiologic biomarkers and environmental processes, which highlights a potential for monitoring the health of wildlife populations vulnerable to environmental change (Cooke & O'Connor, 2010) albeit such evaluations will require recognition of a myriad of identified and unrealized influences on physiologic function.

Polar bear life history characteristics and population dynamics are being influenced by global warming (Atwood, Peacock, et al., 2016; Bromaghin et al., 2015, 2021; Pagano et al., 2018; Rode et al., 2010), and the effects of these changes are expressed at the physiologic level. Our research suggests that physiologic biomarkers varied in association with ecosystem and demographic parameters and may be plastic responses to changes in diet and nutrition resulting from environmental change (Boonstra, 2013). It is important to note that our findings do not imply a cause-and-effect relationship. Our top models often failed to capture the substantial variability inherent in the study system. Accordingly, our models should not be used for predictive purposes; however, the uncertainty does not affect the interpretation of significant variables.

Our findings indicate it may be beneficial to prioritize the evaluation of tightly regulated blood-based biomarkers such as sodium and PCV, as opposed to more widely regulated analytes (e.g., ALT, ALP, BUN, CREA, TP) to inform population-level physiologic perturbations related to climate change. Additionally, biobanking blood and

preserving samples for -omics research (e.g., metagenomics, metabolomics, microbiomics, viromics, epigenetics and transcriptomics), may be valuable for clarifying mechanistic relationships between physiologic and environmental processes (Breithoff & Harrison, 2020). Continuing to explore the physiologic effects of climate change, including the role of clinical pathology in conjunction with community and ecosystem conditions, will further our understanding of the health of wildlife populations (Patyk et al., 2015; Wittrock et al., 2018).

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare. All co-authors have seen and agree with the contents of the manuscript. We certify that the submission is original work and is not under review at any other publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in USGS Alaska Science Center data repository at <https://www.usgs.gov/centers/alaska-science-center/data>; <https://doi.org/10.5066/P9OXCRJ6>.

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REFERENCES

- Ames, E. M., Gade, M. R., Nieman, C. L., Wright, J. R., Tonra, C. M., Marroquin, C. M., Tutterow, A. M., & Gray, S. M. (2020). Striving for population-level conservation: Integrating physiology across the biological hierarchy. *Conservation Physiology*, 8, coaa019.
- Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *The Journal of Wildlife Management*, 74, 1175–1178.
- Atwood, T., Peacock, E., Burek-Huntington, K., Shearn-Bochsler, V., Bodenstein, B., Beckmen, K., & Durner, G. (2015). Prevalence and spatio-temporal variation of an alopecia syndrome in polar bears (*Ursus maritimus*) of the southern Beaufort Sea. *Journal of Wildlife Diseases*, 51, 48–59.
- Atwood, T. C., Duncan, C., Patyk, K. A., Nol, P., Rhyan, J., McCollum, M., McKinney, M. A., Ramey, A. M., Cerqueira-Cézar, C. K., Kwok, O. C. H., Dubey, J. P., & Hennager, S. (2017). Environmental and behavioral changes may influence the exposure of an Arctic apex predator to pathogens and contaminants. *Scientific Reports*, 7, 1–12.
- Atwood, T. C., Marcot, B. G., Douglas, D. C., Amstrup, S. C., Rode, K. D., Durner, G. M., & Bromaghin, J. F. (2016). Forecasting the relative influence of environmental and anthropogenic stressors on polar bears. *Ecosphere*, 7, e01370.
- Atwood, T. C., Peacock, E., McKinney, M. A., Lillie, K., Wilson, R., Douglas, D. C., Miller, S., & Terletzky, P. (2016). Rapid environmental change drives increased land use by an Arctic marine predator. *PLoS One*, 11, e0155932.
- Atwood, T. C., Rode, K. D., Douglas, D. C., Simac, K., Pagano, A. M., & Bromaghin, J. F. (2021). Long-term variation in polar bear body condition and maternal investment relative to a changing environment. *Global Ecology and Conservation*, 32, e01925.
- Blanchet, M., Aars, J., Andersen, M., & Routti, H. (2020). Space-use strategy affects energy requirements in Barents Sea polar bears. *Marine Ecology Progress Series*, 639, 1–19.
- Boonstra, R. (2013). Reality as the leading cause of stress: Rethinking the impact of chronic stress in nature. *Functional Ecology*, 27, 11–23.
- Boonstra, R., Bodner, K., Bosson, C., Delehanty, B., Richardson, E. S., Lunn, N. J., Derocher, A. E., & Molnár, P. K. (2020). The stress of Arctic warming on polar bears. *Global Change Biology*, 26, 4197–4214.
- Bourque, J., Atwood, T. C., Divoky, G. J., Stewart, C., & McKinney, M. A. (2020). Fatty acid-based diet estimates suggest ringed seal remain the main prey of southern Beaufort Sea polar bears despite recent use of onshore food resources. *Ecology and Evolution*, 10, 2093–2103.
- Box, J. E., Colgan, W. T., Christensen, T. R., Schmidt, N. M., Lund, M., Parmentier, F. J., Brown, R., Bhatt, U. S., Euskirchen, E. S., Romanovsky, V. E., & Walsh, J. E. (2019). Key indicators of Arctic climate change: 1971–2017. *Environmental Research Letters*, 14, 045010.
- Breithoff, E., & Harrison, R. (2020). From ark to bank: Extinction, proxies and biocapitals in ex-situ biodiversity conservation practices. *International Journal of Heritage Studies*, 26, 37–55.
- Bromaghin, J. F., Douglas, D. C., Durner, G. M., Simac, K. S., & Atwood, T. C. (2021). Survival and abundance of polar bears in Alaska's Beaufort Sea, 2001–2016. *Ecology and Evolution*, 11(20), 14250–14267.
- Bromaghin, J. F., McDonald, T. L., Stirling, I., Derocher, A. E., Richardson, E. S., Regehr, E. V., Douglas, D. C., Durner, G. M., Atwood, T., & Amstrup, S. C. (2015). Polar bear population dynamics in the southern Beaufort Sea during a period of sea ice decline. *Ecological Applications*, 25, 634–651.
- Burek, K. A., Gulland, F. M. D., & O'Hara, T. M. (2008). Effects of climate change on Arctic marine mammal health. *Ecological Applications*, 18, S126–S134.
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, 33, 261–304.
- Busch, D. S., & Hayward, L. S. (2009). Stress in a conservation context: A discussion of glucocorticoid actions and how levels change with conservation-relevant variables. *Biological Conservation*, 142, 2844–2853.
- Bush, M., & Custer, R. S. (1980). Use of dissociative anesthetics for the immobilization of captive bears: Blood gas, hematology and biochemistry values. *Journal of Wildlife Diseases*, 16(4), 481–489.
- Carlens, H., Lydersen, C., Krafft, B. A., & Kovacs, K. M. (2006). Spring haul-out behavior of ringed seals (*Pusa hispida*) in Kongsfjorden, Svalbard. *Marine Mammal Science*, 22, 379–393.

- Cavaliere, D. J., Markus, T., Hall, D. K., Gasiewski, A. J., Klein, M., & Ivanoff, A. (2006). Assessment of EOS aqua AMSR-E Arctic Sea ice concentrations using Landsat-7 and airborne microwave imagery. *IEEE Transactions on Geoscience and Remote Sensing*, *44*, 3057–3069.
- Cherry, S. G., Derocher, A. E., Stirling, I., & Richardson, E. S. (2009). Fasting physiology of polar bears in relation to environmental change and breeding behavior in the Beaufort Sea. *Polar Biology*, *32*, 383–391.
- Cohen, J., Screen, J. A., Furtado, J. C., Barlow, M., Whittleston, D., Coumou, D., Francis, J., Dethloff, K., Entekhabi, D., Overland, J., & Jones, J. (2014). Recent Arctic amplification and extreme mid-latitude weather. *Nature Geoscience*, *7*, 627–637.
- Cook, N., Oetzel, G., & Nordlund, K. (2006). Modern techniques for monitoring high-producing dairy cows 1. Principles of herd-level diagnoses. *In Practice*, *28*, 510–515.
- Cooke, S. J., Blumstein, D. T., Buchholz, R., Caro, T., Fernández-Juricic, E., Franklin, C. E., Metcalfe, J., O'Connor, C. M., St Clair, C. C., Sutherland, W. J., & Wikelski, M. (2014). Physiology, behavior, and conservation. *Physiological and Biochemical Zoology*, *87*, 1–14.
- Cooke, S. J., Madliger, C. L., Cramp, R. L., Beardall, J., Burness, G., Chown, S. L., Clark, T. D., Dantzer, B., de la Barrera, E., Fangué, N. A., Franklin, C. E., Fuller, A., Hawkes, L. A., Hultine, K. R., Hunt, K. E., Love, O. P., MacMillan, H. A., Mandelman, J. W., Mark, F. C., ... Todgham, A. E. (2020). Reframing conservation physiology to be more inclusive, integrative, relevant and forward-looking: Reflections and a horizon scan. *Conservation Physiology*, *8*(1), coaa016.
- Cooke, S. J., & O'Connor, C. M. (2010). Making conservation physiology relevant to policy makers and conservation practitioners. *Conservation Letters*, *3*, 159–166.
- Cosgrove, A. J., McWhorter, T. J., & Maron, M. (2017). Using individual-condition measures to predict the long-term importance of habitat extent for population persistence: Stress and habitat area. *Conservation Biology*, *31*, 1141–1151.
- Cray, C., Rodriguez, M., Zaias, J., & Altman, N. H. (2009). Effects of storage temperature and time on clinical biochemical parameters from rat serum. *Journal of the American Association for Laboratory Animal Science*, *48*, 202–204.
- Delehanty, B., & Boonstra, R. (2009). Impact of live trapping on stress profiles of Richardson's ground squirrel (*Spermophilus richardsonii*). *General and Comparative Endocrinology*, *160*(2), 176–182.
- DeRepentigny, P., Jahn, A., Holland, M. M., & Smith, A. (2020). Arctic Sea ice in two configurations of the CESM2 during the 20th and 21st centuries. *Journal of Geophysical Research: Oceans*, *125*, e2020JC016133.
- Derocher, A. E. (2005). Population ecology of polar bears at Svalbard, Norway. *Population Ecology*, *47*, 267–275.
- Derocher, A. E., Andersen, M., Wiig, Ø., & Aars, J. (2010). Sexual dimorphism and the mating ecology of polar bears (*Ursus maritimus*) at Svalbard. *Behavioral Ecology and Sociobiology*, *64*, 939–946.
- Derocher, A. E., Nelson, R. A., Stirling, I., & Ramsay, M. A. (1990). Effects of fasting and feeding on serum urea and serum creatinine levels in polar bears. *Marine Mammal Science*, *6*, 196–203.
- Descamps, S., Aars, J., Fuglei, E., Kovacs, K. M., Lydersen, C., Pavlova, O., Pedersen, Å. Ø., Ravolainen, V., & Strøm, H. (2017). Climate change impacts on wildlife in a high Arctic archipelago—Svalbard, Norway. *Global Change Biology*, *23*, 490–502.
- Durner, G. M., Douglas, D. C., Nielson, R. M., Amstrup, S. C., McDonald, T. L., Stirling, I., Mauritzen, M., Born, E. W., Wiig, Ø., DeWeaver, E., Serreze, M. C., Belikov, S. E., Holland, M. M., Maslanik, J., Aars, J., Bailey, D. A., & Derocher, A. E. (2009). Predicting 21st-century polar bear habitat distribution from global climate models. *Ecological Monographs*, *79*, 25–58.
- Ferguson, S. H., Young, B. G., Yurkowski, D. J., Anderson, R., Willing, C., & Nielsen, O. (2017). Demographic, ecological, and physiological responses of ringed seals to an abrupt decline in sea ice availability. *PeerJ*, *5*, e2957.
- Ferguson, S. H., Yurkowski, D. J., Young, B. G., Fisk, A. T., Muir, D. C. G., Zhu, X., & Thiemann, G. W. (2020). Comparing temporal patterns in body condition of ringed seals living within their core geographic range with those living at the edge. *Ecography*, *43*, 1521–1535.
- Frey, K. E., Maslanik, J. A., Clement Kinney, J., & Maslowski, W. (2014). Recent variability in sea ice cover, age, and thickness in the Pacific Arctic region. In J. M. Grebmeier & W. Maslowski (Eds.), *The Pacific Arctic region* (pp. 31–63). Springer.
- Friedrichs, K. R., Harr, K. E., Freeman, K. P., Szladovits, B., Walton, R. M., Barnhart, K. F., & Blanco-Chavez, J. (2012). ASVCP reference interval guidelines: Determination of de novo reference intervals in veterinary species and other related topics. *Veterinary Clinical Pathology*, *41*, 441–453.
- Fry, T. L., Friedrichs, K. R., Atwood, T. C., Duncan, C., Simac, K., & Goldberg, T. (2019). Reference intervals for blood-based biochemical analytes of southern Beaufort Sea polar bears. *Conservation Physiology*, *7*, cozo040.
- Gånheim, C., Alenius, S., & Persson Waller, K. (2007). Acute phase proteins as indicators of calf herd health. *The Veterinary Journal*, *173*, 645–651.
- Hamilton, C. D., Kovacs, K. M., Ims, R. A., Aars, J., & Lydersen, C. (2017). An Arctic predator–prey system in flux: Climate change impacts on coastal space use by polar bears and ringed seals. *Journal of Animal Ecology*, *86*, 1054–1064.
- Hamilton, S. G., & Derocher, A. E. (2018). Assessment of global polar bear abundance and vulnerability. *Animal Conservation*, *22*, 83–95.
- Harwood, L. A., Smith, T. G., Alikamik, J., Alikamik, E., Lea, E. V., Stirling, I., Wright, H., Melling, H., & Zhu, X. (2020). Long-term, harvest-based monitoring of ringed seal body condition and reproduction in Canada's Western Arctic: An update through 2019. *Arctic*, *73*, 206–220.
- Hauser, D. D. W., Laidre, K. L., Stafford, K. M., Stern, H. L., Suydam, R. S., & Richard, P. R. (2016). Decadal shifts in autumn migration timing by Pacific Arctic beluga whales are related to delayed annual sea ice formation. *Global Change Biology*, *23*, 2206–2217.
- Herreman, J., & Peacock, E. (2013). Polar bear use of a persistent food subsidy: Insights from non-invasive genetic sampling in Alaska. *Ursus*, *24*, 148–163.
- Huzzej, J. M., Nydam, D. V., Ospina, P. A., & Overton, T. R. (2014). *Predicting transition cow health and performance-use of blood and fecal biomarkers for herd-level evaluation and diagnostics*. eCommons. <https://hdl.handle.net/1813/36568>
- IPCC. (2018). *Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty* [V. Masson-Delmotte, P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, & T. Waterfield (Eds.)] (630pp).
- Irons, D. B., Anker-Nilssen, T., Gaston, A. J., Byrd, G. V., Falk, K., Gilchrist, G., Hario, M., Hjærnquist, M., Krasnov, Y. V., Mosbech, A., Olsen, B., Petersen, A., Reid, J. B., Robertson, G. J., Strøm, H., & Wohl, K. D. (2008). Fluctuations in circumpolar seabird populations linked to climate oscillations. *Global Change Biology*, *14*, 1455–1463.
- Kirk, C. M., Amstrup, S., Swor, R., Holcomb, D., & O'Hara, T. M. (2010a). Hematology of southern Beaufort Sea polar bears (2005–2007): Biomarker for an Arctic ecosystem health sentinel. *EcoHealth*, *7*, 307–320.
- Kirk, C. M., Amstrup, S., Swor, R., Holcomb, D., & O'Hara, T. M. (2010b). Morbillivirus and toxoplasma exposure and association with hematological parameters for southern Beaufort Sea polar bears: Potential response to infectious agents in a sentinel species. *EcoHealth*, *7*, 321–331.

- Laidre, K. L., Atkinson, S. N., Regehr, E. V., Stern, H. L., Born, E. W., Wiig, Ø., Lunn, N. J., Dyck, M., Heagerty, P., & Cohen, B. R. (2020). Transient benefits of climate change for a high-Arctic polar bear (*Ursus maritimus*) subpopulation. *Global Change Biology*, *26*, 6251–6265.
- Madliger, C. L., & Love, O. P. (2015). The power of physiology in changing landscapes: Considerations for the continued integration of conservation and physiology. *Integrative and Comparative Biology*, *55*, 545–553.
- Madliger, C. L., Love, O. P., Hultine, K. R., & Cooke, S. J. (2018). The conservation physiology toolbox: Status and opportunities. *Conservation Physiology*, *6*, coy029.
- Madliger, C. L., Love, O. P., Nguyen, V. M., Haddaway, N. R., & Cooke, S. J. (2021). Researcher perspectives on challenges and opportunities in conservation physiology revealed from an online survey. *Conservation Physiology*, *9*, coab030.
- McKinney, M. A., Atwood, T. C., Iverson, S. J., & Peacock, E. (2017). Temporal complexity of southern Beaufort Sea polar bear diets during a period of increasing land use. *Ecosphere*, *8*, e01633.
- McKinney, M. A., Iverson, S. J., Fisk, A. T., Sonne, C., Rigét, F. F., Letcher, R. J., Arts, M. T., Born, E. W., Rosing-Asvid, A., & Dietz, R. (2013). Global change effects on the long-term feeding ecology and contaminant exposures of East Greenland polar bears. *Global Change Biology*, *19*, 2360–2372.
- Miller, A., & Lumley, T. (2020). LEAPS: Regression subset selection. R package version 3.1. <https://CRAN.R-project.org/package=leaps>
- Molnár, P. K., Klanjscek, T., Derocher, A. E., Obbard, M. E., & Lewis, M. A. (2009). A body composition model to estimate mammalian energy stores and metabolic rates from body mass and body length, with application to polar bears. *Journal of Experimental Biology*, *212*, 2313–2323.
- Moore, S. E. (2008). Marine mammals as ecosystem sentinels. *Journal of Mammalogy*, *89*, 534–540.
- Moore, S. E., & Huntington, H. P. (2008). Arctic marine mammals and climate change: Impacts and resilience. *Ecological Applications*, *18*(sp2), S157–S165.
- Möstl, E., & Palme, R. (2002). Hormones as indicators of stress. *Domestic Animal Endocrinology*, *23*, 67–74.
- Narayan, E. J., Forsburg, Z. R., Davis, D. R., & Gabor, C. R. (2019). Non-invasive methods for measuring and monitoring stress physiology in imperiled amphibians. *Frontiers in Ecology and Evolution*, *7*, 431.
- Nelson, R. A. (1987). Black bears and polar bears—Still metabolic marvels. In *Mayo clinic proceedings* (pp. 850–853). Elsevier. [https://doi.org/10.1016/S0025-6196\(12\)62341-6](https://doi.org/10.1016/S0025-6196(12)62341-6)
- Nelson, R. A., Beck, T. D. I., & Steiger, D. L. (1984). Ratio of serum urea to serum creatinine in wild black bears. *Science*, *226*, 841–842.
- Nguyen, L., Pilfold, N. W., Derocher, A. E., Stirling, I., Bohart, A. M., & Richardson, E. (2017). Ringed seal (*Pusa hispida*) tooth annuli as an index of reproduction in the Beaufort Sea. *Ecological Indicators*, *77*, 286–292.
- Obbard, M. E., Thiemann, G. W., Peacock, E., & DeBruyn, T. D. (2010). *Polar bears: Proceedings of the 15th working meeting of the IUNC/SSC Polar Bear Specialist Group, Copenhagen, Denmark, 29 June–3 July, 2009*. IUNC.
- Ogi, M., Rysgaard, S., & Barber, D. G. (2016). Importance of combined winter and summer Arctic oscillation (AO) on September Sea ice extent. *Environmental Research Letters*, *11*, 034019.
- Ovsyanikov, N. (1995). Polar bear predation of walrus on Wrangell Island. *Bulletin of the Moscow Association of Natural Scientist, Section of Biology*, *100*, 3–15.
- Pagano, A. M., Durner, G. M., Atwood, T. C., & Douglas, D. C. (2021). Effects of sea ice decline and summer land use on polar bear home range size in the Beaufort Sea. *Ecosphere*, *12*. <https://doi.org/10.1002/ecs2.3768>
- Pagano, A. M., Durner, G. M., Rode, K. D., Atwood, T. C., Atkinson, S. N., Peacock, E., Costa, D. P., Owen, M. A., & Williams, T. M. (2018). High-energy, high-fat lifestyle challenges an Arctic apex predator, the polar bear. *Science*, *359*, 568–572.
- Pagano, A. M., & Williams, T. M. (2021). Physiological consequences of Arctic Sea ice loss on large marine carnivores: Unique responses by polar bears and narwhals. *Journal of Experimental Biology*, *224*. <https://doi.org/10.1242/jeb.228049>
- Patyk, K. A., Duncan, C., Nol, P., Sonne, C., Laidre, K., Obbard, M., Wiig, Ø., Aars, J., Regehr, E., Gustafson, L. L., & Atwood, T. (2015). Establishing a definition of polar bear (*Ursus maritimus*) health: A guide to research and management activities. *Science of the Total Environment*, *514*, 371–378.
- Pilfold, N. W., Derocher, A. E., Stirling, I., & Richardson, E. (2015). Multi-temporal factors influence predation for polar bears in a changing climate. *Oikos*, *124*, 1098–1107.
- R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Ramsay, M. A., & Stirling, I. (1986). On the mating system of polar bears. *Canadian Journal of Zoology*, *64*, 2142–2151.
- Ramsay, M. A., & Stirling, I. (1988). Reproductive biology and ecology of female polar bears (*Ursus maritimus*). *Journal of Zoology*, *214*, 601–633.
- Regehr, E. V., Hunter, C. M., Caswell, H., Amstrup, S. C., & Stirling, I. (2010). Survival and breeding of polar bears in the southern Beaufort Sea in relation to sea ice. *Journal of Animal Ecology*, *79*, 117–127.
- Reynolds, B., Taillade, B., Médaille, C., Palenché, F., Trumel, C., & Lefebvre, H. P. (2006). Effect of repeated freeze–thaw cycles on routine plasma biochemical constituents in canine plasma. *Veterinary Clinical Pathology*, *35*, 339–340.
- Rigor, I. G., Wallace, J. M., & Colony, R. L. (2002). Response of sea ice to the Arctic oscillation. *Journal of Climate*, *15*, 2648–2663.
- Robbins, C. T., Tollefson, T. N., Rode, K. D., Erlenbach, J. A., & Arden, A. J. (2022). New insights into dietary management of polar bears (*Ursus maritimus*) and brown bears (*U. arctos*). *Zoo Biology*, *41*, 166–175.
- Rode, K. D., Amstrup, S. C., & Regehr, E. V. (2010). Reduced body size and cub recruitment in polar bears associated with sea ice decline. *Ecological Applications*, *20*, 768–782.
- Rode, K. D., Olson, J., Eggett, D., Douglas, D. C., Durner, G. M., Atwood, T. C., Regehr, E. V., Wilson, R. R., Smith, T., & St. Martin, M. (2018). Den phenology and reproductive success of polar bears in a changing climate. *Journal of Mammalogy*, *99*, 16–26. <https://doi.org/10.1093/jmammal/gyx181>
- Rode, K. D., Peacock, E., Taylor, M., Stirling, I., Born, E. W., Laidre, K. L., & Wiig, Ø. (2012). A tale of two polar bear populations: Ice habitat, harvest, and body condition. *Population Ecology*, *54*, 3–18.
- Rode, K. D., Regehr, E. V., Bromaghin, J. F., Wilson, R. R., Martin, M. S., Crawford, J. A., & Quakenbush, L. T. (2021). Seal body condition and atmospheric circulation patterns influence polar bear body condition, recruitment, and feeding ecology in the Chukchi Sea. *Global Change Biology*, *27*, 2684–2701.
- Rode, K. D., Robbins, C. T., Stricker, C. A., Taras, B. D., & Tollefson, T. N. (2021). Energetic and health effects of protein overconsumption constrain dietary adaptation in an apex predator. *Scientific Reports*, *11*, 15309.
- Rode, K. D., Wilson, R. R., Douglas, D. C., Muhlenbruch, V., Atwood, T. C., Regehr, E. V., Richardson, E. S., Pilfold, N. W., Derocher, A. E., Durner, G. M., Stirling, I., Amstrup, S. C., St. Martin, M., Pagano, A. M., & Simac, K. (2017). Spring fasting behavior in a marine apex predator provides an index of ecosystem productivity. *Global Change Biology*, *24*, 1–14.
- Rogers, M. C., Peacock, E., Simac, K., O'Dell, M. B., & Welker, J. M. (2015). Diet of female polar bears in the southern Beaufort Sea of Alaska: Evidence for an emerging alternative foraging strategy in response to environmental change. *Polar Biology*, *38*, 1035–1047.
- Routti, H., Atwood, T. C., Bechshoft, T., Boltunov, A., Ciesielski, T. M., Desforges, J.-P., Dietz, R., Gabrielsen, G. W., Jenssen, B. M., Letcher, R. J., McKinney, M. A., Morris, A. D., Rigét, F. F., Sonne,

- C., Styrisshave, B., & Tartu, S. (2019). State of knowledge on current exposure, fate and potential health effects of contaminants in polar bears from the circumpolar Arctic. *Science of the Total Environment*, 664, 1063–1083.
- Scott, M. A., & Stockham, S. L. (2013). *Fundamentals of veterinary clinical pathology*. John Wiley & Sons.
- Serreze, M. C., & Meier, W. N. (2019). The Arctic's sea ice cover: Trends, variability, predictability, and comparisons to the Antarctic. *Annals of the New York Academy of Sciences*, 1436, 36–53.
- Sheriff, M. J., Dantzer, B., Delehanty, B., Palme, R., & Boonstra, R. (2011). Measuring stress in wildlife: Techniques for quantifying glucocorticoids. *Oecologia*, 166, 869–887.
- Stroeve, J., & Notz, D. (2018). Changing state of Arctic Sea ice across all seasons. *Environmental Research Letters*, 13, 103001.
- Stern, H. L., & Laidre, K. L. (2016). Sea-ice indicators of polar bear habitat. *The Cryosphere*, 10, 2027–2041.
- Stirling, I., Spencer, C., & Andriashek, D. (1989). Immobilization of polar bears (*Ursus maritimus*) with Telazol® in the Canadian Arctic. *Journal of Wildlife Diseases*, 25(2), 159–168. <https://doi.org/10.7589/0090-3558-25.2.159>
- Stroeve, J. C., Maslanik, J., Serreze, M. C., Rigor, I., Meier, W., & Fowler, C. (2011). Sea ice response to an extreme negative phase of the Arctic oscillation during winter 2009/2010. *Geophysical Research Letters*, 38. <https://doi.org/10.1029/2010GL045662>
- Thompson, D. W. J., & Wallace, J. M. (1998). The Arctic oscillation signature in the wintertime geopotential height and temperature fields. *Geophysical Research Letters*, 25, 1297–1300.
- Thrall, M. A., Weiser, G., Allison, R. W., & Campbell, T. W. (2012). *Veterinary hematology and clinical chemistry*. John Wiley & Sons.
- Togunov, R. R., Derocher, A. E., & Lunn, N. J. (2017). Windscapes and olfactory foraging in a large carnivore. *Scientific Reports*, 7, 46332.
- Tredennick, A. T., Hooker, G., Ellner, S. P., & Adler, P. B. (2021). A practical guide to selecting models for exploration, inference, and prediction in ecology. *Ecology*, 102, e03336.
- Whiteman, J., Harlow, H., Durner, G., Regehr, E., Amstrup, S., & Ben-David, M. (2018). Heightened immune system function in polar bears using terrestrial habitats. *Physiological and Biochemical Zoology*, 92, 1–11.
- Whiteman, J. P. (2018). Out of balance in the Arctic. *Science*, 359, 514–515.
- Whiteman, J. P., Harlow, H. J., Durner, G. M., Anderson-Sprecher, R., Albeke, S. E., Regehr, E. V., Amstrup, S. C., & Ben-David, M. (2015). Summer declines in activity and body temperature offer polar bears limited energy savings. *Science*, 349, 295–298.
- Wiig, Ø., Aars, J., & Born, E. W. (2008). Effects of climate change on polar bears. *Science Progress*, 91, 151–173.
- Wilson, A. E., Wismer, D., Stenhouse, G., Coops, N. C., & Janz, D. M. (2021). Landscape condition influences energetics, reproduction, and stress biomarkers in grizzly bears. *Scientific Reports*, 11, 12124.
- Wittrock, J., Duncan, C., & Stephen, C. (2018). A determinants of health conceptual model for fish and wildlife health. *Journal of Wildlife Diseases*, 55. <https://doi.org/10.7589/2018-05-118>

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