SEROPREVALENCE OF ERYSIPELOTHRIX RHUSIOPATHIAE IN BEAUFORT SEA POLAR BEARS (URSUS MARITIMUS) IS LINKED TO RINGED SEAL (PUSA HISPIDA) DEMOGRAPHICS

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Seroprevalence of *Erysipelothrix rhusiopathiae* in Beaufort Sea Polar Bears (*Ursus maritimus*) is Linked to Ringed Seal (*Pusa hispida*) Demographics

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ABSTRACT: Polar bear (*Ursus maritimus*) life history is intimately associated with the distribution of sea ice and their prey in Arctic ecosystems. These ecosystems are changing in response to climate warming, resulting in the increased prevalence of pathogens in polar bears. *Erysipelothrix rhusiopathiae* has a long history of infection in domestic species and more recently in wildlife in the Canadian Arctic. As a result of increasing reports of *E. rhusiopathiae* causing morbidity and mortality in Arctic terrestrial mammals, we tested the seroprevalence of *E. rhusiopathiae* in Beaufort Sea polar bears sampled in 1985–87, 1992, 1994, and 2003–11. Our sample of 180 polar bears (117 females, 61 males, two unknown) with a median age of 9 yr (range 1–26 yr) had a seropositivity of 27.2% (49/180 individuals). We used binomial logistic regressions to investigate biotic and abiotic factors that may be linked to seropositivity. The resulting top model found that increased predation on adult ringed seals (*Pusa [Phoca] hispida*) and negative winter Arctic Oscillation Index (AOI) years were associated with a higher probability of seropositivity. Ringed seals may be a reservoir for *E. rhusiopathiae* via their consumption of infected prey, as the pathogen can persist in marine fish, molluscs, and crustaceans. Negative winter AOIs in our data set reflected high ice volume years, which reduced ringed seal natality, resulting in fewer seal pups available as prey. Our results suggest that exposure to *E. rhusiopathiae* in Beaufort Sea polar bears is modulated by a predator–prey mechanism.

Key words: Beaufort Sea, *Erysipelothrix rhusiopathiae*, emerging disease, polar bears, ringed seals.

INTRODUCTION

Erysipelothrix rhusiopathiae, an opportunistic and generalist bacterium, is most widely known for infecting domestic pigs and poultry but has also been observed in many wildlife species (Kutz et al. 2015; Forde et al. 2016; Mavrot et al. 2022). *Erysipelothrix rhusiopathiae* is a gram-positive bacillus with a wide distribution (Wang et al. 2010), infecting a diversity of both marine and terrestrial vertebrates (Conklin and Steele 1979). A unique strain of this bacterium has emerged in the Canadian Arctic Archipelago as an important cause of widespread mortality contributing to population declines in muskoxen (*Ovibos moschatus*) and has been detected in the feces and carcasses of multiple Arctic foxes (*Vulpes lagopus*), wolves (*Canis lupus*), seals (Phocidae), and caribou (*Rangifer tarandus*; Kutz et al. 2015; Forde et al. 2016; Seru 2023). Different, or uncharacterized, strains of *E. rhusiopathiae* have also been detected serologically or by culture from muskoxen, caribou, moose (*Alces alces*), and seals elsewhere in Canada and Alaska, and in Pribilof Island foxes (*Vulpes lagopus* ssp. *pribilofensis*; Forde et al. 2016; Spraker and White 2017; Mavrot et al. 2020; Aleuy et al. 2022; Sudlovenick et al. 2023; S. Kutz, unpubl. data). In domestic animals, death can occur <6 d after infection, but the mortality rate varies across species and individuals (Bobrek et al. 2013). Transmission may occur via contact through damaged skin or mucous membranes (Bobrek et al. 2013); from contact with bacteria shed in feces, urine, and saliva (Brooke and Riley 1999); or via insects as fomites (Wood and Steele 1994). Signs of infection typically include spots or lesions on the skin and regions of hair loss in mammals, and as infection progresses it may lead to sepsis (Peterman 1944; Bobrek et al. 2013). *Erysipelothrix rhusiopathiae* infection may also be maintained in an asymptomatic carrier state (Forde et al. 2016).

The first record of *E. rhusiopathiae* in the Arctic was connected to multiple widespread and severe muskox mortalities on Banks Island and Victoria Island in northwestern Canada (Kutz et al. 2015), with subsequent outbreaks first detected on the Canadian islands of Prince Patrick (2017), Ellesmere (2021–present), and Axel-Heiberg (2022–present). Nevertheless, *E. rhusiopathiae* is not new to the Arctic, with muskoxen seropositive to the bacteria as far back as the earliest available samples: 1976 in Alaska and 1991 in Canada (Mavrot et al. 2020).

Polar bears scavenge muskox remains (Voorhees et al. 2014), so the presence of *E. rhusiopathiae* in the Beaufort Sea region muskoxen suggests that it could be transmitted to polar bears via scavenging. The bacterium was identified in 14 polar bears from a sample of 48 hunter-harvested individuals across Canada during the development of a new method of disease identification (Tschritter et al. 2023). Concerns about exposure to an agent with a pathogenesis such as *E. rhusiopathiae* in polar bears increased after alopecia and reduced body condition were observed in 28% of bears sampled in the southern Beaufort Sea in 2012 (Atwood et al. 2015; Bowen et al. 2015). Elevated numbers of dead and sick ringed seals near Alaska were also reported during the same period (NOAA 2012). Although the cause of these events was not determined, they were suspected to be linked, given the close ecological relationship between polar bears and ringed seals. There are no studies of temporal trends of *E. rhusiopathiae* in polar bears; thus exposure dynamics are unknown.

Marine fish, molluscs, and crustaceans are hosts for *E. rhusiopathiae*, and it can persist in tissues for long periods, surviving in decaying tissues for up to 10 mo and surviving in the exterior mucoid slime of fish without killing them (Brooke and Riley 1999). The Canadian Arctic Archipelago strain of *E. rhusiopathiae* has been cultured from a seal found dead on Victoria Island (Seru 2023), and ringed seals in the eastern Canadian Arctic were seropositive for *E. rhusiopathiae* (Sudlovenick et al. 2023), suggesting that seals may be a source of infection for polar bears through predation. Numerically, ringed seals comprise up to 90% of the prey of polar bears in the Beaufort Sea (Thiemann et al. 2008; Pilfold et al. 2012). Transmission from ringed seals is potentially related to ringed seal age because adult seals consume more fish, which can be carriers of the pathogen (Brooke and Riley 1999). Ringed seals rely on subnivean lairs on the ice for parturition and nursing young, but heavy ice years reduce productivity and lowers pupping success (Smith 1987; Harwood et al. 2000; Nguyen et al. 2017). Pilfold et al. (2012) found that when polar bear seal kills were observed, years of low pup productivity showed a higher proportion of adult ringed seals killed in the Beaufort Sea, with half of the adult seals >21 yr of age, raising the potential that polar bears were exposed to *E. rhusiopathiae* during these periods.

The Arctic is warming at four times the global average, with consequences for both species and ecosystems (Burek et al. 2008; Mallory et al. 2010; Johannessen and Miles 2011; Jacobs et al. 2021; Rantanen et al. 2022). Many of the climate change effects are associated with range shifts in species and changes in habitats, which includes sea ice habitats (Melles et al. 2011; Comiso 2012; Afenyo et al. 2019). Polar bears in the Beaufort Sea are among the most affected by changes in sea ice; have declined up to 50% in abundance (Bromaghin et al. 2015); and have been predicted to undergo further declines (Hunter et al. 2010) because of sea ice decline with ongoing warming (Stern and

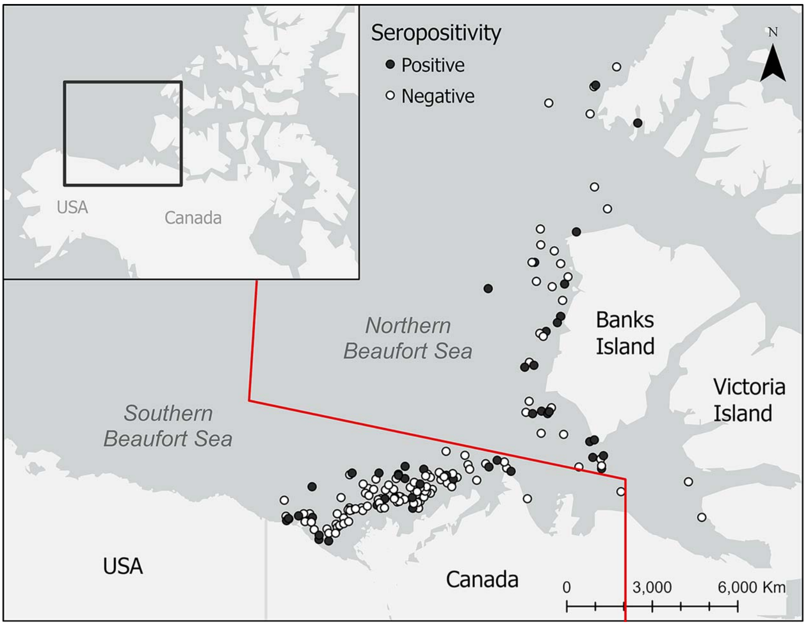

FIGURE 1. Locations of polar bears (*Ursus maritimus*) sampled in the Beaufort Sea, Canada, 1985–2011 for *Erysipelothrix rhusiopathiae*. Black dots are seropositive individuals, white dots are negative. The line shows the delineation between northern and southern Beaufort Sea polar bear populations.

Laidre 2016). Sea ice decline in this region has the potential to make these bears more sensitive to other stressors (Atwood et al. 2016a). An increased prevalence of pathogen exposure has been linked to climate warming (Altizer et al. 2013; Baker-Austin et al. 2013; Cohen et al. 2020; Kafle et al. 2020; Aleuy et al. 2022; Peacock et al. 2022). In the Western Hudson Bay subpopulation, seroprevalence of five different pathogens has increased in polar bears over the past 3 decades; all were correlated to climate-mediated changes in the environment (Pilfold et al. 2021; Buhler et al. 2023).

The objective of our study was to assess the trends in the seroprevalence of *E. rhusiopathiae* in Beaufort Sea polar bears in Canada from 1985 to 2011, and to investigate biotic and abiotic factors that may be linked to infection. We hypothesized that *E. rhusiopathiae* seroprevalence in polar bears would be related to a predator–prey mechanism associated with ringed seals and sea ice patterns. We predicted positive relationships between *E. rhusiopathiae* seropositivity in polar bears and environmental variables that related to predation of adult ringed seals. We also predict relationships between seropositivity and variables that act as proxies for climate change, such as increased seropositivity after years of earlier sea ice breakup.

METHODS

Sample collection

Polar bear sampling occurred in April and May in the Beaufort Sea in 1985–87, 1992, 1994; and 2003–11 in Canada (Fig. 1). The study area included polar bears from the Southern Beaufort Sea and Northern Beaufort Sea subpopulations (Paetkau et al. 1999; Amstrup et al. 2000; Stirling et al. 2011). Polar bears were located and immobilized from a helicopter via remote administration of tiletamine–olazepam (Telazol, Virbac, Carros, France) following Stirling et al. (1989). Blood samples were collected from the femoral vein, centrifuged at 1500 × G, and the serum and cellular portions were then frozen at −80 C until analysis. Age was determined by extracting a vestigial premolar and counting cementum annuli (Calvert and Ramsay 1998); dependent offspring were aged by body size and tooth eruption patterns.

For each sampled bear, sex, body condition, and capture location were recorded. Body condition was ranked from 1 (very skinny) to 5 (very fat) following Stirling et al. (2008b). Capture and handling protocols were approved by the Environment and Climate Change Canada's Western and Northern Animal Care Committee and the University of Alberta Biological Sciences Animal Policy and Welfare Committee, in accordance with the Canadian Council on Animal Care guidelines.

Seroprevalence analysis

To detect anti- *Erysipelothrix* antibodies in the polar bear sera we used an indirect ELISA developed by Giménez-Lirola et al. (2012) and further adapted to wildlife (Mavrot et al. 2020). Commonly used for seroprevalence analyses, ELISAs are highly sensitive (>97%) for determining antibody presence (Trono et al. 2001; Opsteegh et al. 2010). The test outcome is a percent positivity value (PP) of the sample compared with a positive control (serum from a pig vaccinated against *E. rhusiopathiae*). As for many wildlife species, no cutoff value to discriminate between positive and negative samples has been established. We used a mixture-distribution modeling approach to determine the best cutoff value (Mavrot et al. 2020). The PP cutoff for seropositivity was 55.1 (95% confidence interval [CI]: 46.1 – 73.6), where individuals above the cutoff but within the CI were deemed borderline positive and included as a positive in analyses.

Data analyses

Binomial logistic regressions were used to investigate the relationship between *E. rhusiopathiae* seropositivity and potentially predictive variables using RStudio (version 1.2.5033; R Core Team 2020). Positive seroprevalence samples were denoted as 1 and negative samples as 0. We included seven biotic and six abiotic covariates in regression models (Table 1). Following Pilfold et al. (2021), environmental variables were included with a 1-yr lag, suggesting that exposure reflected past conditions rather than at the sampling. Three initial models were chosen a priori to include different covariates to investigate different expected relationships: a biological model, a temporospatial model, and a ringed seal consumption model. A global model with all variables together was also run. All models were linear mixed-effects models, with bear identification (ID) as the random variable, fit with the Nelder Mead optimizer. Pearson correlation between all numerical variables was tested, and any variables with a correlation ≥ 0.50 were not included in the same model. The only correlated variables were year and prey age (described below), with a correlation of 0.64, which were in separate a priori models.

Biological model: Body condition rankings were dummy coded into two binary covariates: a poor body condition covariate with rankings 1 and 2, and a good body condition covariate with rankings 4 and 5, with normal ranking (3) acting as a reference (Table 1). The biological model to investigate biological correlates with seropositivity included bear age, sex, poor body condition, and good body condition as fixed effects, and bear ID as a random effect.

Temporospatial model: The model to investigate potential temporal and spatial patterns included capture year, latitude and longitude of capture, number of low ice days per year, and the date of sea ice breakup as fixed effects; bear ID was a random effect. The length of the sea ice season has been linked to polar bear survival, most often through access to ringed seals (Stirling and Parkinson 2006; Regehr et al. 2007; Molnar et al. 2010; Hamilton et al. 2014). The length of the low ice season corresponds to the amount of time polar bears have a reduced ability to hunt seals, and the sea ice breakup date denotes the start of the low ice season, reflecting the date bears are forced off the ice, their primary habitat.

Ringed seal consumption model: The ringed seal consumption model focused on the suspected effects of ringed seal consumption as a source of exposure, including ringed seal prey age class (prey age, hereafter), female bears with cubs, Arctic Ocean Oscillation Index (AOO), and winter Arctic Oscillation Index (AOI) as fixed effects, and bear ID as a random effect. Prey age is an annual value, calculated by Pilfold et al. (2012). This model uses a proportional width index (PWI) of growth layer groups measured from ringed seal canine teeth that were killed by polar bears and then converted into a body condition index (see Nguyen et al. 2017). Nguyen et al. (2017) found PWI to be positively correlated with ringed seal ovulation rate; thus it may

TABLE 1. Covariates used to model the likelihood of *Erysipelothrix rhusiopathiae* seropositivity in polar bears (*Ursus maritimus*) of the Beaufort Sea, Canada, 1985–2011. All temporal variables were taken from the year before serum sample acquisition to reflect antibodies from exposure in the past year.

Name	Range	Description and source
Biotic		
Age (yr)	1–26	Age of polar bear via tooth histology (Calvert and Ramsay 1998)
Sex	1/0	Field determination with females as reference category (0)
Poor[a]	1/0	Polar bears rated 1 or 2 on 5-point body condition index (Stirling et al. 2008b)
Good[a]	1/0	Polar bears rated 4 or 5 on 5-point body condition index (Stirling et al. 2008b)
PreyAge	0–0.75	Proportion of seal kills detected by aerial surveys that were adult, ≥5 yr old (Pilfold et al. 2012)
PWI[b]	0.267–0.293	Index of ringed seal (*Pusa hispida*) body condition assessed on seal kills (Nguyen et al. 2017)
CUB	1/0	Females with a cub-of-the-year the previous year
Abiotic		
LowIce	86–166 d	Number of days of sea ice concentration <50% as determined by SSM/I (Cavalieri et al. 1996)
BreakUp	136–199	Ordinal date that sea ice concentration dropped and remained <50% as determined by SSM/I (Cavalieri et al. 1996)
AOO	1/0	Index of Arctic wind-driven circulation regimes (Proshutinsky and Johnson 1997), measured annually. Converted to a binary variable, where values <0 are assigned 1
Winter_AOI	1/0	Index of sea-level pressure anomalies north of 20°N (Thompson and Wallace 1998), mean for January–March. Converted to a binary variable where values <0 are assigned 1
Latitude	69.25–76.68	Location of polar bear capture
Longitude	117.36–140.03	Location of polar bear capture

[a] 5-point body condition index dummy-coded, with "average" (3) forming the reference category.

[b] PWI = proportional width index; SSM/I = special sensor microwave/imager; AOO = Arctic Ocean Oscillation Index; AOO = Arctic Oscillation Index.

be associated with ringed seal predation trends in polar bears. Proportional width index data were only available until 2007 (Nguyen et al. 2017), so a separate ringed seal consumption model was run with a truncated time series to test potential effects of PWI. Both winter AOI and AOO may affect both body condition in ringed seals (Nguyen et al. 2017) and polar bear predation (Pilfold et al. 2015). Winter AOI and AOO were converted to binary variables where negative values were denoted as 1 and positive values were 0 because negative AOO and winter AOI years reflected higher ice volume years and were of greater interest. Females with cubs-of-the-year (cubs) were included as a separate group because compared with other polar bears they were expected to feed on a higher proportion of seal pups (Stirling 2002; Stirling et al. 2008a).

Winter AOI and AOO were included in the ringed seal consumption model because they were associated with ringed seal natality (Nguyen et al. 2017) and polar bear predation patterns (Pilfold et al. 2015). Pilfold et al. (2015) described relationships between polar bear kill rates, ringed seal reproduction, ice concentration, and large-scale atmospheric circulation patterns (i.e., winter AOI and AOO) and concluded that kill rates were influenced by a combination of abiotic and biotic factors.

Model selection: There is a recognized temporal pattern in sea ice cover that correlates with ringed seal natality and polar bear predation on ringed seals (Stirling 2002; Pilfold et al. 2015; Nguyen et al. 2017), so interpretation of model results considered relationships between these variables before determining a best-fit model. Temporal trends in prey age were investigated against temporal trends in

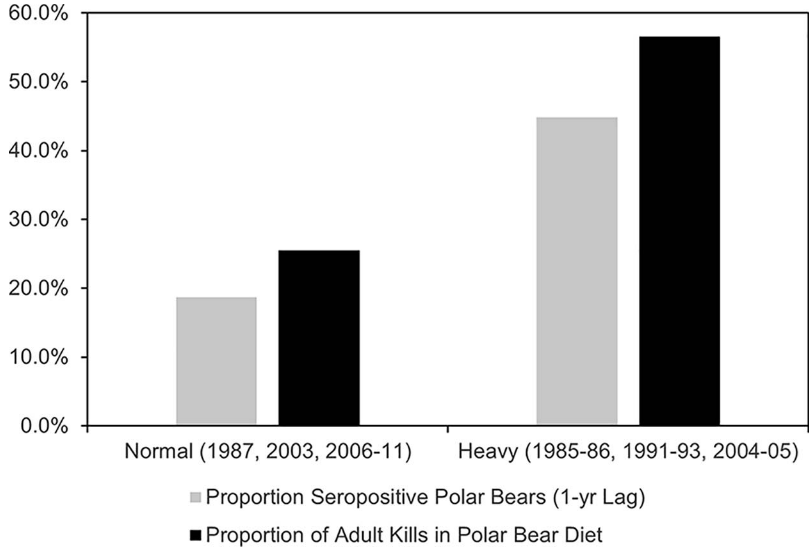

FIGURE 2. Comparison of *Erysipelothrix rhusiopathiae* seropositivity and ringed seal (*Pusa hispida*) prey age in Beaufort Sea, Canada, polar bears (*Ursus maritimus*) sampled 1985–2011 during years of normal and heavy sea ice volume.

seropositivity because of the correlation between year and prey age. When seropositivity was plotted over time, peaks and troughs closely matched peaks and troughs in prey age data, which correlated with periods of normal and heavy sea ice cover, respectively. This pattern was evident when the comparison between ice conditions was plotted (Fig. 2) and suggested that an effect from year could be explained, in part, by prey age, reflecting that the time series began in heavy ice years, where heavy ice reduced ringed seal productivity and ended in years of high ringed seal productivity (Nguyen et al. 2017). Because of the correlation between covariates and this identified trend, year was not included in the top model. $P \leq 0.05$ was considered statistically significant, and $P = 0.05$–0.10 was considered marginally significant for interpreting covariate effect. On the basis of the results from the initial models and Akaike information criterion with a correction for small sample size (AICc) values, where ΔAICc ≥ 2 lower than another model equated to better model fit, a top model was chosen.

RESULTS

Of the 180 polar bears sampled, the median age was 9 yr (range 1–26 yr) and the proportion of females was 0.66. Seropositivity was found in 49/180 (27.2% of samples; 95% CI 21.0–34.4%). Of those that were seropositive, 20 were classified as borderline seropositive, with a PP above the cutoff but within the CI.

The biological model found a marginally significant relationship with sex but no other significant effects (Supplementary Material Table S1). The temporospatial model found a significant negative relationship with year but no other significant effects (Supplementary Material Table S2). The ringed seal consumption model found a significant positive relationship with prey age, as well as marginal significance from winter AOI (Supplementary Material Table S3). The ringed seal model with subset data to include PWI had a marginally significant relationship with winter AOI and a positive significant relationship with prey age (Supplementary Material Table S4). The global model with all covariates included did not converge.

Comparing across all models with the full sample size, the ringed seal consumption model had the lowest AICc value (Table 2). The reduced sample size model (Supplementary Material Table S4) had a lower

TABLE 2. Comparing model-fit Akaike information criterion with a correction for small sample size (AICc) values to inform model selection for models estimating the likelihood of *Erysipelothrix rhusiopathiae* seropositivity in polar bears (*Ursus maritimus*) of the Beaufort Sea, Canada, 1985–2011.

Model	AICc
Biological	212.00
Temporospatial	209.07
Ringed seal (*Pusa hispida*) consumption	171.00
PWI[a] (reduced sample size)	124.11
Final	167.69

[a] PWI = proportional width index.

AICc value but could not be compared directly because of differences in sample size; model results outside of AICc do not suggest that this was the best-fit model. The top model included prey age and winter AOI from the ringed seal consumption model, whereby prey age had a significant positive effect, and winter AOI was marginally significant (Table 3). This top model had a lower AICc (ΔAICc = 3.31) than the original ringed seal consumption model. A model variant was tested with prey age alone to compare with the final model, which had a similar but slightly reduced fit, with a ΔAICc increase of 1.43.

DISCUSSION

When considering infectious diseases, Arctic ecosystems remain data deficient, and as such, lack baseline data (Hoberg et al. 2008; Kutz et al. 2014). This study provides insight on the prevalence of *E. rhusiopathiae* over time in polar bears within the Arctic marine food web. We detected *E. rhusiopathiae* seropositivity in Beaufort Sea polar bears from our earliest samples (1985), suggesting that polar bears in the western Arctic have been exposed for several decades. Seropositivity does not equate to active infection as antibodies often persist longer than a transient infection, although they reduce over time (Gilbert et al. 2013). Antibody persistence varies depending on multiple factors associated with both the host and the pathogen and usually ranges between a few weeks and several years (Secundino et al. 2006; Gilbert et al. 2013). Anti-*Erysipelothrix* antibody persistence in polar bears is unknown and seropositivity in our samples provided no information on when the animal was exposed. As such, although we considered temporal variables, past events and current events may be confounded.

Our time series was limited, with many years lacking samples, and notable previously quantified trends in ringed seal natality and

TABLE 3. Results from the preferred logistic regression model investigating the effects of covariates on the probability of *Erysipelothrix rhusiopathiae* seropositivity in polar bears (*Ursus maritimus*) of the Beaufort Sea, Canada, 1985–2011.

Fixed effects				
Covariate	Estimate	SE	Z value	*P* value
Intercept	−2.593	0.549	−4.727	<0.001[a]
Prey age[b]	2.797	0.971	2.881	0.004[a]
Winter AOI[c]	0.752	0.440	1.709	0.087[d]

Random effect		
Covariate	Variance	SD
Bear identification	1.103	1.05

[a] Significant values ($P < 0.01$).

[b] Proportion of ringed seal (*Pusa hispida*) prey in adult age class.

[c] Annual winter Arctic Oscillation Index.

[d] $P = 0.05$–0.10 was considered marginally significant.

ice volume, so an expected trend of increased infection over time, as was observed in Western Hudson Bay polar bears (Pilfold et al. 2021), was not present but might have been masked by these other effects. Increased seal mortality during the end of our study period (Ferguson et al. 2017; Nguyen et al. 2017) may have also influenced polar bear exposure to *E. rhusiopathiae,* because although ringed seal dynamics were correlated with atmospheric patterns, we speculate that they could also be associated with undocumented *E. rhusiopathiae* infection in the seals. Similarly, the observed *E. rhusiopathiae* muskox epidemic may have reflected a broader ecosystem-level epidemic (Kutz et al. 2015) and could have had an influence on polar bear exposure through scavenging of dead muskoxen and other species.

The initial models each focused on aspects of polar bear ecology. Most covariates related to individual bears had no quantifiable effects on seropositivity, which is similar to the negligible effect individual traits had on *E. rhusiopathiae* seropositivity in Arctic caribou (Aleuy et al. 2022). Most of the spatial and temporal covariates also had no effect on seropositivity. There was marginal significance from sex in the biological model, suggesting that males were more likely to be seropositive. The lack of significance for latitude and longitude suggests that *E. rhusiopathiae* infection was widespread. There was a significant effect from year in the temporospatial model, which suggested a decline in *E. rhusiopathiae* seropositivity over time when considered alone. When considered with ringed seal prey age, we believe that this apparent decline was an artifact of changes in predation associated with changes in ringed seal natality, which was in turn associated with sea ice dynamics (Nguyen et al. 2017; Harwood et al. 2020). The relationship identified between polar bear seropositivity, ringed seal prey age, and ice conditions (Fig. 2) supported choosing prey age over year (they could not both be included because of correlation) for the top model despite its significance in the temporospatial model, as it was probably an artifact of an effect that was better explained by prey age. Interannual variability in *E. rhusiopathiae* infection in caribou has been found to be related to climatic conditions and some waxing and waning in herd immunity (Aleuy et al. 2022), which could be a potential factor in interannual variability in polar bear infection that we were not able to quantify.

The top model was informed by a predator–prey relationship between polar bears and ringed seals, and included the effect of winter AOI, which was linked to ringed seal population dynamics. Polar bears that preyed on a higher proportion of adult ringed seals had a significantly higher probability of seropositivity. Adult seals may have a higher chance of *E. rhusiopathiae* infection because they consume fish, a host for the pathogen, whereas juveniles feed on milk. In a case of infection, it is important to note that seals can also be exposed, infected, and recover without retaining transmissibility, so older seals may not necessarily have higher transmissibility of *E. rhusiopathiae* to polar bears (VanderWaal and Ezenwa 2016), but as an age class (as is included in our model) we can speculate that transmissibility is probably higher in adults versus pups and juveniles. Winter AOI in the model focused on the effects of negative winter AOI years, which reflected years of increased sea ice volume. As such, the positive winter AOI coefficient estimated by the model suggested that probability of seropositivity increased after years with high ice volume. High ice volume was related to reduced pupping success in ringed seals and the age distribution of ringed seals killed by polar bears reflected the availability of pups (Pilfold et al. 2012), so reduced pupping success was connected to an increase in adult seal consumption, and in turn consumption of prey that we can speculate had a higher likelihood of *E. rhusiopathiae* transmission. Ringed seal consumption has been linked to the protozoan parasite *Toxoplasma gondii* in polar bears; this parasite has multiple potential vectors, one of which is the transmission of oocysts from runoff water into filter-feeding fish, which are prey for ringed seals (Massie et al. 2010; Simon et al. 2013). Multiple-host pathogens are generalists, which allows them to be passed through food webs and succeed in multiple taxa (Woolhouse et al. 2001; Lafferty et al. 2008), a probable explanation for the apparent movement of *E. rhusiopathiae* through both the terrestrial and marine food webs.

Multiple aspects of how predator–prey relationships interact with pathogen transmission have been studied, including the effect of predation on pathogen persistence in host species, bioaccumulation in apex predators, and diseases crossing the species barrier from prey to predator (Hsieh and Hsiao 2008; Moore et al. 2010; Su and Hui 2011; Malmberg et al. 2021). In systems where a pathogen can cross from prey to predator, many outcomes are possible, including eradication of the pathogen in the prey from targeted predation, or the pathogen driving the predators to extinction from increased predator infection (Hsieh and Hsiao 2008). The high seroprevalence found in polar bears might indicate that as an apex predator they act as a bioaccumulator for the disease and could be a potential reservoir for it, releasing it in the marine environment. Our results suggest that the food web is a driver of *E. rhusiopathiae* exposure in polar bears, but we do not have enough information within the polar bear ringed seal system to predict how both species are interacting with *E. rhusiopathiae* or how this pathogen may affect predator–prey dynamics into the future. Further information on the occurrence of the bacterium in sympatric seal and fish populations might shed light on whether *E. rhusiopathiae* is maintained in the food web of Beaufort Sea polar bears, versus being a spillover into polar bears from a terrestrial system (through scavenging behavior).

Understanding the prevalence of *E. rhusiopathiae* in polar bears and Arctic ecosystems would be positively affected by an improved surveillance system, inclusive of northern, community-based wildlife health surveillance. Tschritter et al. (2023) have developed sensitive disease surveillance tools for applications in Arctic ecosystems, which included *E. rhusiopathiae* detection, but these methods determine the presence of bacterial DNA, which may not necessarily equate to infection. Various strains of *E. rhusiopathiae* have been found throughout the Arctic; further work to uncover which strain is infecting polar bears, or if there are multiple strains, would be valuable. Progress in detection and inclusive surveillance systems for *E. rhusiopathiae* would help us understand the extent of exposure across the Arctic, and potentially elucidate transmission patterns between regions and species.

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