Assessing stress in western Hudson Bay polar bears using hair cortisol concentration as a biomarker

by

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Abstract

The development of novel biomarkers to help assess whether polar bear (*Ursus maritimus*) health is impacted by long-term physiological stress associated with climate change represents an emerging area of research. With progressively greater reductions in sea ice cover and a corresponding decrease in food availability, polar bears are likely to experience high levels of stress. While stress is adaptive in the short term, chronic stress can have deleterious effects, which may impair individual and population level health. Cortisol is the principal effector hormone of the stress response and has previously been linked to aspects of polar bear biology (e.g. reproduction, growth) that have been shown to be negatively influenced by environmental change.

Understanding stress is important for polar bears at the southern limit of their range, such as those in western Hudson Bay (WH), where changing sea ice phenology threatens population viability. We examined the relationship between the biological and demographic variables of age, reproductive status, and body condition (fatness) and hair cortisol concentration (HCC) in 729 polar bears in WH sampled from 2004 - 2013. Overall, there was a negative relationship between fatness and HCC, suggesting that bears in poorer body condition experienced higher levels of stress. However, when reproductive status was included in our analysis, this relationship only held for male and lone female bears. Females with dependent offspring had consistently low fatness and elevated HCC, likely because of the high cost of maternal care. We also found a positive correlation between HCC and age for bears in: 1) poorer body condition, possibly due to nutritional stress compounding effects of aging; and 2) male bears, potentially due to stress and injury associated with intrasexual mate competition. These findings support the use of HCC as a biomarker for polar bear health. Furthermore, we have established a HCC benchmark against which future effects of continued climate change on polar bear health can be measured.

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Chapter 1 – Introduction

Environmental change

The relationship between an organism and its environment forms the foundation of the discipline of ecology, which identifies the ability of organisms to adapt, survive, and reproduce as essential to life (Emlen and Oring 1977, Hannan and Freeman 1977, Loreau et al. 2001). In the short term (i.e., within a single generation), natural selection favours individuals who are able to adapt to environmental change and maintain a competitive advantage via phenotypic plasticity (Via and Lande 1985, Westeberhard 1989, Schluter 2001). Over longer periods (i.e., across generations), changing genotypes caused by evolutionary adaptation allows species to diversify, and survive more prolonged and severe selective pressures (Lande and Arnold 1983, Wade and Kalisz 1990, Kawecki and Ebert 2004). However, when the speed and magnitude of environmental change outpaces the rate of adaptation and evolution, species are at risk of population declines, extirpation from a region, or extinction (Root et al. 2003, Aitken et al. 2008).

Environmental changes with severe ecological consequences are currently occurring rapidly due to human activities (e.g., Vitousek et al. 1997, Serreze et al. 2000, Parmesan 2006, Halpern et al. 2008). For example, in aquatic ecosystems, overharvesting of fish species of commercial interest has caused large-scale population declines (Jackson et al. 2001) and nutrient input from agricultural runoff has contributed to eutrophication and production of toxic algal blooms (Smith et al. 1999, Heisler et al. 2008). Similarly, terrestrial habitat losses due to deforestation (Brooks et al. 2002, Foley et al. 2005), expansion of agricultural land (Matson et al. 1997, Foley et al. 2005) and desertification (Schlesinger et al. 1990, Kefi et al. 2007) have significantly affected biodiversity around the globe (Pimm and Raven 2000). Harmful industrial contaminants often make their way into watersheds, or are transferred via atmospheric cycling, to remote ecosystems where they can bioaccumulate in the food web (Muir et al. 1992, Cabana and Rasmussen 1994). Contaminants, particularly those that bioaccumulate in organisms and biomagnify up food webs, can have deleterious effects on individual and population health through impaired immune function and neurological development, reduced reproductive success, and death at high concentrations (Van den Berg et al. 1998).

Climate change

Climate warming represents a serious and overarching threat to the biosphere (Walther et al. 2002, Parmesan and Yohe 2003, IPCC 2014). In brief, greenhouse gases (e.g., carbon dioxide (CO_2) methane (CH_4), and nitrous oxide (N_2O)) are being released by anthropogenic sources at rates that cause them to build-up in the atmosphere (IPCC 2014). When the surface of the Earth absorbs solar radiation, some is re-emitted as long-wavelength infrared radiation. Atmospheric greenhouse gases absorb infrared and re-radiate a portion back toward the surface, which causes warming (Crowley 2000, IPCC 2014). Atmospheric CO_2 concentration has recently surpassed 400 ppm and is at a level unmatched in over 800,000 years (Petit et al. 1999, Luthi et al. 2008, IPCC 2014). For comparison, pre industrial levels of CO_2 were about 280 ppm (Luthi et al. 2008). Burning of fossil fuels for use in energy production for industry, transportation, and heating is the greatest contributor to increased CO_2 concentration in the atmosphere (IPCC 2014). Additionally, changes in land use (e.g., deforestation and the associated burning of biomass) to accommodate agricultural expansion releases CO_2 while concurrently impairing the natural sequestration potential of the landscape (Dixon et al. 1994). While atmospheric concentrations of greenhouse gases have fluctuated throughout geological history with corresponding variability in climate, the current rate of climate change is unprecedented (Petit et al. 1999, Luthi et al. 2008), such that the adaptive potential of organisms with long generation times (i.e., years to decades) may be limited (Parmesan and Yohe 2003, Parmesan 2006, Duputie et al. 2015).

The changing Arctic

The circumpolar Arctic is warming faster than more southern ecosystems in response to climate change with several 80-year model-estimated temperature increases being 1.5 – 4.5 times the global mean (Holland and Bitz 2003). A series of positive feedback systems driven by anthropogenic warming contribute to this phenomenon of "Arctic amplification" (Serreze and Francis 2006). Foundational to many of these feedback systems are marked changes to the dynamics of sea ice cover (Screen and Simmonds 2010) where reductions in the area of minimal sea ice extent have exceeded 10% per decade since the 1970s (Stroeve et al. 2012). Coupled with progressively earlier ice break-up and later ice freeze-up, both the duration and extent of open water in the Arctic Ocean are increasing significantly (Stammerjohn et al. 2012). Climate and sea ice projection models predict further declines, with the potential for ice-free summers in the Arctic within the century (Holland et al. 2006, Comiso et al. 2008, Wang and Overland 2009, Liu et al. 2013, Hamilton et al. 2014). Diminishing ice cover is reducing albedo and exposing more open-ocean to absorption of solar radiation, thus, reinforcing further sea ice declines in a system known as surface-albedo feedback (Winton 2006). More exposed ocean during sea ice minimum can increase primary productivity and exacerbate warming of surface waters through direct biological heating (Arrigo et al. 2008, Park et al. 2015); it can also facilitate increased heat exchange between the surface and the atmosphere in a process called ice insulation feedback (Serreze et al. 2009, Screen and Simmonds 2010).

Sea ice – Essential to the ecosystem

As an essential habitat component of Arctic marine ecosystems, changes due to increasing variability and decline of sea ice cover cascade through the entire food web (Bluhm and Gradinger 2008, Laidre et al. 2008). Declines in the proportion of multi-year ice, summer ice extent, and changes to the timing of seasonal melting and freezing have negatively affected more specialized and ice-dependent animals throughout the ecosystem (Arrigo et al. 2008, Laidre et al. 2008). Ice cover is particularly important over the productive waters of the continental shelf. Here, terrestrial runoff enters the relatively shallow and warm waters and fertilizes the abundant plankton life that forms the base of the Arctic food web. Polar cod (*Boreogadus saida*), a keystone consumer and primary prey item for various ice-dependent pinniped species, has a sympagic larval and juvenile life history and preferentially feeds on crustaceans associated with ice-dependent algae (Hop and Gjosaeter 2013). As an essential vector for lipid assimilation and transport to higher trophic levels, variation in the abundance and distribution of polar cod in response to changing ice conditions will have consequences for marine predators further up the food chain. Polar cod comprise a large portion of the diet of ringed seals (*Pusa hispida*) across the Arctic (Holst et al. 2001, Chambellant 2010, Crawford et al. 2015). Ringed seals are similarly dependent on ice for feeding and resting in addition to pup survival (Chambellant 2010). Ringed seal pups are born in subnivean birth lairs in April and remain in the lair for about 6 weeks (Smith and Stirling 1975, Smith 1980). Appropriate snow and ice conditions for the formation of birth lairs are critical to pup survival during a time of heavy polar bear predation (Stirling and Oritsland 1995, Chambellant et al. 2012).

Because of the close predator-prey relationship, ringed seal productivity has been linked to polar bear reproduction and cub survival (Stirling and Oritsland 1995, Rosing-Asvid 2006). Polar bears feed predominantly on ringed seals hunted from the surface of the sea ice (Thiemann et al. 2008); although open water captures are possible, they are rare (Furnell and Oolooyuk 1980). Of particular importance to polar bears is the ringed seal pupping season when they feed extensively on accessible and abundant pups in preparation for a period of near-fasting (Ramsay and Stirling 1988, Ramsay et al. 1991). This fasting period occurs during the summer when polar bears are on land or on thick multiyear ice over relatively unproductive high Arctic water (Stirling and Archibald 1977, Stirling and Oritsland 1995, Pilfold et al. 2012). In part because of the dependence on sea ice as a hunting platform, changing sea ice phenology has been linked to decreases in polar bear body condition (Stirling et al. 1999, Rode et al. 2012), reduced survival (Regehr et al. 2007, Regehr et al. 2010, Bromaghin et al. 2015), reduced reproductive success (Hunter et al. 2010), increased human-bear interaction (Towns et al. 2009) and population declines (Regehr et al. 2007, Bromaghin et al. 2015). With low species richness and many specialized species, the Arctic food web is particularly vulnerable to declines in species at any trophic level (Carscallen and Romanuk 2012). Considering that sea ice is predicted to decline further, the viability of ice-dependent species and the stability of the ecosystem itself may be at risk.

Response to change - Stress

When confronted with threatening stimuli, such as rapid environmental perturbation, animals respond with physiological, behavioural or morphological changes to maintain homoeostasis and increase their likelihood of survival (Reeder and Kramer 2005). The suite of strategies employed to respond to a disruption of homoeostasis are collectively referred to as the stress response (Johnson et al. 1992). In a stressful situation, behaviour is modified to prioritize short-term responses to a perceived threat (fight or flight), while the urgency of longer-term needs (sex, food, sleep) is decreased accordingly (Korte et al. 2005, Reeder and Kramer 2005). In this way, the stress response is adaptive in the short-term.

Physiological response involves simultaneous activation of two important pathways in the central nervous system: the sympathetic nervous system and the hypothalamic-pituitary-adrenal axis (HPA; Johnson et al. 1992, Reeder and Kramer 2005). The sympathetic nervous system reacts rapidly by releasing adrenaline, which can quickly mobilize the stored energy from glucose and lipids needed for short-term survival (Habib et al. 2001, Charmandari et al. 2005). The HPA axis is activated through central nervous system stimulation of the hypothalamus that results in a chain of intermediary hormone messengers being released to the blood stream (Tsigos and Chrousos 2002). When one of these intermediaries, adrenocorticotropic hormone, reaches the adrenal gland, glucocorticoid hormones are released in response (Tsigos and Chrousos 2002). Glucocorticoid hormones are involved in regulating metabolic function under normal conditions, but are elevated above basal levels during stress in quantities proportional to the perceived threat (Reeder and Kramer 2005, Sheriff et al. 2011). In mammals, the primary glucocorticoid hormone is cortisol and its free-circulating concentration corresponds to the intensity of the stress response (Sapolsky et al. 2000). In contrast to the effects of the sympathetic nervous system activation, the HPA response and levels of cortisol peak several minutes after the initial stimulus and remain elevated for minutes to hours (Ulrich-Lai and Herman 2009). Elevated free circulating cortisol boosts energy available in the short-term by stimulating the production of adrenaline while also increasing gluconeogenesis and protein and fat metabolism (Habib et al. 2001, Charmandari et al. 2005, Reeder and Kramer 2005).

Although the stress response is generally adaptive in the short term, prolonged stress and chronically elevated cortisol production can have deleterious effects on many aspects of animal health. Specifically, chronic stress has been linked to diminished growth and reproduction, reduced cognitive ability, increased catabolism of stored energy, and immunosuppression (Johnson et al. 1992, McEwen and Sapolsky 1995, Boonstra et al. 1998, Sapolsky et al. 2000, Habib et al. 2001, Kitaysky et al. 2003, Charmandari et al. 2005). When a consistent unidirectional stress (e.g., progressive environmental change) affects an animal, the chronic elevation of cortisol production may have detrimental health effects.

Measuring stress

Cortisol has been measured as a proxy for stress and used as an early warning indicator of stress-related health effects in laboratory and captive animal studies. Classically, cortisol concentrations have been measured in tissues such as blood, saliva, urine and feces (e.g., Auperin and Geslin 2008, Gatti et al. 2009, Hekman et al. 2012, Romero et al. 2015). However, because of rapid regeneration time, cortisol contained within these samples represents a ‘point’ measurement and can be highly variable within a single day (Davenport et al. 2006, Sheriff et al. 2011). Therefore, cortisol in these tissues cannot be used to assess long-term chronic stress.

Similarly, cortisol in these tissues cannot be used to assess stress levels in free-ranging wildlife because sampling events often require invasive, and potentially stressful, capture techniques (Chow et al. 2011). In contrast, both hair (Davenport et al. 2006, Bechshoft et al. 2012a, Macbeth et al. 2012) and feathers (Bortolotti et al. 2008, Koren et al. 2012) incorporate free-circulating blood cortisol throughout their growth period, thereby representing the average stress burden over a period of weeks to months while remaining uninfluenced by the acute stress of capture (Macbeth et al. 2010, Sheriff et al. 2011, Cook 2012, Meyer and Novak 2012). Additionally, cortisol concentration is consistent through the length of the hair shaft (Davenport et al. 2006) and concentrations do not vary between regions of the body (Macbeth et al. 2010). Intrinsic cortisol concentration is robust to change and is uninfluenced by exposure to the elements (Macbeth et al. 2010) and long-term archiving (Webb et al. 2010, Bechshoft et al. 2012a). Hair can also be effectively washed of external contamination without influencing the internal cortisol concentration (Davenport et al. 2006, Macbeth et al. 2010). Consequently, hair is an excellent matrix for studies of stress in free-ranging wildlife where sampling conditions cannot be carefully controlled. Further, hair can be collected for cortisol concentration analyses opportunistically by non-specialists (e.g., hunters), non-invasively using hair snags (Macbeth et al. 2010, de Groot et al. 2013) and from historic samples (e.g., museums; Bechshoft et al. 2012a).

Study system – Western Hudson Bay polar bears

Hudson Bay is a large inland sea within the Arctic climate zone of central Canada (Figure 1-1). It is an ice-dependent marine ecosystem with seasonal sea ice forming over the Bay from mid-November to December and reaching maximum thickness in April. Ice break-up begins in May, followed by a full open water season by August and a freeze-up beginning in late October

(Hoover 2010). Specific break-up and freeze-up dates (defined as 50% ice coverage) vary between years (Stirling et al. 1999, Gagnon and Gough 2005). However, progressively earlier ice breakup and later ice freeze-up on the Bay has led to an extended ice-free period (Derocher and Stirling 1990, Atkinson and Ramsay 1995, Thiemann et al. 2006, Castro de la Guardia et al. 2013, Hochheim and Barber 2014).

Three polar bear populations, delineated by the movement of resident bears and their fidelity to coastal denning areas, reside in the Hudson Bay region (Stirling 1977, Peacock et al. 2010, Obbard and Middel 2012; Figure 1-1). My study population in western Hudson Bay consists of approximately 1030 polar bears that spend the ice-free period on shore along the coast of Manitoba and Nunavut, Canada (Stirling 1977, Lunn et al. 1997, Stirling et al. 1999, Regehr et al. 2007, Stapleton et al. 2014). Bears in the Western Hudson Bay population have been negatively impacted by the rate and magnitude of changing sea ice phenology (Gagnon and Gough 2005, Castro de la Guardia et al. 2013, Hochheim and Barber 2014). Here, extended ice-free summers have been linked to decreased in body condition (Stirling et al. 1999), reduced survival of young and old bears (Regehr et al. 2007, Bromaghin et al. 2015), increased human-bear interactions (Towns et al. 2009), and population declines (Regehr et al. 2007, Bromaghin et al. 2015). Before 1986, Western Hudson Bay had a higher proportion of females with successfully weaned yearlings and litter sizes that were 6 - 15% larger than more northerly populations. This reproductive success has since declined and reversed (Derocher and Stirling 1995) to the point where models now predict that with continued sea ice loss by mid-century, up to 73% of females could fail to produce a litter due to poor body condition (Molnár et al. 2011). With further lengthening of the ice-free season predicted under several climate scenarios (Castro de la Guardia et al. 2013, Hochheim and Barber 2014), the long-term viability of the Western

Hudson Bay population is uncertain (Molnár et al. 2010, Castro de la Guardia et al. 2013, Molnár et al. 2014). As such, developing novel biomarkers to help assess whether polar bear health is affected by long-term physiological stress is becoming increasingly important.

Research question and hypotheses

In Chapter 2, I examined the influence of body condition, sex, reproductive status and age on the stress levels of the Western Hudson Bay population of polar bears by measuring cortisol concentrations in their hair. Using multivariate analyses, I tested the effectiveness of hair cortisol concentration (HCC) as a proxy (i.e., biomarker) for health in this vulnerable population of free-ranging polar bears. I used this approach to test the following hypotheses:

1. There will be a negative correlation between body condition and HCC, because stored fat is the only significant source of energy for metabolic demands during the ice-free fasting season.

2. Females with dependent offspring will have higher HCC due to the increased energetic demands associated with nursing and offspring care.

3. HCC will be higher in older individuals as the effects of aging impair health and reduce competitive advantage relative to individuals of prime age.

In Chapter 3, I will discuss the implications of my results and their applicability to management of the Western Hudson Bay polar bear population. I will also identify research priorities that extend and build on the results presented in this thesis.

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Figures

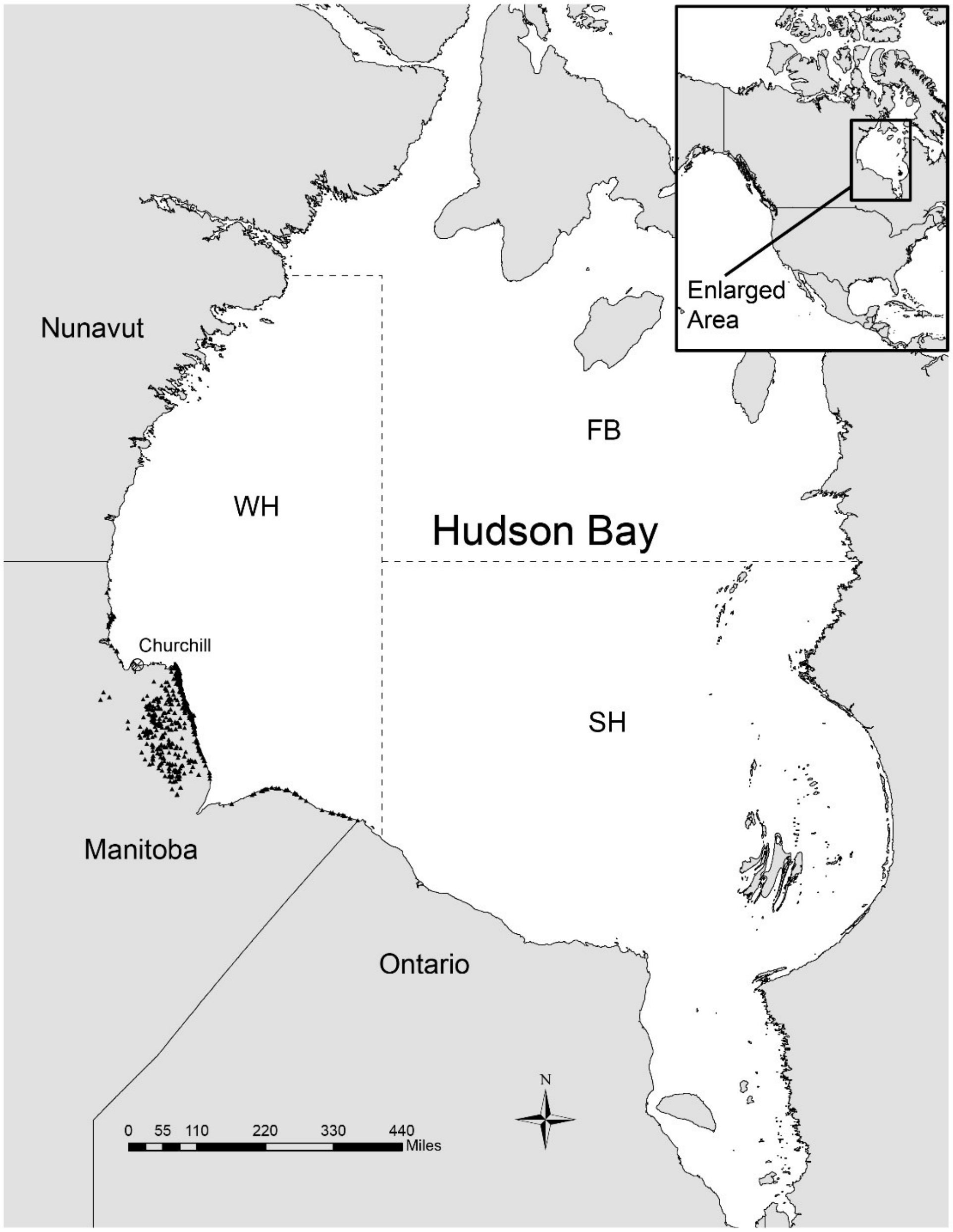

Figure 1-1: Hudson Bay is a large inland sea in the Arctic climate zone of central Canada. Three polar bear subpopulations reside within Hudson Bay – Southern Hudson Bay (SH), Foxe Basin (FB), and the study population for this thesis Western Hudson Bay (WH). Symbols indicate capture locations for 729 samples used in this study.

Chapter 2 – Assessing stress in western Hudson Bay polar bears using hair cortisol concentration as a biomarker

Introduction

The Arctic is warming faster than more southern regions as a consequence of climate change, with the most pronounced effects being the significant reduction in sea ice extent and period of seasonal coverage (Comiso et al. 2008, Stroeve et al. 2012). With positive feedback from solar absorption during an increasing and expansive open water season (Stroeve et al. 2014), as well as rising atmospheric CO_2 concentrations (Solomon et al. 2009, IPCC 2014), further reductions in sea ice extent are predicted (Holland et al. 2006, Liu et al. 2013, Hamilton et al. 2014). Sea ice is the primary habitat for polar bears (*Ursus maritimus)* that use the ice as a platform to travel, hunt, and mate (DeMaster and Stirling 1981, Stirling and Derocher 1993). Earlier ice breakup and a prolonged ice-free period has been linked to decreases in body condition (Stirling et al. 1999, Rode et al. 2012), reduced survival (Regehr et al. 2007, Regehr et al. 2010, Bromaghin et al. 2015), reduced reproductive success (Hunter et al. 2010), increased human-bear interactions (Towns et al. 2009), and population declines (Regehr et al. 2007, Bromaghin et al. 2015).

Polar bears near the southern limit of their range, such as those in the Western Hudson Bay (WH) population, are particularly vulnerable to impacts of a warming climate because of the rate and magnitude of changing sea ice phenology (Gagnon and Gough 2005, Castro de la Guardia et al. 2013, Hochheim and Barber 2014). For these bears, building and maintaining fat reserves is important because of reduced access to their primary prey species, the ringed seal (*Pusa hispida*), during a progressively longer ice-free period in Hudson Bay (Derocher and

Stirling 1990, Castro de la Guardia et al. 2013, Hochheim and Barber 2014). During this ice-free period, polar bears fast onshore (Derocher and Stirling 1995, Polischuk et al. 2002) and use stored fat for metabolic maintenance (Derocher and Stirling 1990, Atkinson and Ramsay 1995). Although polar bears are opportunistic foragers and some are known to use terrestrial food sources (e.g., berries, caribou, seabird and goose eggs) when available (Derocher et al. 1993b, Thiemann et al. 2008, Gormezano and Rockwell 2013, Iverson et al. 2014), the caloric value of these items relative to the energetic cost of acquisition is low and unlikely to compensate for reduced access to ringed seals (Ramsay and Hobson 1991, Rode et al. 2015). Bears that are in poorer condition during the ice-free period are at risk of nutritional stress and increased loss of lean mass (Polischuk et al. 2002, Molnár et al. 2009). Progressively earlier ice break-up and the subsequent extension of the fasting period may compromise the overall health and long-term viability of the WH population (Molnár et al. 2010, Stirling and Derocher 2012, Molnár et al. 2014).

When exposed to environmental disturbance, animals undergo behavioural and physiological changes to increase chances of survival and maintain internal homoeostasis. These changes are part of the stress response that is regulated by the hypothalamic pituitary adrenal axis through the release of glucocorticoid hormones (Sapolsky et al. 2000, Habib et al. 2001). Cortisol is the primary glucocorticoid (Davenport et al. 2006) and has been analyzed in various animal tissues (e.g., blood, saliva, feces, urine) as an indicator of stress levels (e.g., Koren et al. 2002, Bonier et al. 2004, Saeb et al. 2010). Acute stress is an adaptive response to threatening stimuli typified by ‘fight or flight’ physiological changes and behaviour (Habib et al. 2001, Charmandari et al. 2005, McEwen 2007). However, prolonged or chronic stress can be maladaptive and has been linked to diminished growth and reproduction, reduced cognitive ability, increased catabolism of stored energy, and immunosuppression (McEwen and Sapolsky 1995, Boonstra et al. 1998, Sapolsky et al. 2000, Kitaysky et al. 2003).

Behavioural and physiological responses to environmental and ecological disturbances, such as chronically elevated stress, have implications for the stability of a population (Boonstra et al. 1998, Harvell et al. 1999). For polar bears, the positive feedback loop of stress-induced inhibition of fat storage and increased fat catabolism (lipolysis) may exacerbate declines in body condition. As the proportion of chronically stressed individuals in a population increases, the combined influence of reduced reproduction, lower body condition, and immunosuppression may impact population viability. Understanding stress in a population, including differing vulnerabilities, is important for health monitoring and informing conservation and management decisions. A recent meta-survey identified sea ice habitat loss, nutritional stress, and chronic physiological stress as the top three threats to the long-term health and sustainability of polar bears (Patyk et al. 2015).

Stress hormones can be integrated over longer periods in tissues such as hair (Davenport et al. 2006, Bechshoft et al. 2012a, Macbeth et al. 2012) or feathers (Bortolotti et al. 2008, Koren et al. 2012) where free-circulating blood cortisol is incorporated throughout the growth period of the tissue, thereby representing the average stress burden over a period of months (Sheriff et al. 2011, Cook 2012, Meyer and Novak 2012). Hair cortisol concentration (HCC) is not influenced by stress due to sampling events and does not degrade over time (Webb et al. 2010, Bechshoft et al. 2012a). Additionally, hair can be collected for HCC analyses opportunistically (e.g., from hunted bears), non-invasively using hair snags (Macbeth et al. 2010, de Groot et al. 2013) and from historic samples (e.g., museums; Bechshoft et al. 2012a).

In this study, we used hair samples to test whether HCC can be used as a proxy (i.e., a biomarker) to assess health in free-ranging polar bears in WH. We also examined the combined influence of body condition and demographic variables (i.e., age, sex, and the presence of dependent offspring) on HCC.

Materials and methods

Study system - western Hudson Bay

Hudson Bay is a large inland sea that is ice covered in winter and ice free in summer (Hochheim et al. 2010). Seasonal ice forms over Hudson Bay from mid-November to December and reaches maximum thickness in April. Break-up begins in May, followed by a full open water season by August and a freeze-up beginning in late October (Hoover 2010). Significantly earlier break-up and later freeze-up (each defined as 50% ice coverage) has decreased the number of days of ice cover in western Hudson Bay with a corresponding increase in the number of days the bears spend ashore (Stirling et al. 1999, Gagnon and Gough 2005, Cherry et al. 2013).

Hair collection

Hair samples were collected, in late August through early October, as part of ongoing research in WH between 2004 and 2013. While onshore, bears were captured and handled within a 12,000 km^2 area between the town of Churchill, Manitoba and the mouth of the Nelson River (Lunn et al. 2013; Figure 2-1) following methods described by Stirling et al. (1989). Hair samples, consisting of both guard hair and underfur were collected by shaving a patch on the rump as close to the skin as possible with a single-use Feather® disposable surgical scalpel. The hair in these samples would have been grown between May and September (Pedersen 1945, Derocher 2012) following the spring moult.

The age of bears was determined by counting the cementum growth rings in a vestigial premolar tooth extracted during capture (Calvert and Ramsay 1998). Body condition was assessed in the field using a qualitative index of fatness ranging from 1 to 5, with 1 being emaciated and 5 being obese (Stirling et al. 2008). The sex of each bear and the presence of dependent offspring were also recorded.

Cortisol analysis

Guard hairs were subsampled for cortisol analysis, which was performed at the Toxicology Centre, University of Saskatchewan (Saskatoon, SK, http://www.usask.ca/toxicology/). Hair samples were initially washed to remove external contamination. The wash and analysis procedures follow Davenport et al. (2006), which were subsequently modified and validated for use with polar bear hair (Macbeth et al. 2012). In brief, 50 – 80 mg of guard hairs were washed three times with 3 minute agitations in 0.04 ml methanol/mg of hair, then left to dry at room temperature for 48 h. Washed guard hairs were ground to a fine powder in a mixer mill (Retsch Inc., Newtown, PA). Cortisol was extracted from a quantified mass of powdered hair (25 mg for most samples) into methanol (0.02 ml/mg) using 1.8 ml Eppendorf tubes on a slow rotator for 24 h. The resulting methanol extract was centrifuged for 15 minutes at 4500 rpm, after which the supernatant was collected. The sample (pellet) was rinsed again twice with fresh methanol, vortexed, and centrifuged. The resulting pooled supernatant was dried under nitrogen gas and reconstituted with phosphate buffer. Cortisol concentration was determined using an enzyme-linked immunosorbent assay kit (Oxford EA-65 Cortisol EIA kit; Oxford Biomedical, Lansing, MI).

The cortisol extraction efficiency of this procedure was > 95% (Macbeth et al. 2012). Parallelism between serially-diluted hair extracts and cortisol standards provided by the EIA kit manufacturer were observed. Intra-assay and inter-assay coefficients of variation were 9.7% and 11.4%, respectively. The limit of detection for the EIA kit was 0.04 ng/ml, which corresponds to a HCC of 0.32 pg cortisol/mg hair for a 25 mg sample. Results below this threshold were assigned a value half way between 0 and the detection limit (i.e., 0.02 ng/ml on a mass-specific basis; Macbeth et al. 2010, Macbeth et al. 2012).

Statistical analysis

Cortisol concentrations were standardized as z-scores representing the number of standard deviations relative to the mean of the sampling year to remove potentially confounding inter-annual variation while maintaining intra-annual variation. The term cortisol used hereafter represents the values obtained by standardizing cortisol in this way. The relationship between HCC and body condition was examined using a one-way analysis of variance (ANOVA) of mean cortisol values across 4 fatness classifications (only one individual had a fatness 5 so was therefore excluded from the analysis). Means were compared using post-hoc Tukey's t-tests.

We used a linear mixed model to test for the influence of fatness and demographic variables on cortisol. Age was considered a continuous covariate with fatness, sex and presence/absence of dependent offspring (i.e., male, lone female, female with dependent offspring) included as categorical predictors in the model. Both cubs-of-the-year (ca. 8-10 months old) and yearlings (ca. 20-22 months old) were pooled and classed as dependent offspring. To account for potential autocorrelation among repeat measurements of individuals across years, "individual bear ids" were treated as a random variable. The covariance structure associated with the repeat measures that minimized the Akaike's Information Criterion (AIC) was used (based on restricted maximum likelihood estimation). Insignificant interaction terms were removed step-wise to improve the fit of the final model based on maximum likelihood and AIC model selection. Significant two-way interactions were further analyzed using univariate linear regressions and ANOVAs. A second linear mixed model was used to compare females of reproductive age (≥ 5 years) with and without dependent offspring. Statistical analysis was performed using IBM SPSS software (IBM Corp. 2013. IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY).

Results

A total of 729 hair samples were analyzed from 506 individual bears with 350 individuals being sampled once and 156 sampled multiple times (maximum 7 times). The median HCC was 0.62 pg/mg (range: 0.10 to 9.97 pg/mg) with 12 samples below detection limits. There were significant inter-annual differences in HCC ($F_{9, 719} = 9.86$, $p < 0.001$). Our best-fit model included all two-way interactions with the non-significant three-way interaction removed (Table 2-1). HCC differed significantly among the four fatness classifications when all bears were pooled ($F_{3, 723} = 22.08$, $p < 0.001$; Figure 2-2a). In general, HCC declined with increasing fatness. Tukey’s post-hoc means testing showed only a marginally significant decline between fatness indices 1 and 2 ($p = 0.06$), and no difference between fatness indices 3 and 4 ($p = 0.40$). All other differences were significant ($p < 0.001$). The negative relationship between fatness and HCC depended on sex and the presence of dependent offspring (Table 2-1). Specifically, HCC decreased with increasing fatness for male and lone female bears (Figure 2-2b), while females with dependent offspring had lower body condition on average (i.e., were always classified in fatness 1 - 3) and consistently higher HCC.

Increases in HCC with age were larger for bears in poorer body condition (Table 2-1; Figure 2-3). There was no significant relationship between HCC and age for bears in fatness 4, but increases in HCC with age were significant and progressively steeper for bears in fatness indices 3 and 2, respectively (Table 2-2). Fatness 1 had a small sample size (n = 8) and weak statistical power, but followed the same pattern, having the greatest increases in HCC with age. There was only a single individual classified in fatness 5, but this bear had one of the lowest HCC (lower 15% of samples).

Age, sex, and the presence of dependent offspring interactively affected HCC (Table 2-1; Figure 2-4). HCC significantly increased with age in males while there was no significant relationship between HCC and age in females regardless of being alone or accompanied by dependent offspring (Table 2-2). Females with dependent offspring had significantly higher HCC than lone females of reproductive age ($F_{1, 156.1} = 41.42$, $p < 0.001$).

Discussion

Our findings clearly show that HCC can be a useful biomarker for polar bear health by identifying a relationship between fatness (body condition) and HCC. However, this relationship only held for male and lone female bears. In contrast, females caring for dependent offspring had consistently lower body condition (only present in fatness indexes 1-3) and elevated HCC. We also found that HCC of male bears and bears in poor body condition increased with age. Therefore, while, in general, HCC may be a useful proxy to assess polar bear health, other factors, including demographic variables, also significantly influence variability in HCC among individuals.

High HCC in bears with low body fat likely occurred because these animals experienced nutritional stress during the onshore fasting period. Physiological changes associated with using stored fat for metabolic energy during fasting have been linked to elevated circulating cortisol and corticosteroid-binding globulin (Chow et al. 2011). Because polar bears moult in the springtime and regrow hair between May and September (Derocher 2012), the mean free-circulating cortisol associated with nutritional stress should be represented in hair grown during this fasting period (Reviewed in Cook 2012, Meyer and Novak 2012). WH polar bears lose between 0.4 and 0.9 kg of body mass per day (up to 50% of which is fat) for metabolic maintenance while fasting (Derocher and Stirling 1995, Polischuk et al. 2002). Therefore, individuals with insufficient fat stores likely lose more lean mass (Polischuk et al. 2002, Molnár et al. 2009) and experience higher nutritional stress. Importantly, our findings indicate that HCC may be used to track increasing nutritional stress and declining body condition of polar bears. Such a biomarker may prove invaluable as progressively earlier ice break-up may affect polar bear body condition to a point where reproductive failure and starvation mortality become significant enough to have population-level effects (Molnár et al. 2010, Molnár et al. 2014).

Our findings also clearly showed that female bears with dependent offspring had poorer body condition and experienced higher levels of stress relative to other groups. Females with offspring were all ≤ 3 in fatness, consistent with the known negative association between body condition and rearing offspring (e.g., Ramsay and Stirling 1982, Derocher et al. 1993a, Atkinson and Ramsay 1995, Derocher and Stirling 1998). However, our study also revealed a measurable endocrine stress response associated with the physiological demands of offspring care by showing that females supporting dependent offspring had consistently elevated HCC. Increased stress in females with offspring is likely explained by the high energetic and nutritional cost of lactation (Derocher et al. 1993a, Arnould and Ramsay 1994). Polar bear offspring are partially dependent on their mother's milk through their first 1.5 years and may nurse for up to 2.5 years (Arnould and Ramsay 1994, Derocher and Stirling 1995). Polar bear milk contains high fat content (up to 30%) with equivalently high demand on mobilization of stored energy from the mother (Ramsay and Stirling 1988, Derocher et al. 1993a, Thiemann et al. 2011). Declining body condition in WH polar bears associated with a progressively longer ice-free period (Stirling et al. 1999) may compound high levels of nutritional stress already experienced by polar bear mothers, leading to chronically elevated cortisol. HCC in polar bear cubs-of-the-year correlates with that of their mothers while HCC of yearlings does not (Macbeth et al. 2012). This could be caused by direct cortisol transfer during lactation, similar phenotypic responses to shared environmental stressors, genetic heritability, or contributions from all three (Macbeth et al. 2012). Regardless of the mechanism, polar bear cubs may be vulnerable, in their first year, to the effects of elevated cortisol transferred from their mother. A continued decline in body condition in WH could result in reproductive failure, premature cessation of nursing, reduced cub survival, and diminished size and health of surviving offspring in addition to further increasing stress levels (Derocher et al. 1993a, Thiemann et al. 2006, Rode et al. 2010). The deleterious effects of chronically elevated stress (e.g., reduced reproduction, reduced growth, immunosuppression) may compound these issues to further affect population viability.

For polar bears in poor body condition, increases in HCC with age may be explained by long-term stress over an individual lifetime compounded by the deleterious physiological effects of aging. Chronic nutritional stress experienced by bears in poor body condition can increase the rate of cellular senescence, causing earlier onset of, and greater susceptibility to, age-related health effects (Epel et al. 2004). Cellular senescence, in turn, is a major part of organismal aging and can impair an animal's ability to handle stress, fight disease, and maintain internal homoeostasis (Kay and Makinodan 1976, Ames et al. 1993, Rudolph et al. 1999). Additionally, the compromised immune systems of older bears and those in poor body condition likely increase their vulnerability to disease (Reviewed in Lesourd 2006), which may be particularly important in WH where a warming climate may facilitate the introduction of novel pathogens from more southern habitats (Weber et al. 2013).

Higher concentrations and increased mobilization of lipophilic contaminants (e.g., persistent organic pollutants) by bears in poor body condition may contribute to increases in HCC with age. Bio-accumulating contaminants cause deleterious effects including immunosuppression in polar bears (see review by Sonne 2010), and several contaminants (e.g., mercury, organohalogens) have been linked to cortisol concentrations (Oskam et al. 2004, Bechshoft et al. 2012b, Bechshoft et al. 2015). Industrial pollutants accumulate in the Arctic as a consequence of long-range transport, and polar bears often carry high burdens of contaminants (Bernhoft et al. 1997, Smithwick et al. 2005, St Louis et al. 2011). Although body condition does not influence total contaminant load, the bioavailability of contaminants in bears in poor body condition may be high as they have less fat to partition away lipophilic compounds during the fasting period when contaminants are remobilized (Norstrom and Muir 1994, Polischuk et al. 1995, Polischuk et al. 2002, Sonne 2010). In contrast, fat bears have a more diluted contaminant burden and are likely buffered against the deleterious effects of lipophilic contaminants with age (Polischuk et al. 2002, Sonne 2010).

The accumulation of injuries associated with competition between males during the mating season may explain why HCC increased with age in male bears, but not females (alone or with offspring). Serious injuries associated with mate competition, such as broken canine teeth, broken bones and deep lacerations, can impair the ability of male polar bears to hunt and compete (Derocher et al. 2010) thereby likely contributing to stress. The onset of mate competition in male polar bears around 6 years of age (Derocher et al. 2010) corresponds with the age at which we found higher HCC relative to females. In addition to intrasexual competition, nutritional stress associated with increased fasting by male bears during the spring mating seasons may also contribute to increase HCC levels (Ramsay and Stirling 1986, Cherry et al. 2009). The additional body condition deficit likely caused by this reproductive behaviour may further increase stress levels relative to female bears. In contrast, we found that HCC in female bears was likely affected by reproductive stressors associated with dependent offspring and did not increase with age. While there is the potential for older females to experience cumulative health effects due to raising multiple litters over their reproductive lifetimes, the cost may be mitigated by reducing the number of cubs per litter in late life (Ramsay and Stirling 1988). Additionally, increased maternal and hunting experience may help older mothers build and maintain better body condition while nursing potentially offsetting some of the stress due to cumulative health effects (Atkinson and Ramsay 1995). Therefore, the positive relationship between age and HCC demonstrated only in male polar bears may be attributable in part to differences in life history and intersexual reproductive strategies.

There is a need to identify the impacts of rapid climate change and ongoing sea ice habitat loss on vulnerable Arctic species. Our study provides evidence that HCC may provide an effective health biomarker to monitor the status of polar bear populations by demonstrating a link between body condition and HCC in a multivariate framework using a large sample size. Our study also established HCC benchmarks against which to assess future effects of continued climate change on polar bear health in WH. Importantly, use of HCC as a biomarker could potentially allow researchers to monitor bear populations using non-invasive sampling, such as hair snags. Nonetheless, our discovery that relationships between body condition and HCC depended on interactions with age and demographic group suggests that using HCC as a tool to monitor the health of polar bear populations may be most appropriate when demographic information is known. Further, the large amount of variability in HCC among individuals suggests that detecting meaningful trends in HCC in polar bear populations may require large sample sizes.

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Tables

Table 2-1: Results of the linear mixed effects model investigating the effects of Western Hudson Bay polar bear age, fatness and presence/absence (P/A) of offspring (for male, lone female, females with offspring) on standardized HCC for 2004 – 2013.

Effect	Numerator df	Denominator df	F	p-value
Intercept	1	281.0	0.25	0.62
Fatness	3	162.2	1.27	0.29
P/A offspring	2	128.8	0.56	0.57
Age	1	379.3	1.16	0.28
Fatness * P/A offspring	4	105.1	4.06	< 0.01
Fatness * Age	3	47.8	2.79	0.05
P/A offspring * Age	2	36.4	6.22	< 0.01

Table 2-2: Univariate linear regression coefficients of standardized HCC against age for predictor variables in Western Hudson Bay polar bears sampled from 2004 – 2013. Each univariate regression explores significant interaction terms from the full linear mixed effects model (Table 2-1). β represents the unstandardized beta coefficient of the regressions.

Variable	n	β	Std. E	t	p-value	R^2
Lone Females	166	-0.01	0.01	-1.49	0.14	0.01
Females + Offspring	169	-0.01	0.02	-0.28	0.78	0
Males	394	0.05	0.01	5.70	< 0.01	0.08
Fatness 1	8	0.25	0.22	1.12	0.31	0.17
Fatness 2	200	0.03	0.01	2.76	< 0.01	0.04
Fatness 3	417	0.02	0.01	3.00	< 0.01	0.02
Fatness 4	102	0.01	0.01	1.00	0.32	0.01
Fatness 5	1	-	-	-	-	-

Figures

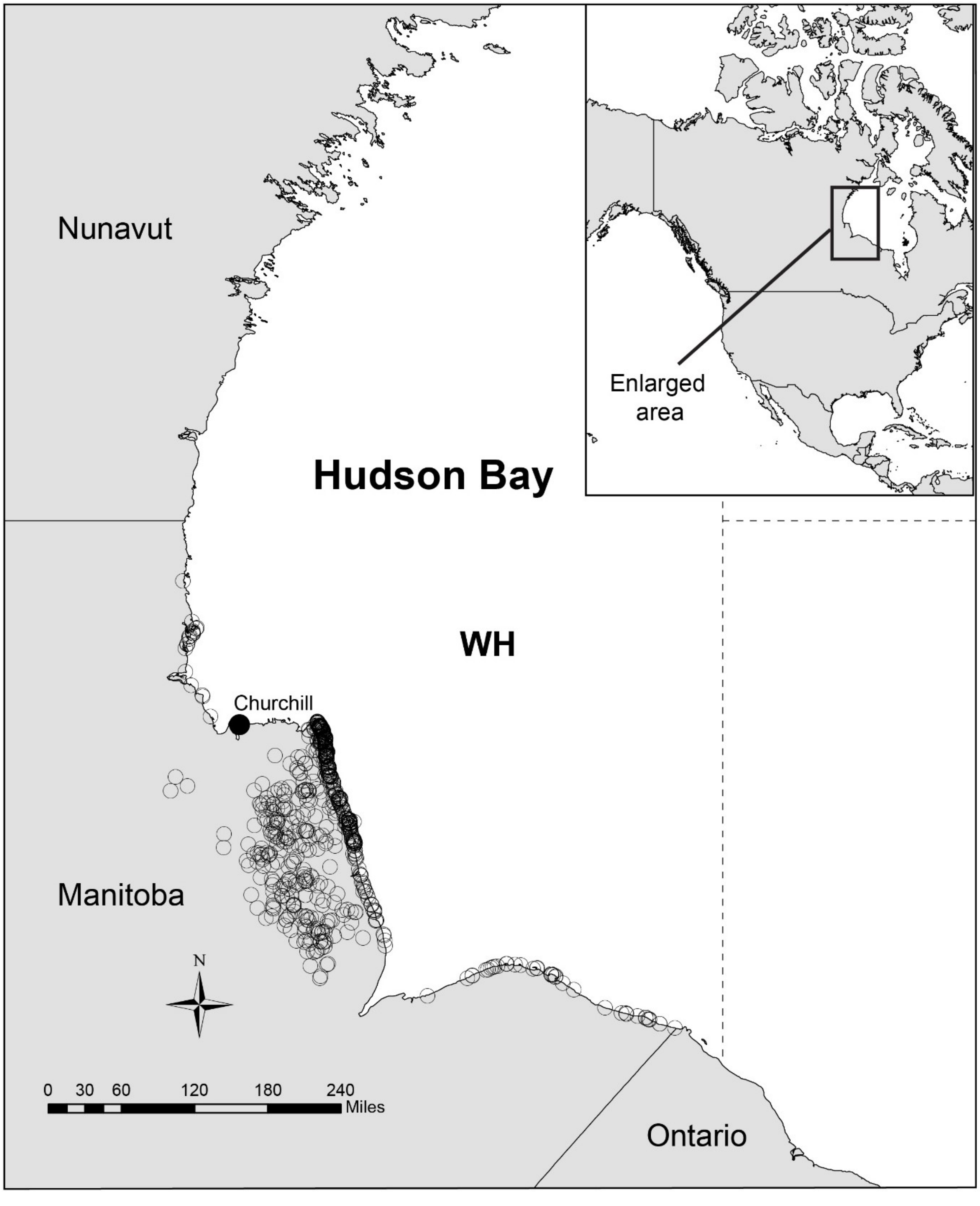

Figure 2-1: The management boundaries of the Western Hudson Bay (WH) study population and locations where samples were collected 2004-2013, are indicated by open circles.

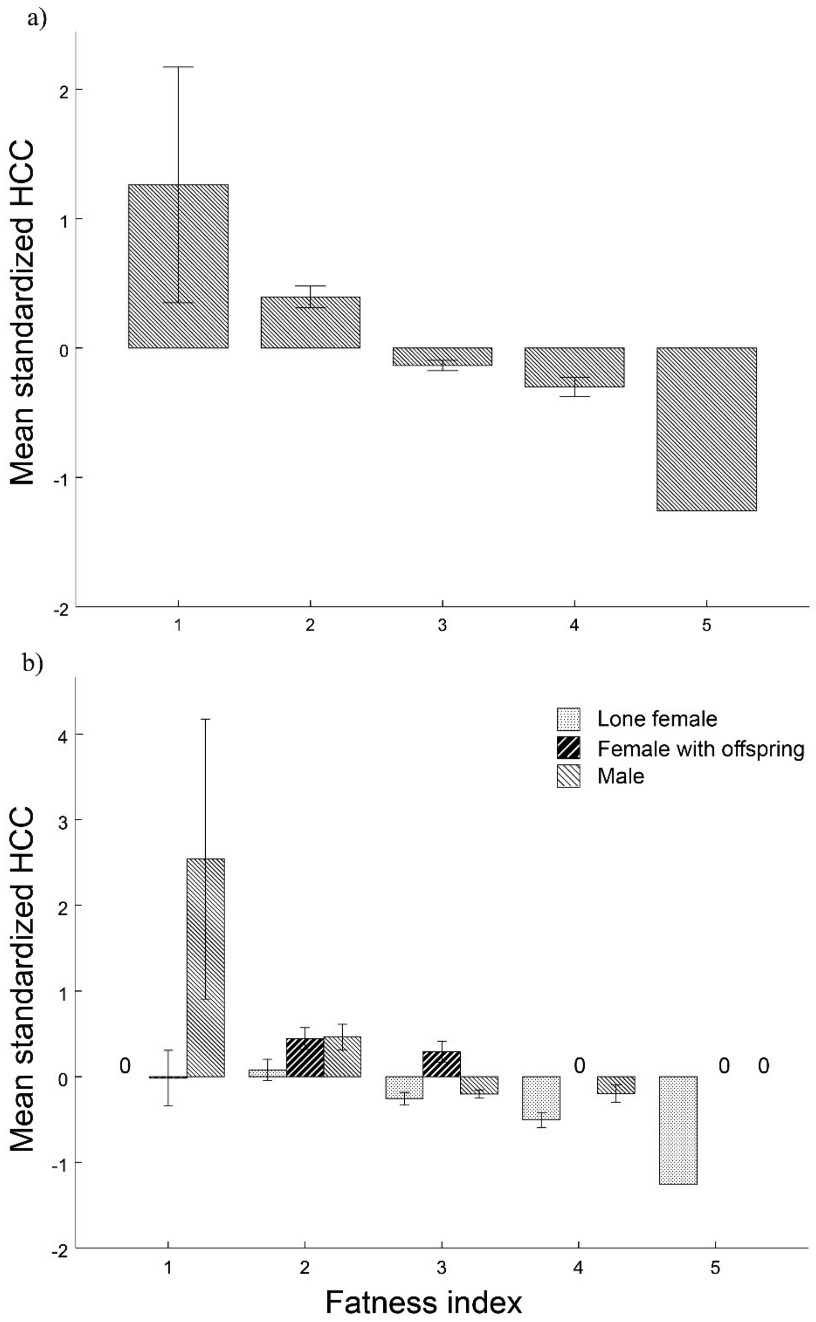

Figure 2-2: Mean Western Hudson Bay polar bear hair cortisol concentration (HCC) (standardized; 2004 – 2103) across **a)** 5 fatness classifications (with 1 being emaciated and 5 being obese) where all bears are pooled and **b)** separated by demographic grouping (male, lone female, female with offspring). Fatness index 5 contains only 1 individual. Vertical bars represent ±1 standard error.

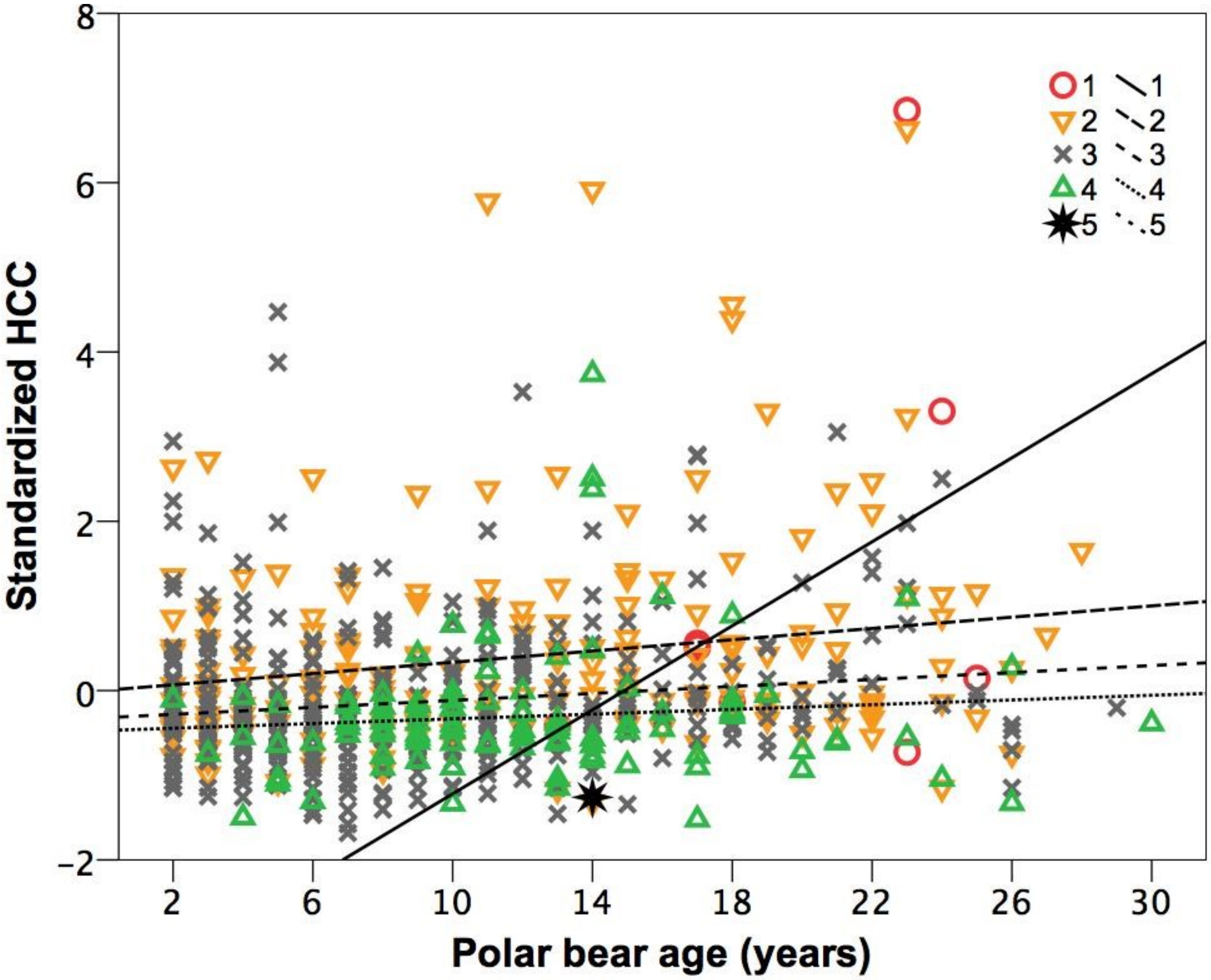

Figure 2-3: Linear regressions investigating the relationship between age and hair cortisol concentration (HCC) (standardized; 2004 – 2013) across 5 fatness classifications (with 1 being emaciated and 5 being obese) for Western Hudson Bay polar bears. Each fatness classification is marked with a line of best fit (Table 2-2).

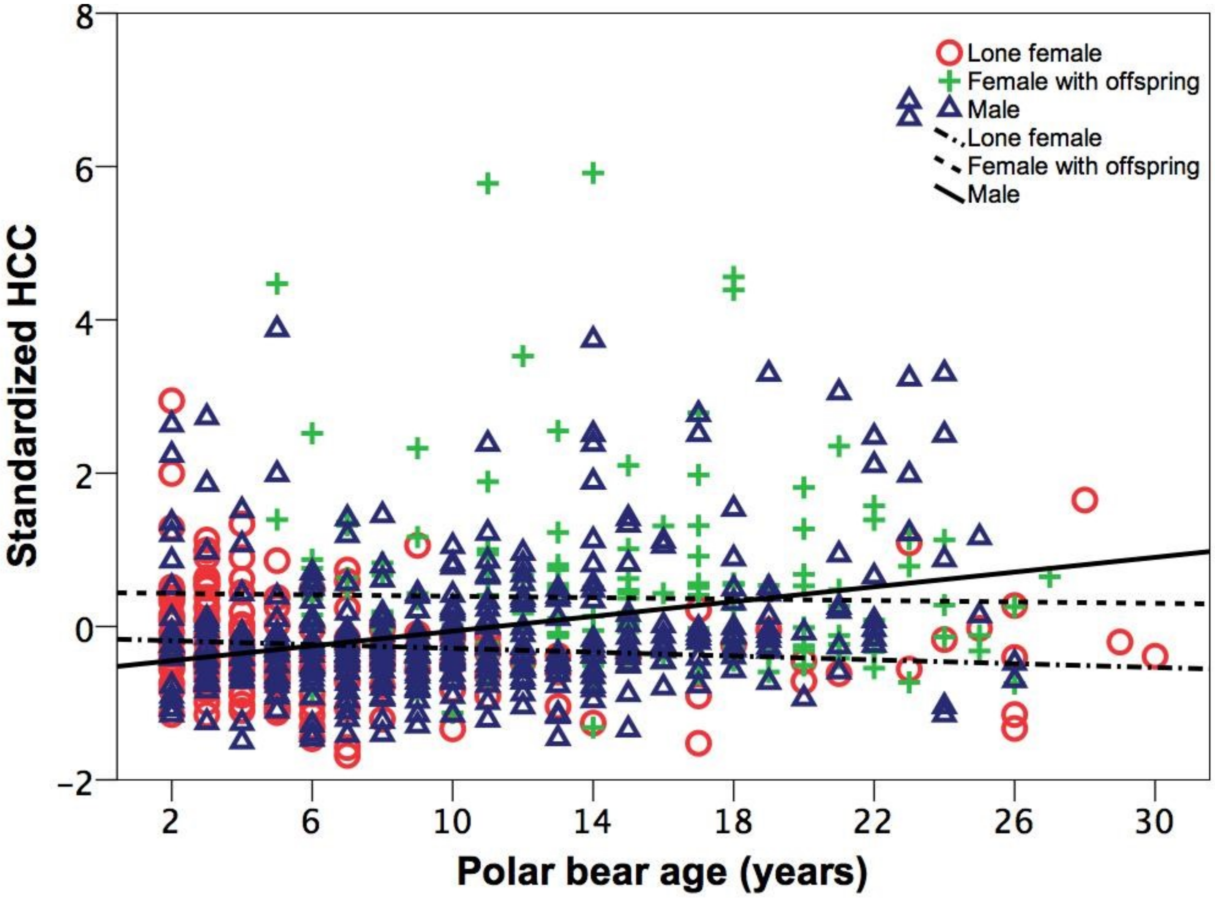

Figure 2-4: Linear regressions investigating the relationship between polar bear age and HCC (standardized) across demographic classifications (male, lone female, female with offspring) for Western Hudson Bay polar bears sampled from 2004 – 2013. Each demographic classification is marked with a line of best fit (Table 2-2).

Chapter 3 – Conclusions

Hair cortisol concentration (HCC) is increasingly used as a proxy for stress in free ranging wildlife. My finding that HCC was positively associated with body condition in polar bears (*Ursus maritimus*) supports the use of HCC as an effective biomarker of health in this species. Declining body condition likely leads to higher HCC in polar bears, particularly those in western Hudson Bay (WH), because they are highly dependent on stored fat to survive the summer months when sea ice break-up forces them ashore, restricting access to seals (Stirling 1977, Derocher and Stirling 1990). With body fat as the primary source of metabolic energy during this approximately 4-month period, bears in poorer body condition are at increased risk of loss of lean mass and nutritional stress (Polischuk et al. 2002, Molnár et al. 2009). When the relationship between HCC and body condition is considered in a multivariate context with demographic variables, I found that females with dependent offspring had consistently lower body condition and correspondingly elevated cortisol relative to male or lone female bears. Higher HCC in females with dependent offspring could be explained by the increased draw on the mother's fat reserves for lactation during the 1.5 – 2.5 years a cub may nurse (Derocher et al. 1993a, Arnould and Ramsay 1994).

My hypothesis that older bears would have higher HCC relative to individuals of prime age due to the deleterious effects of aging was supported, but depended on body condition and demographic grouping. Bears in lower body condition had correspondingly greater increases in HCC with age potentially due to the deleterious effects of aging being exacerbated by the influence of increased nutritional stress (Epel et al. 2004). In contrast, the fattest bears did not show an age-related increase in HCC. I also found that, unlike females (alone or with cubs), male bears had significant increases of HCC with age, potentially due in part to stress associated with cumulative injuries accrued by older individuals through intrasexual mate competition (Ramsay and Stirling 1986, Derocher et al. 2010). Female bears showed no increase in HCC with age, but females with cubs had consistently elevated HCC relative to lone females, reinforcing the conclusion that maternal care is stressful.

My hypotheses were all supported, at least conditionally, suggesting that future studies assessing HCC should consider their results in the context of biological and demographic variables. Previously, studies measuring HCC in free-ranging bears have had small sample sizes and, in some cases, limited supporting demographic information. Because there seems to be considerable variation in HCC between individuals, studies with small sample sizes may not have the statistical power to identify the same relationships between HCC and biological and demographic variables seen here.

Management implications

Sea ice is an essential habitat component of the Arctic ecosystem and increasing variability in the extent and duration of seasonal coverage is having negative effects on wildlife throughout the region (Bluhm and Gradinger 2008, Laidre et al. 2008). Because of their dependence on ice as a hunting platform (DeMaster and Stirling 1981, Stirling and Derocher 1993), changing sea ice phenology is causing declines in polar bear health with reductions in body condition, survival, and reproduction (Stirling et al. 1999, Rode et al. 2012, Bromaghin et al. 2015). Declines in the fitness of individual bears are, in turn, having negative consequences on the health of the Hudson Bay population (Reviewed in Stirling and Derocher 2012). With further reductions in sea ice predicted, particularly in the southern limits of their range (Stroeve et al. 2007, Stroeve et al. 2012, Castro de la Guardia et al. 2013, Hochheim and Barber 2014), it is becoming increasingly important to monitor the response of polar bears to habitat loss and changing environmental conditions (Vongraven et al. 2012). Although global stressors, such as climate change, cannot be entirely ameliorated by local management, understanding the responses of threatened populations to environmental change provides managers with insight into how local mitigation action may best curb the negative consequences of such stressors. However, educating the public on the effects of climate change, particularly on a high profile animal like the polar bear, may help inspire meaningful large-scale action to mitigate greenhouse gas release.

By identifying important relationships between HCC, biological and demographic variables, my research highlighted the potential for HCC to be used as proxy for population health. My study also established a baseline of HCC in the Western Hudson Bay polar bear population against which to gauge the effects of future environmental change. In particular, my finding that female bears with dependent offspring have consistently elevated HCC relative to male and lone female bears suggests that understanding the effect of chronic stress on this demographic group should be a research priority, especially given that the health of reproductive-age female bears is critical for ensuring long-term population stability. Sea ice declines in have been linked to reductions in litter size, cub size, and cub survival (Regehr et al. 2007, Rode et al. 2010, Molnár et al. 2011). With progressively earlier ice break-up predicted, a tipping point may eventually be reached whereby the body condition of female bears is poor enough to substantially reduce reproduction in a season (Derocher et al. 1992, Molnár et al. 2011). Collectively, these negative influences of changing sea ice conditions on cub recruitment may result in an overall trend toward an aging population in WH. My finding that the HCC of bears in poor body condition increased significantly with age suggests that WH population, which is both aging and showing declines in mean body condition (Stirling et al. 1999, Regehr et al. 2007), may be highly susceptible to the deleterious effects of chronic environmental stress. Coupled with higher starvation mortality, earlier ice break-up may threaten the viability of the WH population (Molnár et al. 2010, Molnár et al. 2014) and monitoring HCC may provide a warning signal before a tipping point is reached.

Cortisol contained in the hair shaft is robust to environmental exposure, degradation over time, and contamination (Macbeth et al. 2010, Bechshoft et al. 2012a). It is therefore, possible to collect samples non-invasively using hair snags without compromising the intrinsic cortisol concentration (e.g., Macbeth et al. 2010, de Groot et al. 2013). This technique is not commonly used for sampling of polar bears but could be applied in field conditions to aid monitoring while also being setup, managed, and harvested by local people. Instead, collection of biomonitoring data on polar bears typically involves sedation via remote injection from a helicopter by specialists, a process that may be both stressful for the animal and costly for the researcher. While incorporating demographic information (i.e., age, sex, reproductive status) into my analysis helped account for variability in cortisol levels, my findings suggest that mean HCC collected using snags could provide a coarse, but easily implemented, method for assessing population health. Further, the use of hair snags would allow for remote population monitoring and reduce handling of wildlife.

Extensions

Previous work investigating HCC in free-ranging bears involved small sample sizes with limited longitudinal breadth because of the challenge and cost associated with sample collection. To date, HCC has been examined in grizzly bears (*Ursus arctos*)(e.g., Macbeth et al. 2010, Bryan et al. 2013) and polar bears (e.g., Bechshoft et al. 2011, Bechshoft et al. 2012a, Macbeth et al. 2012), with most early studies aiming to validate methodology. More current research has built on this work to begin assessing factors that may influence HCC in bears including biological and demographic variables (Macbeth et al. 2012), nutrition (Bryan et al. 2013), and contaminants (Bechshoft et al. 2015). My study is the first to assess HCC using a large dataset, which involved 729 samples spanning 10 years. However, in doing so, I discovered that there was a considerable amount of residual variation in HCC that was not explained by age, demographic group or body condition. This finding suggests that other unmeasured environmental and biological factors likely contribute to variation in HCC among individual bears. Although a growing body of evidence supports the use of HCC as a measure of stress in free-ranging wildlife, further research is needed for a more complete understanding of the complexities of the physiological stress response. Below I have highlighted three research priorities that are natural extensions of this study, each with important conservation and management implications.

Research priority #1 – Evaluate the generality of HCC trends across populations

To date, studies investigating HCC in polar bears have focused on well-studied populations where hair samples have been collected as part of established monitoring programs or from Inuit subsistence kills (Bechshoft et al. 2011, Macbeth et al. 2012). However, less is known about more remote polar bear populations where high field-operating costs and challenging logistics make study difficult. Of the 19 populations of polar bears around the circumpolar arctic, 9 are data deficient with unknown trends in population growth (IUCN/PBSG 2014). Methods of monitoring stress using HCC developed in well-studied systems like WH can be similarly applied to gain insight into the effect of changing climatic conditions on the health of bear populations in more remote regions.

An important next step is to determine whether the relationships between HCC and demographic groups found in the WH population are generalizable to other populations. This can be accomplished using similar methodology to assess trends in HCC of other well-studied populations (e.g., South Hudson Bay, South Beaufort Sea, Barents Sea). Although populations will experience different combinations and intensities of stressors, correlations between HCC and some biological variables may be universal for polar bears. For example, females nursing dependent offspring are likely to always have poorer body condition and experience a corresponding increase in cortisol relative to other demographic groups. Likewise, male bears are likely to experience stress associated with injury from intrasexual mate competition regardless of population. If it is discovered that HCC can be predictively linked to demographic variables across populations, the use of HCC as a biomarker for health in more remote regions of the Arctic would be strongly supported.

Research priority #2 – Investigate drivers of interannual variation in HCC

I discovered significant interannual variation in HCC in WH polar bears. However, determining drivers of this variation was beyond the focus my study. As such, this variation was removed before the model analysis by transforming HCC to standard deviation units relative to the sampling year mean. Using the same dataset, future research could test the hypothesis that polar bears are experiencing increased stress associated with directional changes in environmental variables.

Polar bears depend on sea ice as a platform from which to travel hunt and mate (DeMaster and Stirling 1981, Stirling and Derocher 1993). Variation in the date of ice break-up and ice freeze-up has led to progressively longer ice-free periods in Hudson Bay (Gagnon and Gough 2005, Joly et al. 2011, Hochheim and Barber 2014), forcing polar bears to fast for longer periods with proportionally less time to build the fat reserves needed to survive during fasting (Polischuk et al. 2002, Castro de la Guardia et al. 2013, Hochheim and Barber 2014). Considering the close relationship this study identified between HCC and body condition, it seems to follow that sea ice break-up date, having been shown to influence body condition (Stirling et al. 1999), would have an equally close association with HCC. However, a preliminary analysis using the 10 years of data from this study revealed that, although break-up date can help explain interannual variation in HCC, a suite of environmental variables likely influences mean annual HCC in the WH population. Therefore, other unmeasured environmental factors could obscure the influence of break-up date. Further, detecting trends in HCC will likely require models that account for multi-year effects and lagged effects of environmental variables on HCC.

In addition to changing sea ice cover, other environmental variables such as snowfall, rainfall, surface temperature, and the pattern of ice break-up could influence mean HCC in the WH population. Further, seal productivity, which is also influenced by these environmental variables (Ferguson et al. 2005), has been linked to polar bear reproduction and cub survival

(Rosing-Asvid 2006) and may be a driver of HCC. Consequently, environmental factors may have both direct and indirect effects on polar bears by influencing the survival and productivity of their main prey species, the ringed seal (*Pusa hispida*) (Ferguson et al. 2005, Chambellant 2010, Chambellant et al. 2012). Because of the importance of the ringed seal pupping season for storing fat in advance of the ice-free period, a year with low reproduction or high pup mortality could have a pronounced effect on polar bear body condition and nutritional stress. In addition, environmental variables can have non-additive interactive effects on populations (Crain et al. 2008), and therefore a multivariate analysis including interactive terms will be necessary to identify how multiple, potentially interacting, environmental variables influence mean HCC across years. Structural equation modeling may also provide a useful tool for disentangling the relative importance of direct versus indirect drivers of HCC.

Research Priority #3 – Influence of movement on HCC

As sea ice break-up occurs progressively earlier, WH polar bears can either move ashore and endure longer periods of fasting or follow the retreating ice to the southeast, continuing to hunt but facing a long transit back to summer grounds (Derocher et al. 2004, Durner et al. 2009, Cherry et al. 2013). This decision reflects a trade-off between energy conservation (e.g., coming ashore earlier, but closer to familiar territory) and acquisition (e.g., increased energetic uptake and cost of continuing to hunt on the retreating and deteriorating ice) (Mauritzen et al. 2003). Further, the decline of ice conditions through early thinning and fragmentation may force bears to travel extended distances to find suitable productive hunting grounds with high associated energetic costs (Derocher et al. 2004, Auger-Méthé et al. 2015). Increased movement and extended migration may lead to declines in body condition and correspondingly, may act as a driver of interannual variation in HCC.

Ice break-up is typically defined as the date when coverage falls below 50% (Stirling et al. 1999) and is often used as a ‘catch-all’ metric for assessing annual ice conditions. However, the pattern of ice meltu may influence quality of hunting habitat before coverage falls below this threshold of break-up. Further, wind and counter-clockwise currents in Hudson Bay may push fragmented ice further offshore resulting in greater transit distances for migrating bears (Derocher et al. 2004) even if percent ice coverage remains high. Therefore, break-up date alone may not tell the whole story about quality of changing ice conditions between years and direct measurements of polar bear movement may be a stronger predictor of interannual variation in HCC.

Using telemetry data collected over several years from WH polar bears, space use and migration distance could be compared to several metrics of sea ice condition (e.g., rate of decline, fragmentation, percent cover, location to shoreline) during the critical hyperphagic period preceding ice break-up (e.g., Cherry et al. 2013). Combined, ice condition and movement data could be then compared to HCC of the collared polar bears across years to test the hypothesis that average migration distance is positively associated with mean interannual HCC variation.

Conclusions

This study has built on the growing body of literature supporting HCC as a biomonitoring tool for free-ranging wildlife, validated the methodology for use in polar bears with a large dataset, and introduced novel interactions between HCC, age, body condition and reproductive status. Further, it has allowed for the comparison of demographic trends in HCC to other well-studied polar bear populations. With further study and development of HCC as a biomonitoring tool, non-invasive collection techniques could be employed and more remote and data deficient populations could be sampled with increased frequency providing greater insight into population health.

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