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Beyond the Ridge: Rethinking Thermal Windows in Beluga Whales

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Across evolutionary time, marine mammals have developed a range of thermoregulatory adaptations to survive in a highly conductive and thermally variable environment (Berta et al. 2005). As highly mobile species, both pinnipeds and cetaceans may encounter a broad range of temperatures as they dive up to hundreds of meters below the surface and/or migrate thousands of kilometers between high-latitude summering habitats and lower-latitude wintering regions (Favilla and Costa 2020). Routine movements through the water column during foraging—and annually across ocean basins during migration—require a specialized level of thermal flexibility. These include a suite of dynamic thermoregulatory adaptations to maintain internal homeostasis across a wide range of thermal conditions (Davis 2019).

Although blubber is important to aid insulation, decades of research suggests that blubber serves many additional functions, including providing buoyancy and maneuverability, acting as an endocrine organ, and functioning primarily as an energy reserve (Cornick et al. 2016; George et al. 2021; Kanwisher and Ridgway 1983; Noren et al. 1999; Werth and Ford 2012). The ability of smaller-bodied cetaceans and pinnipeds that have relatively thin blubber layers to inhabit polar waters, sometimes year-round, suggests that many cetaceans are over-insulated (Kasting et al. 1989; George et al. 2021). This, paired with a metabolic rate 1.4–2.9 times higher than similarly sized terrestrial mammals, puts cetaceans in a constant state of heat dissipation (Kasting et al. 1989; Williams 2022). During exercise (i.e., diving or foraging) or in warmer temperatures, cetaceans dissipate excess heat through localized thermal windows—areas with visible borders that show higher temperatures than surrounding skin (Erdsack et al. 2012; Mauck et al. 2003; McGinnis

et al. 1972; Noren et al. 1999). Thermal windows are primarily observed in body regions like the pectoral fins, flukes, and dorsal fin (Schmidt-Nielsen 1997), where there is little insulation and a high surface-area-to-volume ratio, allowing for rapid heat transfer through regulated blood flow (Favilla and Costa 2020; Meagher et al. 2008). To conserve heat, cetaceans as well as pinnipeds utilize a countercurrent heat exchange system, allowing for the transfer of warm arterial blood to cool venous blood, minimizing heat loss from the extremities. Depending on the animal's thermal demands, blood flow to peripheral appendages can either facilitate heat dissipation—bypassing the countercurrent heat exchange system and increasing flow through superficial veins—or conserve heat by maintaining countercurrent exchange within the fins and flukes (Hampton et al. 1971; Meagher et al. 2008; Noren et al. 1999; Scholander and Schevill 1955). Due to the challenges of collecting data on wild cetaceans in their natural environment, research on cetacean thermoregulation has largely focused on individuals in human care, particularly small odontocetes such as harbor porpoises (*Phocoena phocoena*), spotted dolphins (*Stenella attenuata*), common bottlenose dolphins (*Tursiops truncatus*), and spinner dolphins (*Stenella longirostris*) (Meagher et al. 2008; T. M. Williams et al. 2017; Worthy and Edwards 1990). However, partnerships with subsistence hunters have enabled researchers to investigate morphometrics, physiology, and body composition of cetaceans that otherwise would be inaccessible, providing critical insights into thermoregulatory mechanisms that would be difficult to measure in the wild (J. C. George et al. 2021).

Arctic cetaceans challenge conventional thermoregulatory strategies, as species like beluga whales (*Delphinapterus leucas*), narwhals (*Monodon monoceros*), and bowhead whales

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(*Balaena mysticetus*) lack a dorsal fin—an important thermal window (Favilla and Costa 2020; Ford et al. 2013; O'Corry-Crowe 2009). According to Bergmann's rule, polar species tend to evolve larger body sizes to minimize heat loss, while Allen's rule suggests they develop shorter appendages with less surface area and more compact body shapes to conserve heat (Adamczak et al. 2020; Torres-Romero et al. 2016). Because beluga whales are highly insulated and constantly have excess heat to dump, the absence of a dorsal fin is likely not due to heat conservation and is most likely an adaptation that allows for better navigation beneath the ice (Kasting et al. 1989; Dietz et al. 2007; Werth 2007; Ford et al. 2013). However, as Arctic conditions continue to warm, there is potential for increased thermal stress for cold water adapted species (Rantanen et al. 2022; Williams et al. 2021).

Without a dorsal fin, Arctic cetaceans must rely on alternative morphology to regulate body temperature and heat loss. Supplemental heat dissipation strategies have been documented for bowhead whales (as well as other mysticetes), including vascular retia at the hard palate and the root of the tongue that prevent or facilitate heat loss depending on activity (Ford et al. 2013; Werth 2007). Given that beluga whales and narwhals lack dorsal fins, it is unclear if additional body regions participate in these known processes to supplement thermoregulation.

To answer this, we investigated beluga whale thermal windows to identify how and where they dissipate heat. The beluga whale is an ideal study model because it is a common Arctic cetacean kept in human care, and it lacks a dorsal fin. While many temperate cetaceans rely on the dorsal fin as a primary site of heat dissipation, several species that occupy temperate waters can also lack a dorsal fin, including gray whales (*Eschrichtius robustus*), North Atlantic right whales (*Eubalaena glacialis*), and northern right whale dolphins (*Lissodelphis borealis*), suggesting that alternate pathways for heat dissipation exist. The absence of a dorsal fin in temperate cetaceans is thought to favor maneuverability rather than thermoregulatory function, further motivating investigation into alternative heat dissipation pathways (Dietz et al. 2007). We hypothesized that in the absence of a dorsal fin, beluga whales would utilize regions not typically considered heat dissipation zones (i.e., low surface-area-to-volume ratio sites). For temperate cetaceans like bottlenose dolphins, the dorsal fin exhibits thermal windows, while areas with lower surface-area-to-volume ratios, like the flank, do not (Favilla et al. 2024; Hampton et al. 1971). Using infrared thermography, we examined the thermoregulatory patterns of beluga whales and how they might differ due to the absence of a dorsal fin. If belugas offload heat from the dorsal ridge (DR) in addition to other areas of the body (i.e., the flank), it could unveil previously undocumented heat dissipation techniques.

We measured surface temperatures from the dorsal and lateral sides of trained beluga whales (*Delphinapterus leucas*) using infrared (IR) thermography during routine resting trials. This study included three adult females and one juvenile female beluga whale, housed at the Georgia Aquarium (Atlanta, GA, USA). Experiments took place in temperature-regulated indoor saltwater pools (average water temperatures of 15°C) with a maximum depth of 7.3 m. Trials conducted in April 2023 were not performed under fasted conditions (> 8 h since

the last feeding). All procedures were approved by the Georgia Aquarium Institutional Research Committee and the University of California, Santa Cruz Institutional Care and Use Committee following the National Institutes of Health guidelines. The research was conducted under Marine Mammal Protection Act permits issued through the NOAA Fisheries Office of Protected Resources (NMFS Permit #24054).

All thermal images were taken at rest, which was determined by sedentary steady-state behavior while the animal voluntarily floated at the surface following routine, relatively calm behaviors prior to the trial's start (1–5 min) (John et al. 2024). A thermal camera (FLIR C3, Teledyne FLIR, Wilsonville, OR, USA) was used for IR thermography (emissivity = 0.98; distance to object = 1 m; angle of incidence = 0°; reflected temperature = 20°C). Atmospheric temperature and relative humidity were set to 20°C and 50%, respectively, within the indoor facility at the Georgia Aquarium. These environmental parameters were adjusted within the camera's settings prior to data collection. Top-down thermal images were taken of the DR ($n = 15$ trials) and the flank ($n = 11$ trials) (Figure 1), which represent a site of thermal windows and an insulated region, respectively, as described in the literature for other species of odontocetes (Favilla and Costa 2020; Meagher et al. 2008; Noren et al. 1999).

Thermal images were analyzed using FLIR Studio (v.2.0.21). Image quality was evaluated and only in-focus images were used. From the thermal images, temperature measurements of thermal windows were taken from the DR and flank, along with a “baseline” point within each image where no heat dissipation was observed, to capture baseline skin temperature (Figure 1). Baseline points were determined by locating areas of the body that had little thermal activity. Care was taken to avoid areas covered by water, which can distort surface temperature measurements (Playà-Montmany and Tattersall 2021). Thermal windows were defined as areas with visible borders that show higher temperatures than the surrounding skin. We identified anywhere between 1 and 6 thermal windows on a single body region (Flank/DR). When thermal windows were observed (DR: $n = 90$ thermal windows analyzed; flank: $n = 66$ thermal windows analyzed), we recorded the number of distinct thermal windows present as well as their mean and maximum surface temperatures. Means and standard deviations of the number of thermal windows per body region were also calculated.

All analysis was performed in R (v4.4.1; R Core Team 2024) using packages from the *tidyverse* suite (Wickham et al. 2019). The effect of body region and thermal window presence on mean and maximum temperatures were each analyzed using generalized linear mixed models (GLMM) with *glmmTMB* function from the “glmmTMB” package (Brooks et al. 2017). For all models, a gaussian distribution was selected and residuals were visually inspected for normality using the diagnostic plots. Separate models were used to compare mean (m1) and maximum (m2) temperature differences across body regions. For both models, we included an interaction between body region and site type (thermal window, baseline) and also included animal ID as fixed effects to account for site-specific temperature differences and variation attributable to individual animals. Session ID (animal, date, time) was included as a random effect to account for the variability in thermal window appearance observed throughout

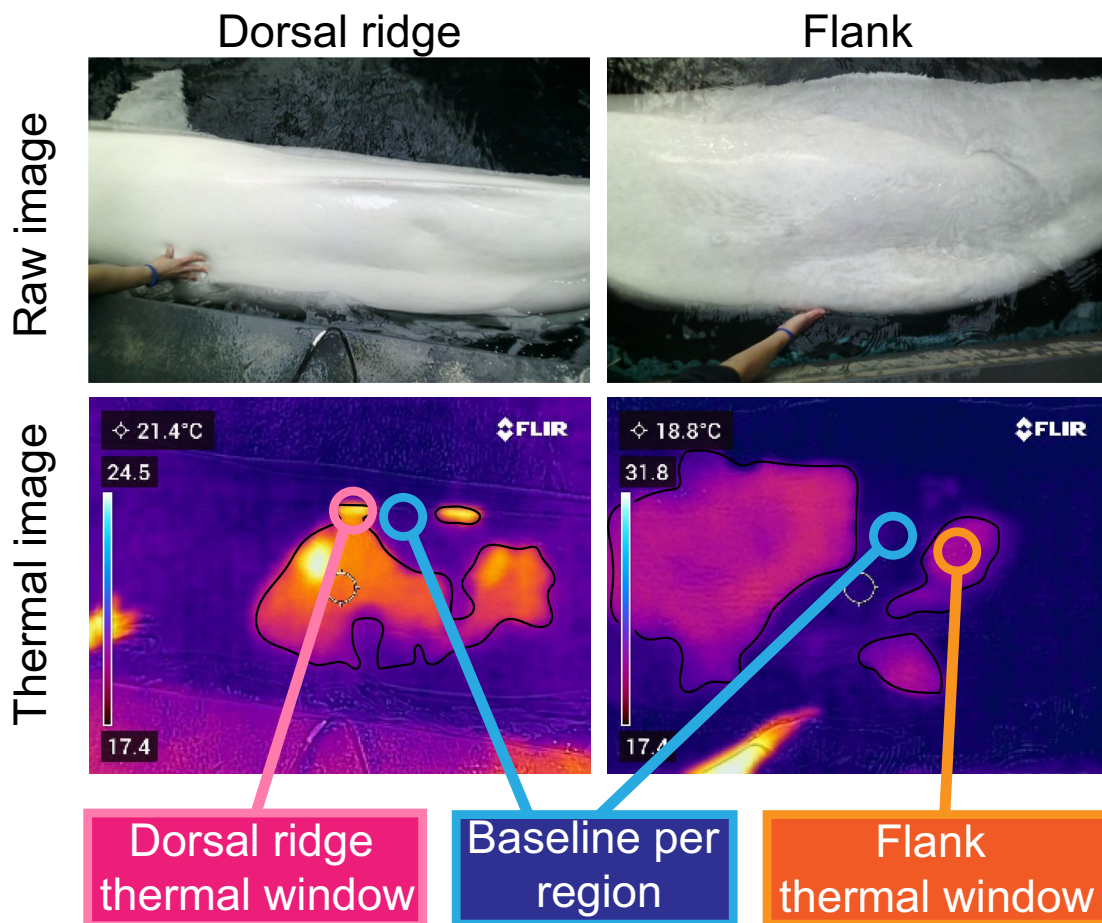


FIGURE 1 | Figure depicting example point measurements of site-specific (dorsal ridge vs. flank) thermal windows and baseline regions. Thermal windows were regions with clear borders that were hotter than the surrounding area, while baseline points were areas with no heat signature. The top row shows the original raw images, and the bottom row shows the associated thermal image. Black outlines depict how we classified distinct thermal windows within a given thermal image according to the definition from Mauck et al. (2003).

data collection. Additional models were used to separately assess mean and maximum temperatures within the dorsal ridge (m3, m4) and flank (m5, m6). Site type and animal ID were included as a fixed effect, and session ID was included as a random effect. Following model development, *post hoc* Tukey Tests using the *emmeans* and *contrast* functions from the “emmeans” package were used to compare thermal windows across body regions (m1, m2) or thermal windows to baseline sites (m3, m4, m5, m6) (Lenth 2025).

For Arctic cetacean species that lack a dorsal fin, such as narwhals and beluga whales, it has been unclear if the absence of this appendage hinders their ability to offload heat to their environment (O’Corry-Crowe 2009). Our results indicate that thermal windows routinely appear on both the DR (mean $\pm$ sd: 2.20 ± 1.33) and flank of beluga whales (0.9 ± 0.8 , Figure 2a). For the DR, the mean temperature from the thermal windows was 2.7°C hotter ($19.0^\circ\text{C} \pm 2.2^\circ\text{C}$; $p < 0.0001$; m3) than baseline temperatures along the DR ($16.3^\circ\text{C} \pm 0.84^\circ\text{C}$; Figure 2b). Similarly, the maximum temperature on the DR was 5.6°C ($21.9^\circ\text{C} \pm 3.9^\circ\text{C}$; $p < 0.0001$; m4) hotter than the baseline ($16.3^\circ\text{C} \pm 0.84^\circ\text{C}$; Figure 2c). Unexpectedly, spatially dynamic thermal windows appeared on the flank, with mean temperatures being 1.2°C hotter ($17.4^\circ\text{C} \pm 1.3^\circ\text{C}$; $p = 0.0013$; m5; Figure 2b) and maximum

temperatures being 1.8°C hotter ($18.0^\circ\text{C} \pm 1.5^\circ\text{C}$; $p = 0.0001$; m6) than baseline points along the flank ($16.2^\circ\text{C} \pm 0.82^\circ\text{C}$; Figures 1 and 2c). This is different from bottlenose dolphins, where heat dissipation via distinct thermal windows along the flank has not been described (Hampton et al. 1971; Heath and Ridgway 1999; Noren et al. 1999; Williams et al. 1999). Additionally, the beluga whale DR likely still serves as the primary thermal window, as maximum temperatures remained significantly hotter than those recorded along the flank ($+ 3.9^\circ\text{C}$; $p = 0.0005$; m2). Mean temperatures between the thermal windows located along the DR and flank, however, were not significantly different ($p = 0.0578$; m1). As such, thermal windows located along the flank may be used as an important site for heat loss, supplementing the use of their DR to maintain thermal homeostasis; however, it is largely unknown how their morphology and/or vasculature enable the use of the flank as a thermal window.

One system that beluga whales may utilize to support thermal windows in the flank includes specialized vascularization. Such systems are the *rete mirabile*, a dense network of arteries and veins that facilitate a countercurrent heat exchange system, and arteriovenous anastomoses, highly innervated vascular structures that bypass capillaries to regulate skin blood flow and heat loss (Bisaillon et al. 1988; Romano et al. 1993; Vogl and

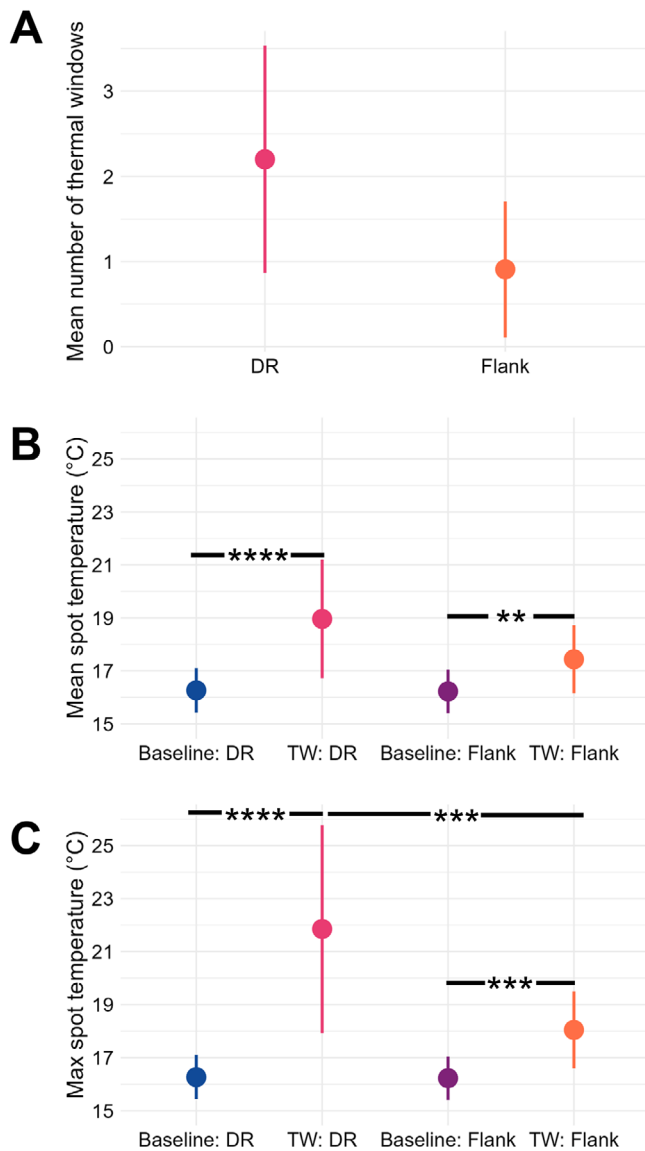


FIGURE 2 | (A) Mean number of distinct thermal windows (TW), (B) mean temperature and (C) maximum temperatures of each TW observed along the dorsal ridge (DR; $n=15$) and flank ($n=11$). (A) displays the mean ± 1 s.d. (standard deviation) of the number of TWs detected on the DR and flank. (B) reports the mean ± 1 s.d. of the mean temperature and statistical results from m1. (C) reports the mean ± 1 s.d. of the maximum temperature and statistical results from m2. Baseline measurements plotted in (B) and (C) represent the surface temperatures of areas outside of a TW boundary as identified using the FLIR images. Significant differences between body regions and TW or baseline sites are indicated with an asterisk. A single asterisk (*) indicates $p < 0.05$, two asterisks (**) indicate $p < 0.01$, three asterisks (***) indicate $p < 0.001$, and four asterisks (****) indicate $p < 0.0001$.

Fisher 1982). A key thermoregulatory adaptation of phocids is the increased presence of arteriovenous anastomoses across the entire body, rather than only the extremities, suggesting the vasculature is a primary mechanism for heat thermoregulation (Molyneux and Bryden 1978). To accommodate the wide range of temperatures beluga whales experience, they may possess a similar adaptation of a denser network of arteriovenous anastomoses in additional body regions than typical cetaceans.

Further investigation into beluga blubber vascularization will be central to understanding the anatomy behind thermal windows located in the flank.

In addition to possible vascular adaptations, belugas have large subcutaneous adipose stores (blubber) that play a critical role in minimizing conductive heat loss and may influence where thermal windows are located along the flank (Ball et al. 2017; Cornick et al. 2016; Doidge 1990). Blubber distribution is not uniform across the body, and it has been suggested that heat loss is inversely proportional to insulation thickness (Doidge 1990; Iverson 2009; Werth and Ford 2012). Belugas exhibit their thickest blubber layer along the dorsal ridge (extending from mid-body to the caudal peduncle), followed by the flank, fluke, and pectoral fins (Cornick et al. 2016; Werth and Ford 2012; Doidge 1990).

To better understand the potential morphological mechanisms behind beluga thermal windows, we compared the beluga FLIR images to previously described patterns of blubber thickness (Doidge 1990) to determine whether regions of observed heat loss corresponded to areas with relatively lower insulation. Contrary to expectations, we observed considerable variation in heat loss across both the DR and flank, with no consistent relationships between areas of greater blubber thickness and reduced heat loss (Figure 3). This suggests that while blubber thickness may influence heat loss, it is not the sole factor driving thermoregulatory patterns within belugas. Additional factors, such as vascular adaptations or differences in tissue properties, may also influence heat loss. Previous theoretical modeling has shown that large cetaceans must bypass the blubber layer to dissipate heat and avoid hyperthermia (Hokkanen 1990). Specialized vascular mechanisms enabling blood to bypass the blubber and reach the skin surface or conversely to retain heat in deeper tissues have been proposed as essential strategies for dynamic thermoregulation (Heath and Ridgway 1999; Scholander and Schevill 1955). Belugas also possess unique musculature along their lateral pontoons that aid in locomotor control, which could also contribute to these heat loss patterns (Werth and Ford 2012).

Tissue properties such as stratification, lipid content, lipid class, and collagen content can influence the thermal conductivity of blubber and vary across body regions, further complicating the relationship between blubber morphology and thermal function (Doidge 1990; George et al. 2021; Krüger 2025). George et al. (2021) demonstrated in bowhead whales that the thermal conductivity of blubber differs regionally, and high surface area appendages that are involved in heat loss were more conductive than core regions like the thorax. In contrast, beluga whales appear to dissipate heat through thick blubber layers along the flank that are not considered to be typical areas of heat dissipation. This raises the possibility that the blubber in the flanks of belugas may exhibit elevated thermal conductivity, similar to what is observed in the appendages. The deep blubber layer has also been proposed as a phase change material, where it can store or release heat as blood flows through the blubber layer. Through this role, blubber may act as a buffer, delaying heat transfer to the surface and moderating large temperature gradients (Dunkin et al. 2005; Favilla et al. 2024). Further research is needed to better understand the mechanisms underlying the

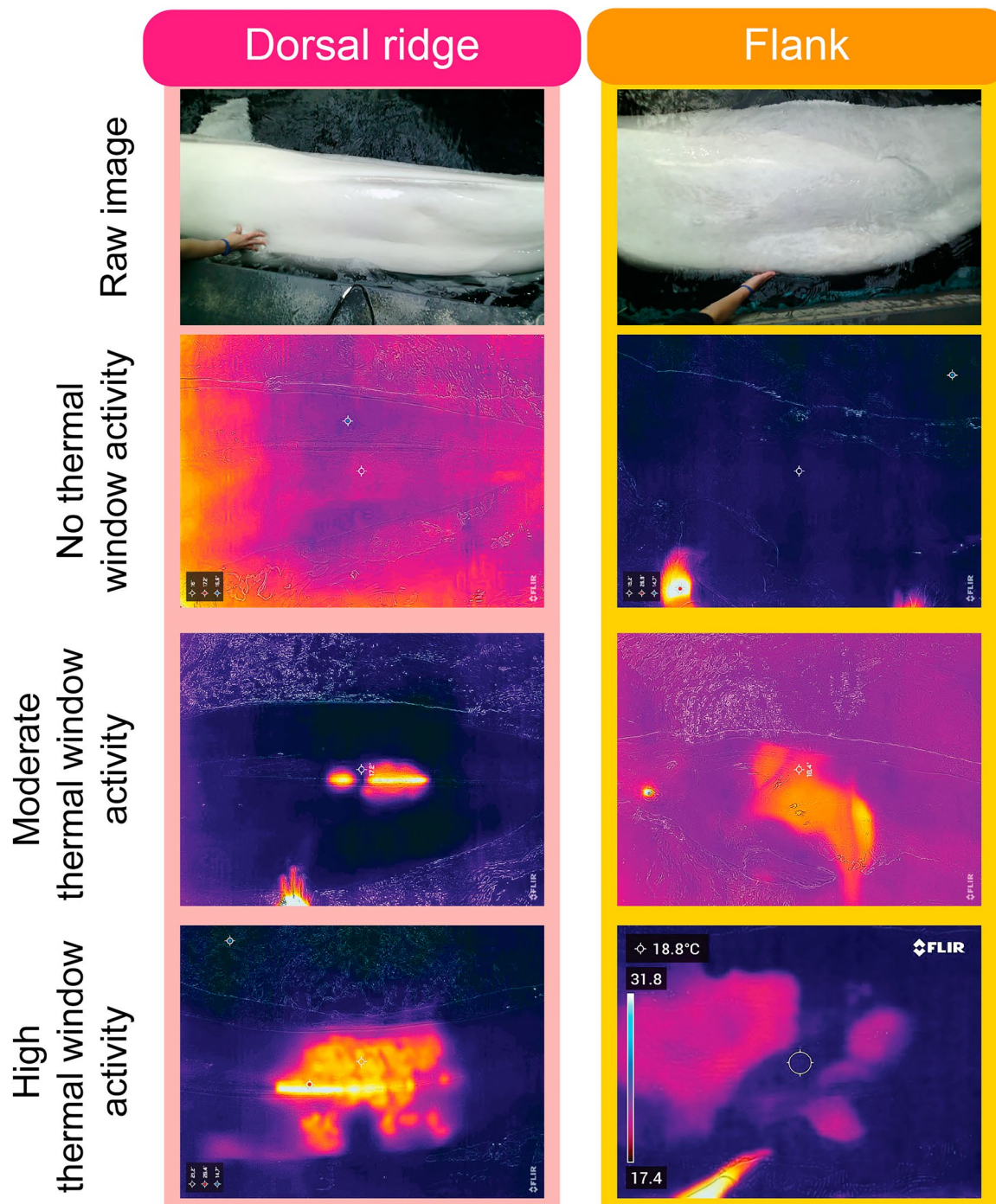


FIGURE 3 | FLIR images of thermal window variability in a resting beluga whale. The right FLIR images show the flank, while the left images display the dorsal ridge. Rows indicate the level of thermal window activity detected (low, moderate, high). The observed variability suggests that thermal hot spots do not consistently align with blubber thickness and may follow a non-random pattern. An agreement scale was used to compare thermal hot spots identified in FLIR images with the blubber thickness distribution described by Doidge (1990).

high variability and location of thermal windows (and resultant heat loss) in beluga whales.

Our results suggest interesting and previously unexplored beluga whale thermoregulatory patterns. Follow-up studies are needed to gain a better understanding of how thermal windows along the flank may be used under a range of conditions. Future behavioral studies on beluga whales in human care should extend

these findings beyond resting trials to conditions in which beluga whales produce excess metabolic heat by exercising. Future work should also include both male and female beluga whales from different stocks across the Arctic and Subarctic. Data in the present study were exclusively collected from females, potentially influencing the observed thermal patterns. Previous work examining respiration rate as a proxy for metabolic rate suggests that adult male beluga whales exhibit slightly higher metabolic

demand than females, particularly during summer months, indicating a potential sex-specific difference in heat production and dissipation (George and Noonan 2014). Male cetaceans must also cool intraabdominal testes, using cold blood from appendages like the fluke, and may exhibit dissimilar spatial or temporal patterns of heat dissipation (Rommel et al. 1992). Continuous observations recording heat loss along the DR and flank in both sexes would lend insight into the dynamism of the site-specific thermal windows and the time scales over which these physiological adjustments can occur. Further, beluga whales from different stocks vary in size and can experience markedly different environmental conditions, possibly influencing their strategies for heat loss.

In addition to implementing behavioral modifications into the study design, additional anatomical studies would strengthen this line of research. Examining regional variation in vasculature, thermal window size, and blubber conductivity may provide a more comprehensive understanding of the full role of heat dissipation along the flank. Further research should also evaluate how thermal windows in the flank function in relation to established heat exchange structures, such as the flukes, to better understand how belugas integrate multiple heat dissipation pathways in response to varying degrees of cold and heat stress. Collaboration with subsistence hunters could provide valuable insights into the tissue properties of beluga whales, as Inuit communities have worked with researchers to document variations in blubber thickness and quality (Breton-Honeyman et al. 2016; Doidge 1990). Such observations could help fill important gaps in the literature of beluga whale physiology by documenting spatial variation in blubber conductivity and the distribution of vascular networks, providing insight into the physical processes supporting their flexible use of thermal windows.

Lastly, this work was conducted in indoor pools with water temperatures that are considerably higher than those encountered by free-ranging cetaceans in the Arctic. As polar temperatures increase, beluga whales will likely not have the option to migrate to cooler waters. Thus, understanding how the use of thermal windows may vary with water temperature is an important next step for understanding their utility.

Our findings offer new insights into the thermal plasticity of beluga whales, enhancing our understanding of their capacity to adapt to future environmental variability and human disturbance. With Arctic sea temperatures rising four times faster than the global average, wild belugas may face growing challenges in maintaining thermal balance (Rantanen et al. 2022; R. Williams et al. 2021), yet their thermoregulatory strategies have remained poorly understood. This work highlights the dynamic use of thermal windows located along the flank of beluga whales in managed care, in environmental conditions that are likely more controlled than those experienced by wild populations. Thus, the thermoregulatory plasticity observed with these animals may lend important insight into the ability for free-ranging cetaceans to offload heat as ocean temperatures rise. Such adaptations may be especially critical for this species, as behavioral adjustments, including shifting their range to higher latitudes and cooler water temperatures, will likely not be an option for belugas in the Arctic (Rivas et al. 2024).

Author Contributions

Sam Bartosik-Velez: conceptualization, investigation, writing – original draft, methodology, visualization, writing – review and editing, formal analysis, data curation, funding acquisition. **Emily C. Nazario:** conceptualization, investigation, funding acquisition, writing – original draft, visualization, writing – review and editing, formal analysis. **Amelia H. Reynolds:** conceptualization, investigation, funding acquisition, writing – original draft, visualization, writing – review and editing, formal analysis, funding acquisition. **Philippine Chambault:** conceptualization, investigation, funding acquisition, writing – review and editing. **Traci L. Kendall:** writing – review and editing, project administration, supervision. **Katherine L. Flammer:** writing – review and editing, data curation, project administration, supervision, funding acquisition. **Dennis R. Christen:** writing – review and editing, project administration, supervision, funding acquisition. **Terrie M. Williams:** conceptualization, writing – review and editing, project administration, supervision, funding acquisition.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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