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C H A P T E R

3

Thermoregulation

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Abstract

The aquatic environment poses unique thermoregulatory challenges for marine mammals due to its high thermal conductivity. Despite these challenges, dolphins have adapted to a multitude of thermal regimes across their cosmopolitan distribution. This chapter addresses the thermoregulatory adaptations of dolphins, and other whale species, that allow them to inhabit such a wide range of habitats. We discuss the role of blubber, body size, and morphology in maintaining thermal balance, as well as associated physiological adaptations (e.g., countercurrent heat exchangers, peripheral vasoconstriction). Additionally, we discuss the importance of behavior for thermoregulation, such as the role of exercise and diving. We demonstrate the importance of morphological, physiological, and behavioral adaptations that enable dolphins to survive in their respective thermal habitats. We show that thermoregulatory demands often conflict with other physiological processes such as reproduction, integument repair, and energy storage. This chapter provides a holistic view of the thermoregulatory adaptations of a widely distributed species, the bottlenose dolphin.

Introduction

Water is roughly 25 times more conductive than air (Dejours, 1987). Thus, heat is quickly drawn away from the body in the aquatic environment, even across relatively small temperature gradients. Still, marine mammals maintain a constant and relatively high core body temperature (~37°C) across a range of ambient temperatures defined by their thermoneutral zone (Fig. 1). This gives marine endotherms an energetic advantage over their ectothermic equivalents at colder temperatures (Cairns et al., 2008; Grady et al., 2019). However, maintaining a large temperature gradient between the core and surrounding water requires significant energetic expenditure.

Marine mammals have a basal metabolism that ranges from 1–3 times that of terrestrial eutherian mammals. The thermoregulatory requirements associated with resting metabolism account for 70% of their daily energy expenditure (Williams et al., 2001; Davis, 2019). Within their thermoneutral zone, the metabolic rate is constant over a range of ambient temperatures and is bounded by the lower and upper critical temperature thresholds (Fig. 1). Over this range, compensation to heat flux variations is managed by insulation adjustments (i.e., peripheral blood flow) and blood flow to the appendages. At ambient temperatures outside of this range, animals employ mechanisms to produce or dissipate heat that requires increased energy expenditure and consequently an increase in metabolism (Fig. 1). For most marine mammals, heat conservation is the primary concern. As such, marine mammals have various adaptations for minimizing heat loss, such as increasing their insulation. Still, mechanisms for heat dissipation are needed, especially during periods of activity or when they are in warmer habitats that exceed their upper critical temperature (UCT).

Yet, it is important to remember that thermoregulation is a balancing act—not only in terms of heat balance but also for the coordination of competing physiological demands associated with diving, exercise, digestion, molting, and skin growth/repair (Favilla and Costa, 2020). For example, daily activities, such as foraging and transiting, elevate metabolism above basal levels and thus increase heat production, impacting calculations of the thermoneutral zone. Additionally, cardiovascular adjustments are integral to these responses, and those required for thermoregulation may, at times, conflict with other concurrent demands. For example, blood flow patterns for dissipating excess heat generated from intense foraging activity would conflict with oxygen conservation during a dive. Thus, thermoregulation is not an isolated response, but rather it depends on the coordination of several responses based on the animal's current homeostatic conditions.

The Physiology of Dolphins
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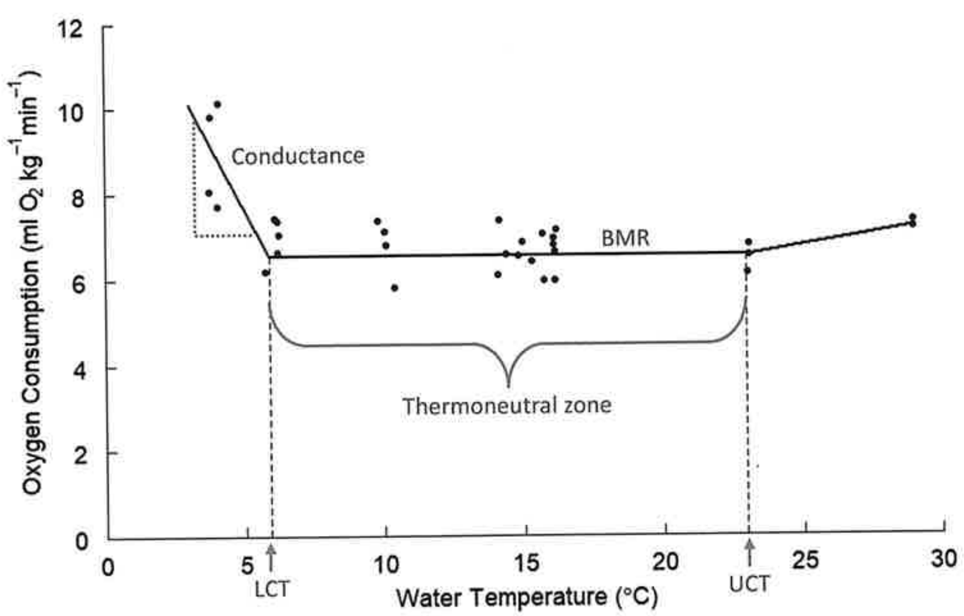

FIG. 1 The relationship between resting metabolic rate and water temperature for three adult male, post-absorptive bottlenose dolphins (mean body mass = 148.6 kg). Dolphins were acclimatized to a water temperature of 15.4°C. Each point represents a single measurement. The thermoneutral zone is the range of temperatures where the metabolic rate is at a minimum, i.e., BMR = 6.53 0.16 mL O_2 kg^{-1} min^{-1}, mean for all three dolphins. Above the UCT (23.0°C) and below the LCT (5.9°C), metabolic rate increases due to the physiological mechanisms required to reestablish thermal balance. *Adapted with permission from Williams et al. (2001).*

To take our understanding of thermoregulation to the next level, it is best to use a study species that inhabits a range of thermal regimes and can be accessed both in laboratory and wild settings. The best-studied dolphin is the bottlenose dolphin (*Tursiops* spp.), a cosmopolitan species inhabiting coastal and offshore waters (Wells and Scott, 2018) and kept in managed care in several research facilities and aquaria worldwide. Coastal nonmigratory populations in Sarasota Bay, FL, experience considerable seasonal changes in water temperature, ranging from 11 to 33°C (Barbieri et al., 2010), whereas other populations off Scotland withstand temperatures as low as ~5°C in the winter (Wilson et al., 1997; Fougères, 2008). In addition to seasonal temperature variation, populations that perform deep dives offshore or periodically transition to inshore habitats will experience abrupt temperature changes over short timescales.

This chapter describes the morphological, physiological, and behavioral adaptations that allow homeothermy in bottlenose dolphins, and some other cetaceans, across a broad range of thermal habitats. In addition to region-specific thermal challenges, the tradeoffs between thermoregulation, reproduction, integument repair, and energy storage are considered. We examine how form meets function by comparing the thermoregulatory adaptations and costs in bottlenose dolphins across different thermal habitats, different ages, and reproductive states.

Avenues of heat transfer

Dolphins are fully aquatic and must maintain thermal balance in a highly conductive environment with limited avenues of heat transfer. Typically, animals exchange heat with their environment via radiation, convection, conduction, and evaporation. However, for aquatic animals, such as the bottlenose dolphin, heat exchange predominantly occurs via conduction and convection. Conductive heat transfer occurs through direct contact with a solid or nonmoving fluid material. In contrast, convective heat loss is associated with heat transfer as a fluid moves across the animal's body surface. Both mechanisms depend on the temperature difference between the animal's body surface and environment. Animals minimize heat loss by reducing the temperature differential between their skin and the environment. Marine mammals employ various adaptations to maintain their skin temperature within a few degrees of water temperature (Irving and Hart, 1957; Barbieri et al., 2010).

In contrast, radiation and evaporation are less important mechanisms of heat exchange in bottlenose dolphins. Radiation is the emission of infrared energy by all objectives due to its temperature. This form of heat transfer is

relatively insignificant compared to the other forms of heat flux because radiation is quickly absorbed by water. Similarly, respiratory evaporative heat loss only occurs while breathing at the water's surface. Dolphins, like other cetaceans, lack nasal turbinates that reduce heat and water loss while breathing (Hillenius, 1992). In seals, respiratory heat loss contributes to roughly 10% of the total heat dissipation [gray seals; (Folkow and Schytte Blix, 1987)]. As dolphins lack nasal turbinates, their respiratory evaporative heat loss is likely to be higher, however, differences in respiratory patterns between pinnipeds and cetaceans may also contribute to different levels of respiratory evaporative heat loss. Due to the increased permeability of their skin, some cetaceans have high cutaneous water loss. However, this water loss is primarily associated with osmoregulation (Hui, 1981; Ortiz, 2001; Costa, 2018). As dolphins are entirely aquatic, they cannot rely on evaporative heat loss. They must therefore rely on other mechanisms besides sweating to dump heat.

Thermal adaptations span morphology, physiology, and behavior

Heat loss (Q; $W m^{-2}$) can be estimated using Newton's law of cooling: $Q = C(T_b - T_a)$ where C is thermal conductance ($W m^{-2} \cdot °C^{-1}$), T_b is core body temperature (°C), and T_a is ambient temperature (°C). However, this requires that skin temperature is at or near water temperature, core body temperature is constant (no heat storage or net heat loss), and there is no evaporative heat loss. As water temperature changes, marine mammals can maintain their core body temperature at ~37°C by adjusting their thermal conductance or heat production. For example, metabolism increases when ambient temperatures drop below the lower critical temperature (LCT), whereas thermal conductance decreases to keep the body temperature constant (Fig. 1). Thermal conductance is a measure of how much heat transfers through a material and is dependent on the material's thermal properties and thickness. Thermal conductance can be broken down into two components: whole-body conductance and blubber conductance. Whole-body conductance is represented by the slope of the line relating changes in metabolism to ambient temperatures below the LCT (Ryg et al., 1993). Long-term changes in whole-body conductance (days to months) vary with changing blubber thickness and composition. Blubber generally has low thermal conductance and thus high insulating capability because insulation is the inverse of conductance. However, blubber conductance can change within seconds as peripheral blood flow through the blubber layer changes. Both mechanisms effectively modify the thermal conductance of the periphery, albeit on different timescales (i.e., days vs seconds, respectively).

As changes in insulation are constrained by morphology and physiology, marine mammals can also increase their metabolic heat production to maintain thermal balance in cold water. Marine mammals have elevated metabolisms compared to terrestrial animals as a mechanism to offset the greater thermal demands of the aquatic environment (Williams et al., 2001; Costa and Maresh, 2017; Davis, 2019). Some authors dispute this and argue that there is no difference in the metabolism between terrestrial and marine mammals (Lavigne et al., 1986a, b; Innes and Lavigne, 1991). However, many factors determine mammals' resting or basal metabolic rate (BMR), including body mass, body composition, diet, reproductive status, age, sex, and phylogeny (McNab, 2001). More importantly, marine mammals are composed of at least five different evolutionary lineages and may exhibit distinctly different metabolic adaptations associated with their phylogeny.

The BMR of bottlenose dolphins has been measured (Williams et al., 1999a; Noren et al., 2013; van der Hoop et al., 2014; Noren et al., 2017; Pedersen et al., 2020), in addition to measurements from the spinner dolphin (*Stenella longirostris*; Hampton and Whittow, 1976), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*; Rechsteiner et al., 2013), harbor porpoise (*Phocoena phocoena*; Kanwisher and Sundnes, 1965), killer whale (*Orcinus orca*; Worthy et al., 2014), beluga whale (*Delphinapterus leucas*), and a gray whale calf (*Eschrictius robustus*; Wahrenbrock et al., 1974). Although results are equivocal among cetacean species (e.g., Worthy et al., 2014), bottlenose dolphins have a BMR 2.5–3 times the predicted BMR of terrestrial carnivores or eutherian mammals, respectively (Williams et al., 2001; Davis, 2019). They are also among the few cetacean species for which their lower and upper critical temperatures have been empirically determined (Fig. 1). However, these thermal limits that define the thermoneutral zone curve will differ when daily activities are considered since field metabolic rate is up to 3–6 times the predicted basal metabolic level in bottlenose dolphins (Costa and Williams, 2000; Rimbach et al., 2021).

Activity is essential in maintaining thermal balance for some delphinids, a family of small to medium-sized odontocetes. Like the Hawaiian spinner dolphin, smaller dolphin species remain active in cold water to keep warm (Hampton et al., 1971; Hampton and Whittow, 1976). This allows them to use the heat generated by working muscles to offset thermoregulatory costs. In contrast, the larger Pacific bottlenose dolphins may need to dissipate excess heat during activity to prevent overheating (McGinnis et al., 1972). As discussed further below, size plays an important role in mediating heat flux and thus thermal balance.

The role of size and morphology

Morphology, or an animal's size and shape, plays an important role in thermoregulation. The surface area-to-volume helps determine the heat lost to the environment relative to metabolic heat production. Heat loss occurs across the body surface, whereas metabolic heat production occurs throughout the body's volume. The surface area-to-volume ratio is predominantly modulated by size due to the scaling of each component relative to body length. Surface area scales with size squared (length^2), whereas volume scales with size cubed (length^3). Therefore, larger animals have a greater volume for a given surface area, resulting in lower ratios. The smaller exposed surface area for a given amount of heat produced also means larger animals will have a greater ability to retain heat. Conversely, smaller animals have larger surface area-to-volume ratios, yielding higher heat loss.

Facilitated by the reduced gravitational field and fluid dynamics of the marine environment, marine mammals have converged on a hydrodynamic body shape and relatively large body size. Cetaceans in particular contain many of the largest species (e.g., the blue whale, *Balaenoptera musculus*) that have a much lower surface area-to-volume ratio than their terrestrial counterparts. In addition to thermoregulation, body size and shape also play an important role in hydrodynamics. The streamlined body shape of marine mammals aids in reducing drag and locomotion costs (Fish, 1994; Fish et al., 2008). Additionally, an animal's shape can inform its foraging strategy (Woodward et al., 2006). Therefore, morphology is ultimately a result of optimizing body size and shape for all these functions. Interestingly, the thermoregulatory implications of body size are thought to be a fundamental constraint that has determined the minimum body size of marine mammals (Gearty et al., 2018).

Bergmann's and Allen's rules

Thermoregulatory costs are not only influenced by body size (and thus surface area-to-volume ratios) but also appendage size. Latitudinal changes in these morphological features are associated with the thermal constraints of living in a cold environment (Worthy and Edwards, 1990; Adamczak et al., 2020). Larger animals with lower surface area-to-volume ratios typically inhabit colder climates at higher latitudes, which is known as Bergmann's rule. Allen's rule posits that terrestrial animals inhabiting colder climates typically have smaller appendages to decrease surface area. Cetaceans and other marine endotherms follow Bergmann's rule across taxa (Torres-Romero et al., 2016) and within taxa (e.g., Adamczak et al., 2020). However, there is conflicting evidence for Allen's rule in cetaceans (e.g., Fougères, 2008; Adamczak et al., 2020).

The broad distribution of bottlenose dolphins provides the opportunity to further explore Bergmann's rule within a species (Fougères, 2008). When examining dolphin populations spanning 48 degrees latitude in the northern hemisphere, the largest dolphins in total length inhabit the coldest waters off Scotland. In contrast, the smallest dolphins in total length and surface area were found where the mean summer temperature was warmest (i.e., coastal FL in Fougères, 2008). Similarly, when looking at populations spanning both the northern and southern hemispheres (Fig. 2), dolphins in Shark Bay, Australia, are smaller in total length than bottlenose dolphins in FL, as well as greater in surface area-to-volume ratio than bottlenose dolphins in FL and Scotland. Thus, Shark Bay dolphins have a much larger surface area relative to size across which to dissipate heat. Their small size may be in part due to the thermoregulatory challenges of living in warm waters. However, optimal body size is also influenced by other physiological and ecological processes, such as the increased diving ability associated with larger body size and the environmental advantages or disadvantages of body size related to prey distribution (Hückstädt et al., 2016).

Allometric morphological changes also influence thermal dynamics with ontogenetic growth. As dolphins mature, their surface area-to-volume relationship changes. Their surface area increases slower than the corresponding increase in volume. These allometric changes have thermal consequences due to the scaling between body volume and metabolic heat production. Younger (i.e., smaller) animals have higher total energy expenditure than those of conspecific adults, yielding more internal heat production relative to their size (Rimbach et al., 2021). The large size of Scottish dolphins should correspond with lower mass-specific metabolic rates than their warmer water counterparts, but this would conflict with the need to maintain thermal balance in their cold habitat. It remains to be determined if there are differences in metabolism along with the factors that drive these ontogenetic and population differences in surface area-to-volume relationships.

Appendage shape and size play an important role in thermoregulation as appendages can increase an animal's surface area without significantly increasing internal heat production, thereby increasing heat loss. Allen's rule was formulated based on terrestrial animals, with those inhabiting colder climates having smaller appendages to reduce

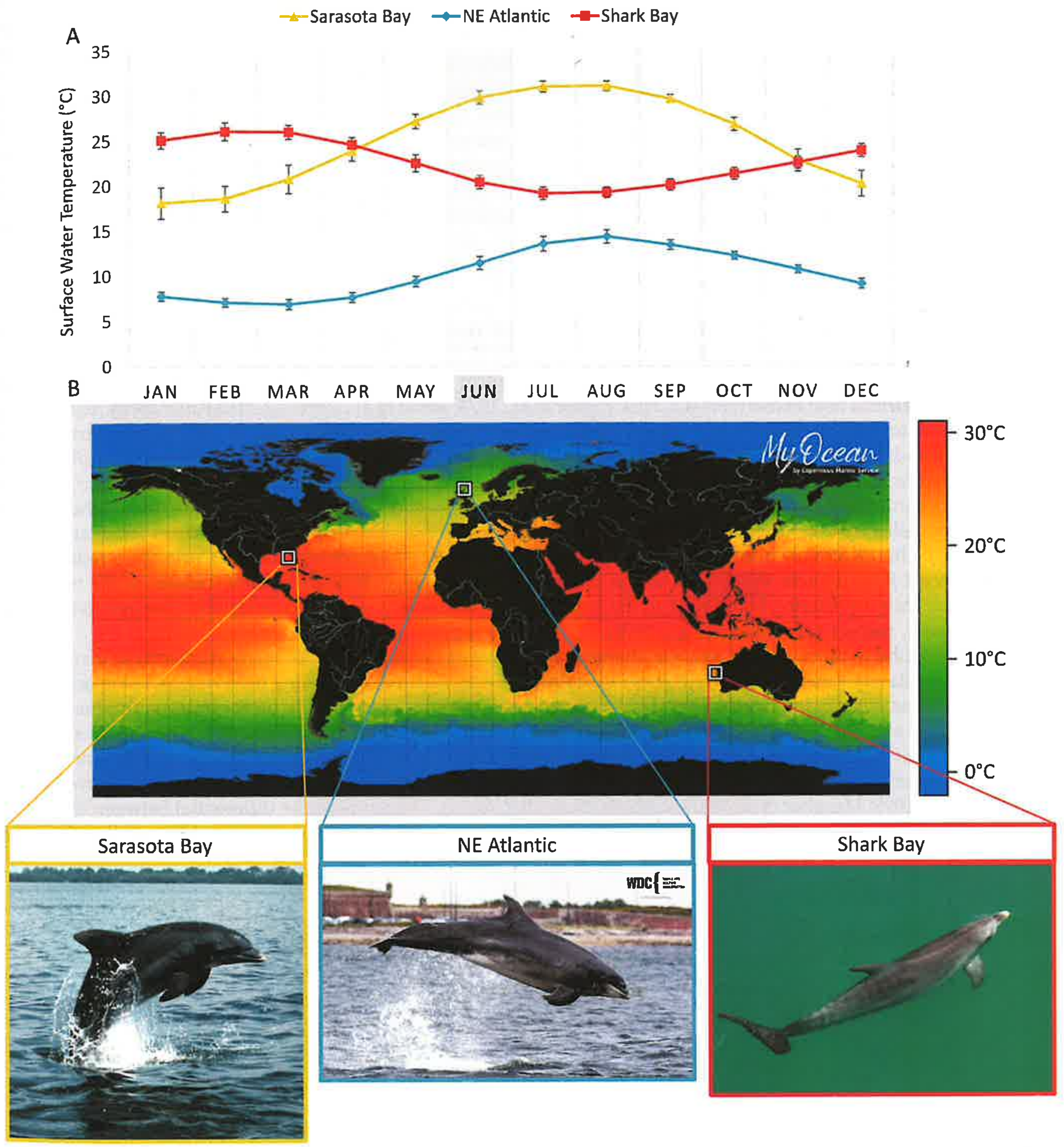

FIG. 2 Annual trend of average monthly climatology (1993–2019) of surface water temperatures off northern UK in Moray Firth (58.0°N, 3.0°W), Sarasota Bay, FL (27.36°N, 82.59°W), and Shark Bay, Australia (25.65°S, 113.65°E), with error bars showing standard deviation. The locations of the three bottlenose dolphin populations are shown on the map, with average monthly surface water temperatures in June 2019 depicted by colour. *Data and maps obtained from the E.U. Copernicus Marine Service Information, Product GLOBAL_MULTIYEAR_ PHY_001_030. Sarasota Bay dolphin photo by the Chicago Zoological Society's Sarasota Dolphin Research Program, taken under NMFS permit no. 638. NE Atlantic dolphin photo by Charlie Phillips WDC. Shark Bay dolphin photo by Jana Watson-Capps, Shark Bay Dolphin Research Project.*

heat loss. Interestingly, some cetaceans exhibit a pattern of appendage size opposite that of Allen's rule. For example, the northern species (higher latitude) of pilot whale has a larger overall appendage surface area than their more southern (lower latitude) counterparts (Adamczak et al., 2020). Given the large body size and thick blubber layer of the northern species of pilot whale, larger appendages likely provide excellent thermal windows that can dissipate heat during activity and conserve heat while resting. However, the potential reversal of Allen's rule is less clear for bottlenose dolphins as appendage size appears to be more related to coastal or offshore habitats than a function of water temperature or latitude. Coastal bottlenose dolphin populations have a greater appendage surface area than offshore populations, which could improve maneuverability in a more complex coastal habitat (Fougères, 2008). If chasing prey in the coastal environment requires greater bursts of activity, larger appendages could also facilitate heat loss as thermal windows.

Appendages as thermal windows: Where morphology and physiology meet

Large appendages serve as dynamic thermoregulatory control surfaces because they are mostly uninsulated and contain countercurrent heat exchangers (CCHEs; Elsner et al., 1974; Pabst et al., 1999). CCHEs function by juxtaposing outgoing, warm arterial blood with cool venous blood returning from the periphery (Fig. 3). The vascular structure of CCHEs in appendages allows for efficient heat exchange control between the arterial and venous blood supply. Major arteries are located centrally within a ring of thin-walled veins to conserve heat in the body's core. The rate of blood flow is key for controlling heat regulation through CCHEs. High blood flow into the appendages expands the circumscribed artery, reducing venous return within the CCHE and providing little time for heat exchange (Scholander and Schevill, 1955). This effectively dumps heat into the environment. When heat conservation is a priority, a reduction in peripheral blood flow reduces the flow of warm blood to the appendage, facilitating heat transfer to the returning venous blood. Thus, by altering blood flow in the appendages, the tissue conductance is rapidly changed to conserve or dissipate heat, respectively (Elsner et al., 1974).

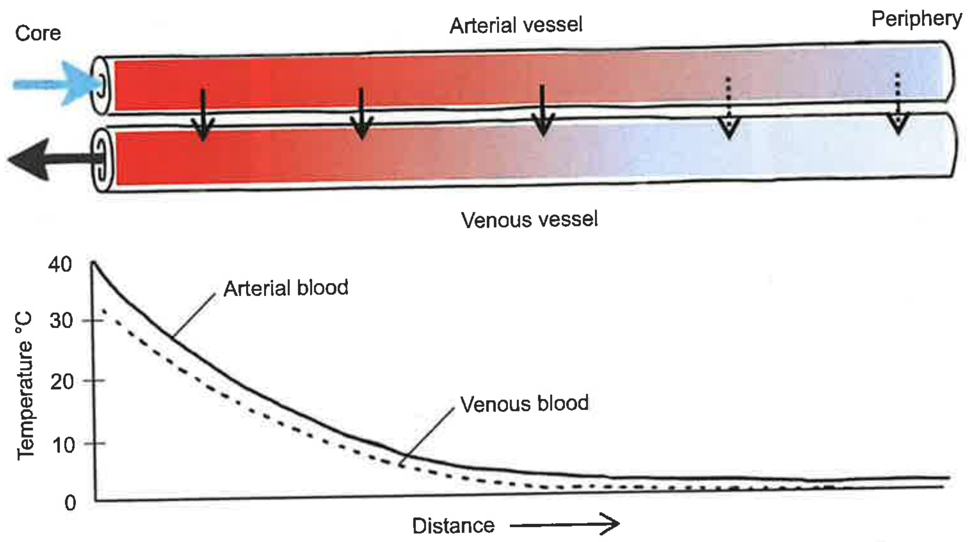

FIG. 3 Schematic of countercurrent heat exchanger showing how heat transfers between juxtaposed arterial and venous vessels. Warm arterial blood traveling from the core transfers heat to cool venous blood returning from the periphery, resulting in temperature gradients along the length of the vessel such that blood in the core body is kept warm. *Reprinted with permission from Davis (2019).*

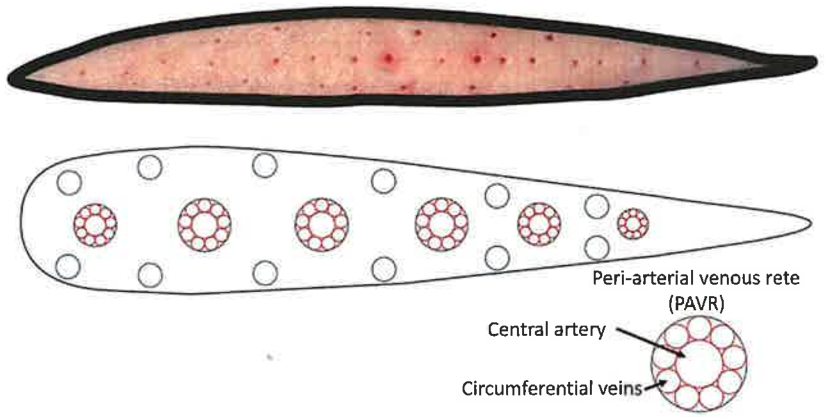

FIG. 4 Dorsal fin cross section from a harbor porpoise (photo courtesy of The Long Marine Lab Marine Mammal Stranding Network) and schematic showing the arrangement of countercurrent heat exchangers in the dorsal fin. Countercurrent heat exchangers contain central arteries surrounded by veins that form peri-arterial venous retia (PAVR). *Redrawn from Meagher et al. (2002).*

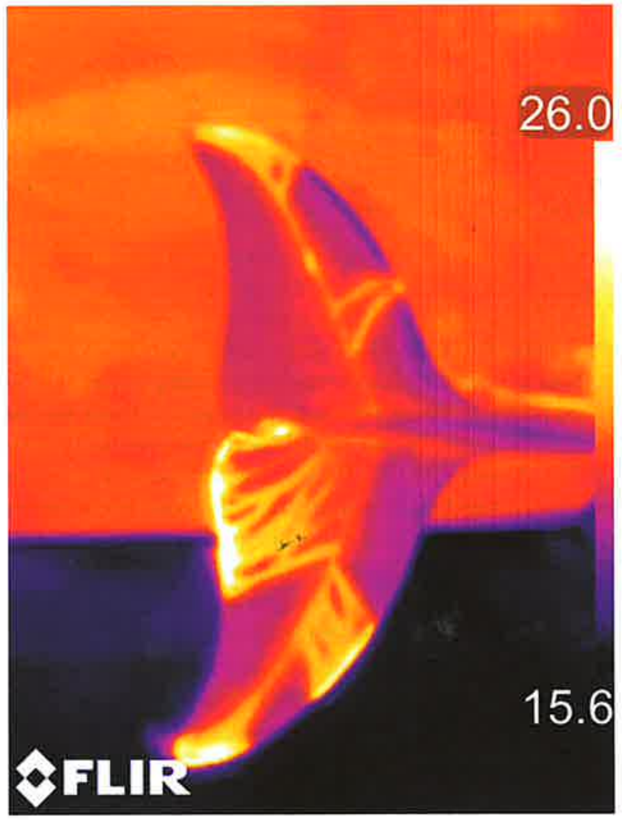

FIG. 5 Infrared thermal image of a bottlenose dolphin fluke showing warmer areas in white and yellow that correspond to vasculature in the appendage. *Image used with permission from NMFS, permit #24054.*

CCHEs are found in the dorsal fin, pectoral flippers, and flukes of cetaceans (Fig. 4). Many studies have investigated their thermoregulatory function relative to water temperature, activity level, and diving behavior, focusing on the dorsal fin of dolphins. The underlying vasculature in the dorsal fin results in a spatially heterogeneous thermal surface (Fig. 5, Meagher et al., 2002; Plön et al., 2018). The regulation of blood flow results in temporal changes in skin temperature and heat flux. Skin temperature of the dorsal fin responds to changes in behavioral state (McGinnis et al., 1972; Westgate et al., 2007) and water temperature and is usually within 1°C of water temperature (Noren et al., 1999; Williams, 1999; Meagher et al., 2002, 2008; Barbieri et al., 2010). The temperature differential between the dorsal fin and ambient water is constant across seasons, thus resulting in a large change in the temperature gradient between the body core and surface when water temperatures are lower (Fig. 6; Barbieri et al., 2010). A temperature gradient between body core and surface as large as 23°C in the winter (compared to 4–7°C in the summer) is possible due to changes in blubber thickness and lipid content (Barbieri et al., 2010). Seasonal patterns in heat flux suggest that appendages consistently dump heat in the summer but are more variable thermoregulatory surfaces in the winter. Greater variability within seasons in heat flux in the appendages also supports their flexible role as heat dissipators (Meagher et al., 2008).

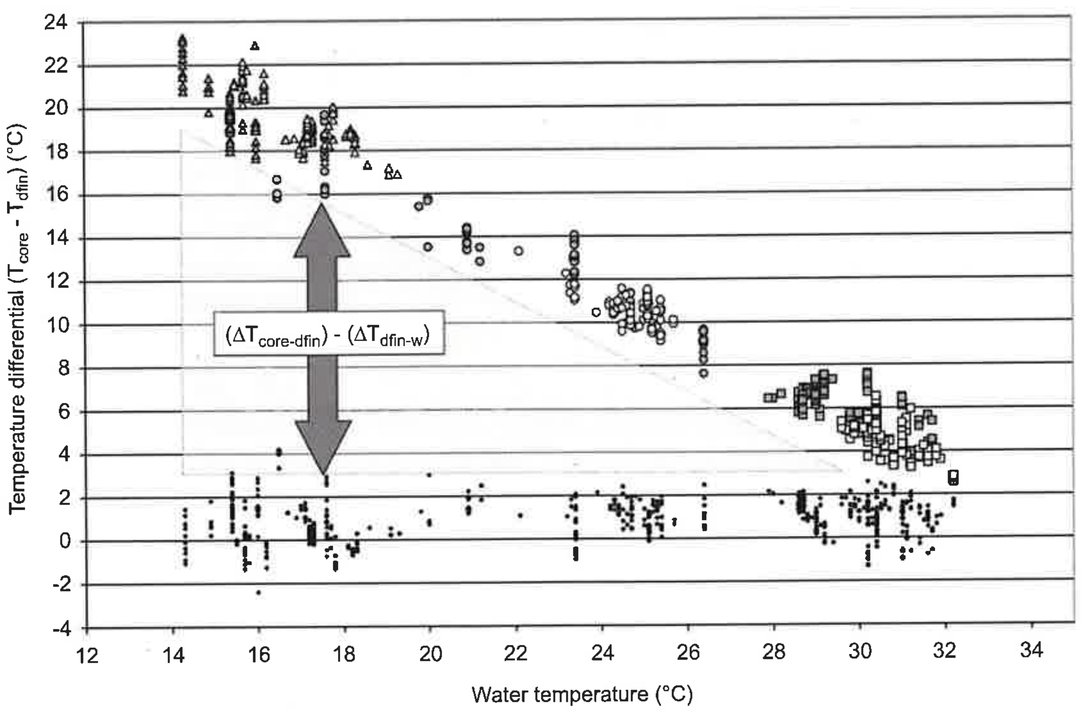

FIG. 6 Difference between temperature differentials of bottlenose dolphins. Temperature differential decreases with increasing water temperatures from 14 to 33°C as depicted by the shaded region. Small dots represent temperature differential between the dorsal fin and water ($\Delta T_{dfin\text{-}w}$). Larger shapes represent temperature differential between core body temperature (assumed to be 37°C) and dorsal fin ($\Delta T_{core\text{-}dfin}$) in different field seasons (filled circle, November 2002; open circle, November 2003; filled square, June 2003; open square, June 2004; filled triangle, February 2003; open triangle, February 2004). *Reprinted with permission from Barbieri et al. (2010).*

Thermal effects of exercise and diving

The ability to induce rapid, short-term changes in heat flux using CCHEs in the appendages is beneficial for adjusting thermal balance after exercise (Kanwisher and Sundnes, 1966; Hampton et al., 1971; Meagher et al., 2008). Another mechanism to avoid activity-induced thermal stress is to use the separate thick-walled superficial veins in the appendages as conduits to bypass the CCHE (Fig. 4). When cold blood preferentially returns in these vessels, the body is cooled (Scholander and Schevill, 1955). A separate CCHE near the reproductive organs facilitates regional cooling with the body core (Fig. 7). Mammalian testes need to be cooler than the core body temperature, or they become infertile. However, dolphins have internal testes. They use cold blood from the dorsal fin and fluke to keep the intraabdominal testes cooler than 37°C (Rommel et al., 1992). This mechanism is especially critical during exercise since the reproductive organs of dolphins lie in between two major locomotor muscles, which generate a lot of heat. Colonic temperatures taken at rest and immediately after exercise in male dolphins showed regional cooling (up to 1.3 and 0.5°C, respectively) and provided evidence for the function of the reproductive CCHE (Rommel et al., 1994; Pabst et al., 1995).

Similarly, for pregnant females, a CCHE brings cool blood to the uterus. This dissipates excess heat and avoids increases in fetal temperature that could result in detrimental developmental effects (Fig. 7; Rommel et al., 1993, 1998). For most mammals, some fetal heat (~15%) is generally dissipated through the mother's abdomen. However, in dolphins, the locomotory muscles and the insulating blubber layer make this unlikely. The CCHE near the uterus allows the temperature gradient between the fetus and surrounding maternal tissue to be favorable for dissipating fetal heat even during exercise.

As previously described, changes in peripheral blood flow are associated with the thermal demands of the animal. However, peripheral blood flow is also modulated by the dive response. To conserve oxygen during a dive, blood flow is reduced to the more hypoxic tolerant organs and tissues, including the appendages. While diving in cold water, the dive response and the thermal response are synchronized, and decreased blood flow to the appendages attenuates heat dissipation at depth (Noren et al., 1999; Williams et al., 1999b). Studies using trained dolphins showed that when the animal returns to the surface at the end of the dive, heat flux increases at the dorsal fin—likely due to enhanced blood flow associated with the anticipatory tachycardia—and remains elevated during the surface interval. Dissipating heat at depth would require temporarily overriding the dive response to perfuse peripheral thermal windows. However, this does occur in certain situations. Attenuation of heat dissipation at depth was recorded in a bottlenose dolphin that had performed several jumps out of the water before diving (Noren et al., 1999). Because cardiovascular adjustments are integral to the dive response, exercise response, and thermoregulation, a balancing act is required to meet these potentially conflicting physiological demands to maintain homeostasis.

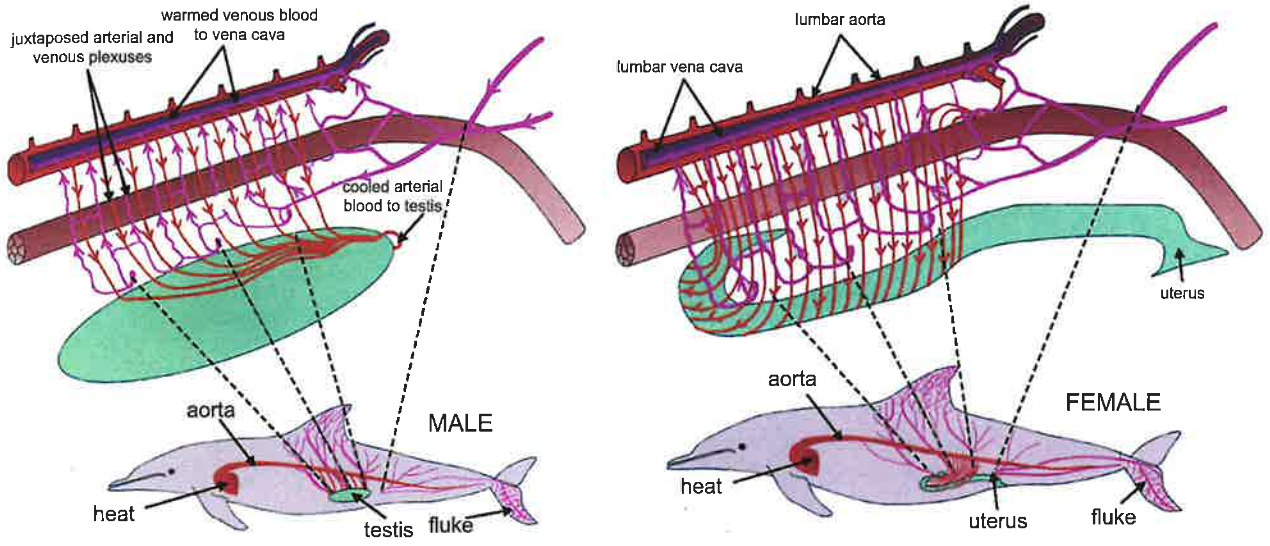

FIG. 7 Countercurrent heat exchanger associated with the intra-abdominal testis of males (left) and uterus of females (right). Cool blood returning from the dorsal fin and fluke forms a venous plexus that is juxtaposed with arteries. Blood from the aorta is cooled before reaching the reproductive organ to prevent overheating of the testis or developing fetus in the uterus. *Adapted with permission from Rommel et al. (1998).*

While appendages, particularly the dorsal fin, are the principal body surfaces to regulate thermal balance, the body trunk provides a large surface area for heat transfer. The vascularization of the blubber layer also facilitates changes in the body conductance in response to changing water temperature or activity level. For example, dolphins chased in the Eastern Tropical Pacific tuna fishery had elevated body surface temperatures, consistent with greater peripheral blood flow to the integument for dissipation of excess heat (Pabst et al., 2002). The fact that blubber is internal and vascularized allows for the easy bypass of this thick insulation when necessary. The following section details how blubber's structure and composition affects its thermal properties and how that changes with ontogeny, reproductive state, season, and diet. All these factors influence the thermoregulatory role of blubber, which is only one of its many roles, resulting in many tradeoffs.

Blubber structure and its thermoregulatory function

Blubber is the vascularized adipose tissue that serves important physiological roles supporting energy balance, maintaining water balance while fasting, streamlining, and aiding in thermoregulation for dolphins and other cetaceans (Iverson, 2009). Dolphin blubber is a lipid-rich tissue filled with adipocytes, or fat cells, typically composed of triacylglycerols (TAGs). While deeper-diving cetacean species have blubber that is predominantly composed of waxy esters (WEs), most dolphin species examined to date have little to no WEs in their blubber (Pabst et al., 1999; Koopman, 2007, 2018; Bagge et al., 2012). Here, we focus on how blubber quality (i.e., the insulative properties) and quantity (i.e., the amount of insulation) relate to dolphin thermoregulation, while noting the competing functions that it serves.

The insulative properties of blubber are heavily dictated by blubber lipid content. Blubber lipid content is driven by the size and density of adipocytes. Adipocytes form during fetal development and proliferate throughout the gestational period (Struntz et al., 2004). However, it is posited that postnatal changes in blubber lipid content are driven by changes in adipocyte size rather than the addition or subtraction of adipocytes (Struntz et al., 2004). Mean adipocyte size typically increases until maturity (Fig. 8).

In contrast, bottlenose dolphin blubber lipid content increases until the animal reaches a juvenile stage and declines into adulthood (Fig. 9; Struntz et al., 2004; Dunkin et al., 2005). Blubber thickness, relative to total body size, begins to decline at the juvenile stage as the rate of adipocyte growth is slower than total body growth. In emaciated animals, the

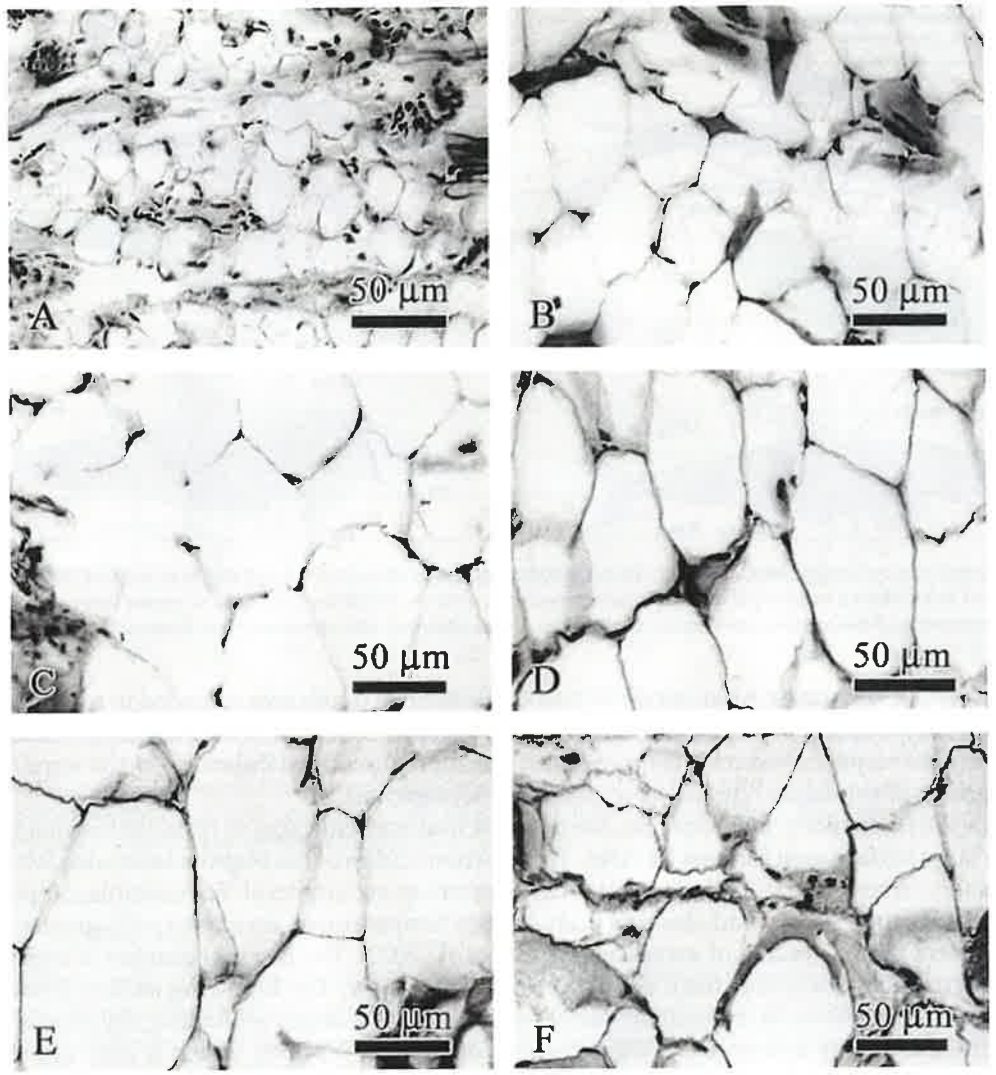

FIG. 8 Light micrographs of blubber from the mid-thoracic region of bottlenose dolphins showing the difference in adipocyte size in a fetus (A), neonate (B), juvenile (C), subadult (D), adult (E), and emaciated adult (F). *Reprinted with permission from Struntz et al. (2004).*

adipocytes shrink, resulting in a blubber lipid content that mimics a neonate's (Fig. 8; Struntz et al., 2004; Dunkin et al., 2005). Similarly, emaciated animals and neonates have a high blubber water content due to the inverse relationship between blubber lipid and water content (Dunkin et al., 2005). Sub-adult and pregnant dolphins have the most insulative blubber due to the complex relationship between body size, blubber lipid content, and blubber insulative properties. In contrast, fetuses and emaciated adults have blubber with higher conductivity and thus are more poorly insulated (Fig. 9; Dunkin et al., 2005).

Although the entire blubber layer serves some insulative purpose for a dolphin, blubber is stratified into superficial, middle, and deep layers that serve slightly different functions. The superficial blubber layer has a high density of structural fibers and a low adipocyte cell count, suggesting its importance in streamlining rather than insulating (Montie et al., 2008). The middle blubber layer has the highest blubber lipid content resulting in a greater insulative capacity (Montie et al., 2008; McClelland et al., 2012). Middle and deep blubber layers typically have more vasculature than superficial layers (McClelland et al., 2012). Blood flow to these layers is critical for accessing and depositing fat stores, but peripheral perfusion also increases blubber conductivity resulting in a tradeoff between blubber as insulation and energy storage. However, the initial thermoregulatory costs of depositing fat stores may be offset by the thicker blubber layer that is often a response to seasonal changes in temperature or food availability, which is discussed further in the next section. This tradeoff is less of a concern in the superficial blubber layer that has reduced vasculature. With fewer veins carrying warm blood reaching the animal's surface, heat dissipation is reduced in this superficial layer. At times when heat conservation is a priority, reducing blood flow to the entire blubber layer will decrease blubber conductivity and minimize heat loss (McGinnis et al., 1972).

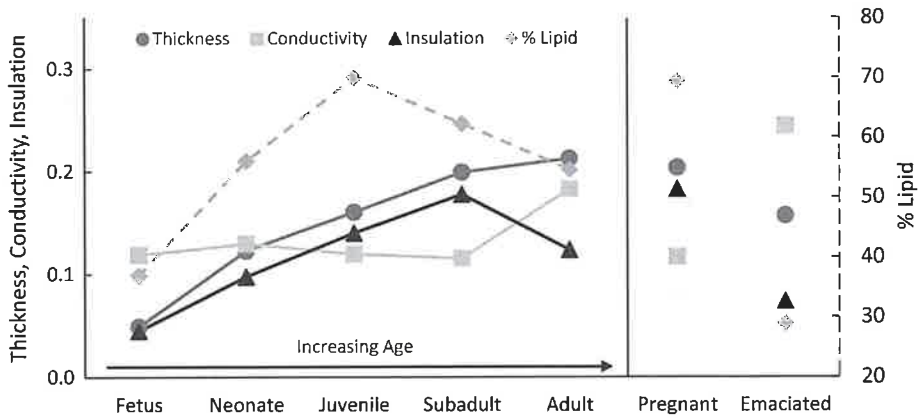

FIG. 9 Blubber thickness (dm, circles), thermal conductivity ($W m^{-1} deg.^{-1}$, squares), insulation ($m^2 deg. W^{-1}$, triangles), and lipid content (%, diamonds) shown for bottlenose dolphins of different age classes. For comparison, values for pregnant and emaciated adults are shown. *Redrawn from Dunkin et al. (2005).*

Intrinsic and extrinsic factors affecting blubber

The thickness of the blubber layer, often driven by the size of adipocyte cells, can change as a function of intrinsic factors such as sex, age, reproductive state, and nutritional state (Fig. 9) (Struntz et al., 2004; Dunkin et al., 2010; Ball et al., 2015). However, blubber thickness alone is typically a poor indicator of the insulative properties of blubber across different ontogenetic stages (Dunkin et al., 2005). Blubber thickness steadily increases from birth to maturation but can be modulated by energetically costly reproductive events such as pregnancy (Struntz et al., 2004; Dunkin et al., 2005).

Because of the multipurpose nature of blubber, dolphins must balance their thermoregulatory needs with the other necessary functions that blubber serves, including buoyancy and energy stores. During nutritional stress, adipocyte cells typically shrink as the lipid is mobilized, decreasing the thickness and insulating quality of the blubber layer, which may become too thin to provide sufficient insulation. A thick blubber layer is essential for thermoregulation and provides energy stores when food is scarce. However, a thick blubber layer also increases buoyancy and may increase energy expenditure to overcome buoyancy when diving (e.g., Adachi et al., 2014; Nousek-McGregor et al., 2014). The animal may also be at greater risk of heat stress due to the increased insulative quality of the blubber as adipocyte cells grow.

Blubber thickness and its associated tradeoffs between thermoregulation and energy stores vary seasonally with changes in water temperature. Typically, blubber thickness and mass decrease in warmer water (Meagher et al., 2008; Noren and Wells, 2009; Adamczak et al., 2021). Decreases in blubber thickness typically yield higher thermoregulatory costs for both male and female dolphins. We examined this relationship by modeling the average adult male and female dolphin (mass = 225 and 184 kg, respectively) using morphometric data provided by the Sarasota Bay Dolphin Research Project. For individuals with an average blubber depth of approximately 2 cm, thermoregulatory costs are relatively low, with temperatures above ~17°C resulting in no thermoregulatory costs for both sexes (Fig. 10). In colder water, a thicker blubber layer is required (~2.5 cm at 5°C) to reach a thermoregulatory cost of zero. However, in warmer water, the primary challenge may be dumping heat. In contrast to adults, younger dolphins are less capable of adjusting their blubber thickness in response to water temperatures despite being more vulnerable to the cold due to their small size (Noren and Wells, 2009).

Blubber's dynamic role in thermoregulation

Interestingly, blubber may aid in both heat generation and dissipation for dolphins. Dolphins have brown adipocytes within the deep blubber layer. These form a layer of brown adipose tissue along the entire body (Fig. 11; Hashimoto et al., 2015). Brown adipose tissue (BAT) is found in most mammals. It plays a vital role in producing heat through non-shivering thermogenesis. Through the futile cycling of protons across a protein (UCP1) in the mitochondrial membrane, BAT tissue generates heat without producing usable energy in the form of ATP. Thus, BAT upgrades the function of the blubber layer from merely insulating as a "conventional blanket" to producing heat as an "electric blanket."

Four species—bottlenose dolphin, Pacific white-sided dolphin, Dall's porpoise (*Phocoenoides dalli*), and harbor porpoise—that are known to have BAT all occur in the North Pacific Ocean where water temperatures are relatively cool. This enhanced heat generation capacity allows these species to survive in waters colder than their insulation alone

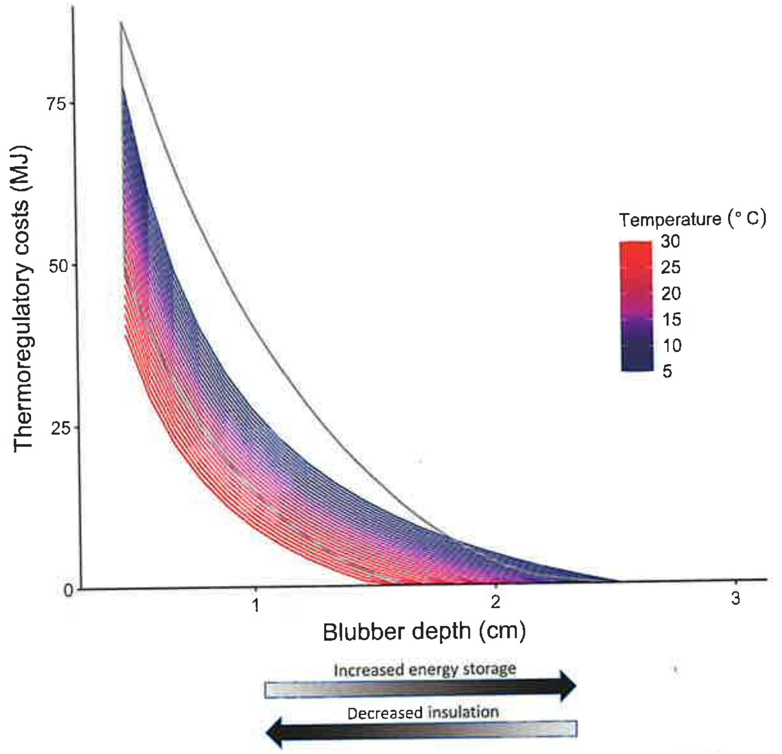

FIG. 10 Thermoregulatory costs were calculated as a function of blubber depth for an adult female bottlenose dolphin for water temperatures ranging from 5 to 30°C. Thermoregulatory costs between 5 and 30°C for an adult male bottlenose dolphin are represented by the gray polygon. Arrows depict the conflicting energy demands of blubber relative to its thickness. Costs are calculated using equations put forth by Hind and Gurney (1997).

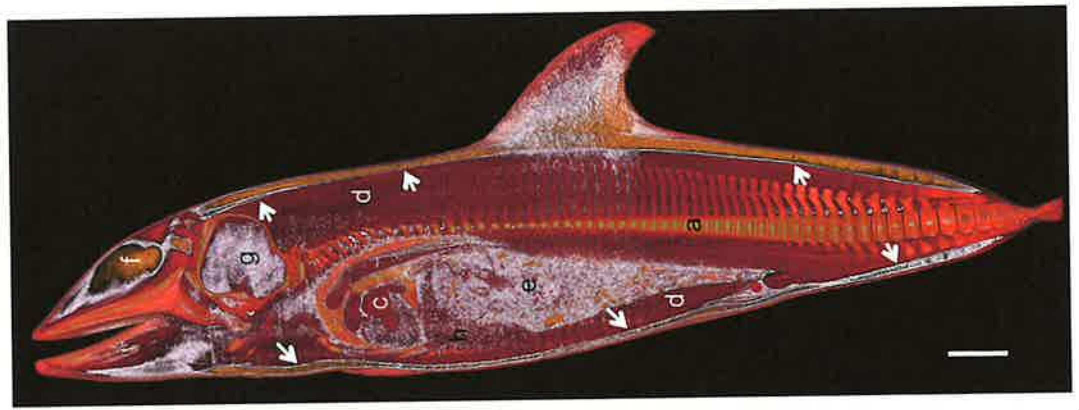

FIG. 11 CT scan of a Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) showing the distribution of brown adipose tissue (denoted by the white arrows) along the entire body. *Reprinted from Hashimoto et al. (2015).*

would allow. It may also help maintain thermal homeostasis during periods of inactivity (Hashimoto et al., 2015). Interestingly, the body sites where BAT was not found included the rostrum, fins, and flukes, of which the latter two are important thermal windows.

In contrast to the heat-generating properties of BAT, blubber may also play a role in dissipating heat for dolphins in warmer waters. Dolphins typically swim in warm coastal waters without overheating. This may be attributed to the redistribution of heat from the internal body to the blubber in times of thermal stress, which simultaneously decreases the rate of heat transfer from the warm water to the dolphin and cools the inner body to maintain normal function (Heath and Ridgway, 1999). Further, the deep layer of blubber has been described as a phase change material, meaning that it may act to store and release heat when necessary (Dunkin et al., 2005). When heat is shunted to the periphery via blood flow, blubber may temporarily store this heat and serve as a buffer zone when experiencing large temperature gradients (Dunkin et al., 2005; Bagge et al., 2012).

Thermoregulatory considerations for epidermal growth and repair

Besides the hypodermal blubber layer, the integument is composed of the dermal and epidermal layers, which provide some additional thermal resistance. These layers' quality and proper functioning are critical for ensuring a protective yet dynamic barrier.

As bare-skinned mammals, dolphins typically maintain their skin at or near ambient temperature. In cold water, this creates a problem as most mammalian tissues, including epidermal cells, have a limited ability to survive prolonged exposure at low temperatures. Further, most are not capable of cell division at low temperatures (Feltz and Fay, 1966). Wound repair and epidermal regeneration are typically associated with increased peripheral blood flow to the skin. However, in a cold environment, thermoregulatory requirements necessitate a reduction in peripheral blood flow. To circumvent this potential conflict, sea lions and seals haul out of the cold water to molt in a more favorable thermal environment (Paterson et al., 2022). While on land, they can increase the blood flow to the periphery to regenerate new hair and epidermal tissue without compromising their heat balance. How dolphins and other fully aquatic marine mammals solve this dilemma is unclear but is likely related to the complex structure of their dermal papillae (see below).

Unlike the annual molt of amphibious marine mammals, dolphins experience continuous epidermal growth facilitated by the structure of their dermal layer. Dolphins have a thick epidermis (roughly 15–20 times thicker than that of humans) with highly innervated dermal papillae protruding roughly half its thickness (Sokolov, 1960; Palmer and Weddell, 1964; Brown et al., 1983). The convoluted nature of the papillae provides a high surface area for epidermal cell proliferation (Fig. 12). This, alongside an increased rate of cell replication, leads to enhanced skin renewal and wound healing capacities (Bruce-Allen and Geraci, 1985). The outermost layer of skin is renewed roughly 12 times per day. While this high sloughing rate is energetically expensive, it is critical for maintaining a clean, smooth outer surface. Besides improving hydrodynamics (Pavlov, 2006), it allows cells to be mitotically active and replicate for wound healing (Hicks et al., 1985).

Observations of skin lesions in wild dolphin populations in regions with different environmental conditions have shown that the prevalence and severity of skin lesions are correlated with water temperature and salinity (Fig. 13) (Wilson et al., 1999; Croft et al., 2020; McClain et al., 2020). Dolphins near Scotland experience the lowest water temperatures and salinity and have the most severe lesions (Wilson et al., 1999). Although epidermal cells can proliferate at temperatures as cold as 17°C, the optimal temperature for proliferation is close to core body temperature (pinnipeds; Feltz and Fay, 1966). The grooves of the dermal papillae that sit deeper in the epidermis will be more shielded from the cold water. They may allow for faster proliferation compared to more superficial cells (Feltz and Fay, 1966). While warmer waters enhance cellular mitotic rate, a higher salinity helps create a degenerative layer of cells to serve as a buffer zone for the underlying wound since dolphins do not form scabs in the healing process (Bruce-Allen and Geraci, 1985; Corkeron et al., 1987). Therefore, the effectiveness of the skin as a physical barrier is dependent on environmental factors; water temperature is a significant determinant of skin health and blubber thickness.

The major effects of water temperature, specifically on skin health and regeneration, are clearly seen in another cosmopolitan delphinid species, the killer whale. Although much larger than bottlenose dolphins, they are the smallest cetacean to regularly inhabit Antarctic waters, where subzero water surface temperatures are typical (Durban and

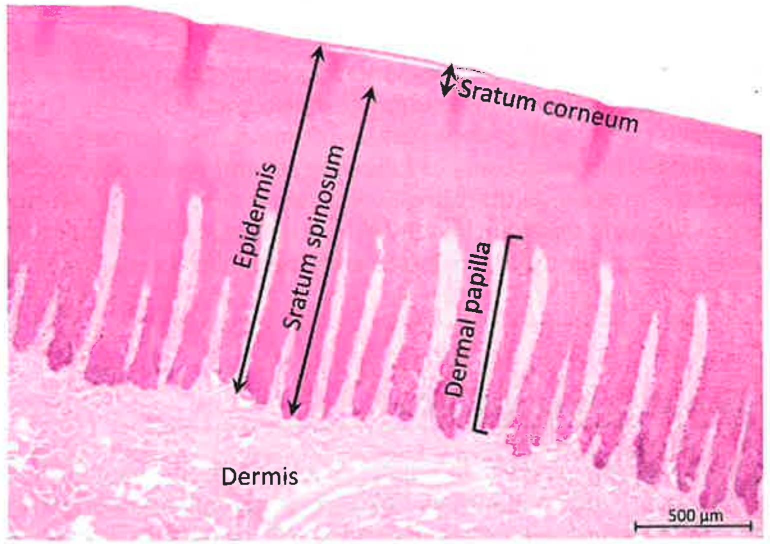

FIG. 12 Hematoxylin and eosin (H&E) stained photomicrograph of the dorsal skin of a bottlenose dolphin depicting the dermis, epidermis, stratum spinosum, dermal papilla, and stratum corneum. *Adapted with permission from Garten and Fish (2020).*

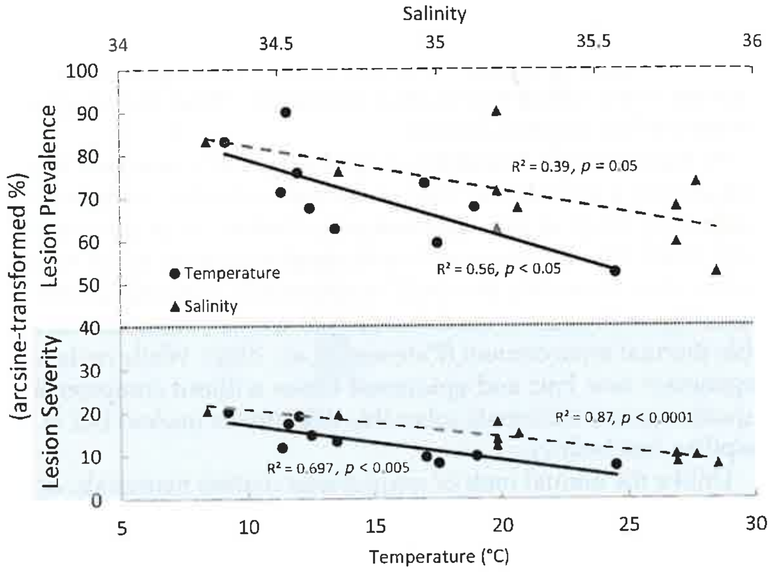

FIG. 13 Prevalence (data > 40%) and severity (data < 40%) of epidermal lesions in bottlenose dolphins from 10 coastal populations (Moray Fifth, Scotland; Shannon Estuary, Ireland; Cardigan Bay, Wales; Cornwall, England; Brittany, France; Doubtful Sound, New Zealand; Kvarnevic, Croatia; Sado Estuary, Portugal; Beaufort, North Carolina USA; Sarasota Bay, FL) in relation to mean annual water temperature (circles, solid lines) and salinity (triangles, dotted lines). *Redrawn from Durban and Pitman (2012).*

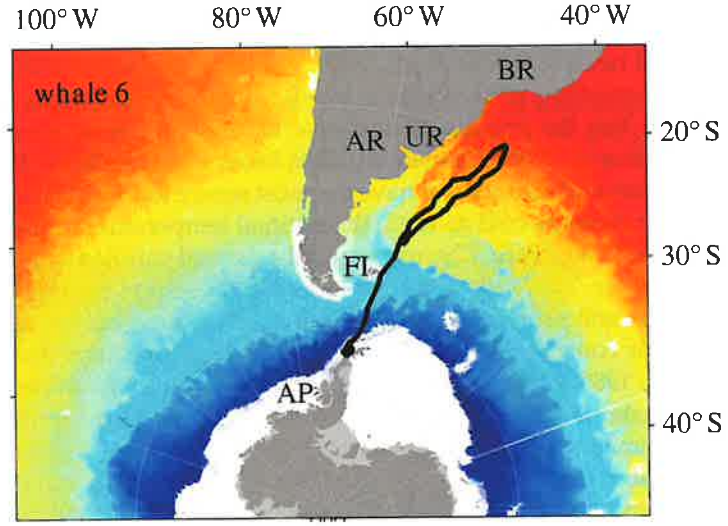

FIG. 14 Track (black line) of an adult female killer whale (ecotype B) tagged in 2010 (Feb 13–May 21) showing movement away from the Antarctic Peninsula (AP) northward past the Falkland Islands (FI) and reaching latitudes off Uruguay (UR) and Brazil (BR). *Adapted from Durban and Pitman (2012).*

Pitman, 2012). Tracking data revealed directed long-distance migrations from their Antarctic foraging grounds to subtropical waters off Uruguay and Brazil, where warmer waters would allow epidermal replacement (Fig. 14). These migrations were short (6–8 weeks) and occurred on a facultative, rather than seasonal, time frame (Pitman et al., 2019). Additionally, a yellowish film of diatoms on the whales' skin was observed following several weeks of foraging in Antarctic waters (Fig. 15). These observations support the hypothesis that trips to warmer waters serve a thermoregulatory role. Here they can molt in more favorable conditions to maintain healthy skin. Another strategy that other cetacean species foraging in the Antarctic may employ is timing their molt to coincide with their migration to warmer breeding grounds (Pitman et al., 2019).

Energetic tradeoffs with thermoregulation

The cost of thermoregulation can be represented by the energy needed to maintain constant body temperature minus internal heat generation from other metabolic processes (Hind and Gurney, 1997). Thermoregulatory costs vary with size, activity level, and reproductive state because internal heat generation depends on these factors. To explore how different metabolic demands influence thermoregulatory costs, we used equations put forth by Hind and Gurney (1997) for an average female bottlenose dolphin (184 kg and 249 cm; data provided by Sarasota Dolphin Research Program). As basal metabolism increases, which often occurs due to changes in mass resulting from growth, thermoregulatory costs steadily decline. This is because increases in basal metabolism result in greater heat generation, which will offset thermoregulatory costs in a cold environment. In contrast, the impact of increased activity levels resulting from locomotion on thermoregulatory costs is not quite as straightforward. At low velocities, internal heat generation is high enough to counteract heat loss from the animal's surface. However, at higher velocities (around 6 m/s for an average adult female dolphin) heat loss from the skin rapidly increases as cool water passes over the skin, resulting in convective heat loss. This results in an increase in thermoregulatory costs at high swim speeds (Hind and Gurney, 1997; Gallagher et al., 2018).

FIG. 15 A killer whale (ecotype B2) photographed near Gerlache Strait, Western Antarctic Peninsula showing a skin condition possibly related to an inability to molt properly while in frigid waters. *Reprinted from Pitman et al. (2019).*

Increased costs from reproduction may similarly influence thermoregulation. A pregnant female has increased internal heat production due to the heat of gestation and energy input into fetal tissue development. Although gestation results in a slight increase in internal heat production from the growing fetus, it does not counteract heat loss from the skin surface (Fig. 16). However, lactation, the most energy-intensive part of reproduction, results in no thermoregulatory costs due to excess internal heat generation. Interestingly, the swimming speed at which heat production

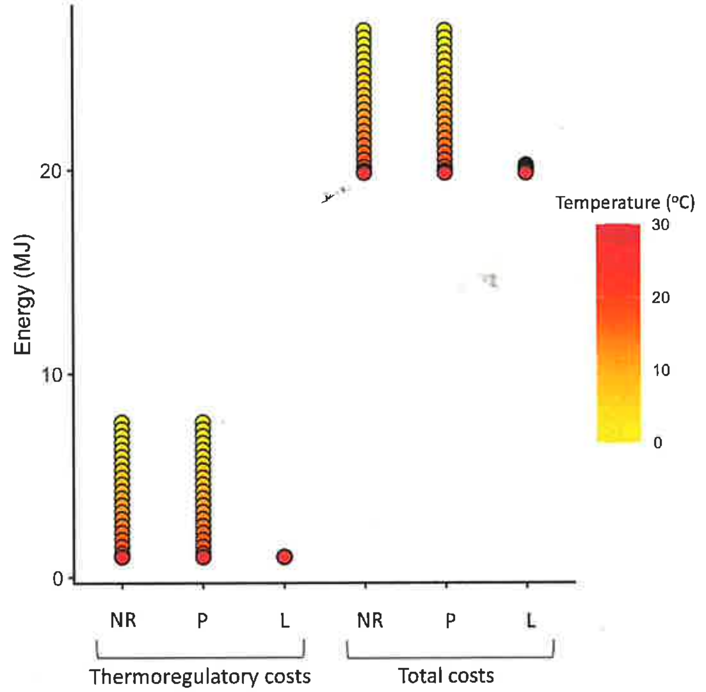

FIG. 16 Thermoregulatory and total energetic costs of a mature female in different reproductive states (NR, nonreproductive; P, pregnant; L, lactating) for water temperatures ranging from 5 to 30°C. Thermoregulatory costs are calculated using equations put forth by Hind and Gurney (1997). Pregnancy costs are calculated for a female with a near-term fetus and include the cost of fetal tissue investment (Boult et al., 2018) and the heat of gestation (Brody, 1968). Lactation cost derived from milk energy output (Cockcroft, 1989).

exceeds thermoregulatory needs for pregnant bottlenose dolphins was found to be only 1.5 m/s, while the optimal speed for dolphins is higher between 1.9 m/s and 3.2 m/s (Yazdi et al., 1999). This indicates that offloading heat may be more important to reproductively-active dolphins than generating heat due to their already heightened metabolic heat production.

There are two contrasting costs associated with foraging. The first is the cost of warming cold prey. The second is the energy liberated as a function of that prey's digestion and biochemical processing. The heat generated from the digestion of prey is known as the heat increment of feeding (HIF), also known as the specific dynamic action (Kleiber, 1975). HIF is characterized by an increase in metabolic rate following food consumption. For dolphins, it has been found that metabolic rate increases by a maximum of 57.1% following consumption of fish (Yeates and Houser, 2008). In other marine mammal species, such as the sea otter, HIF is an essential mechanism for heat production to offset heat loss while resting (Costa and Kooyman, 1984). It is unknown whether dolphins incorporate HIF as part of their thermal budget.

Due to these numerous energetic tradeoffs, the cost of thermoregulation fluctuates throughout an animal's lifetime (as a result of age, mass, and reproductive state) and even throughout the day (as a result of activity level and prey intake). Although the information presented here focuses on the costs associated with heat generation, there are likely costs associated with heat dissipation. The energetic consequences of dissipating heat in times of thermal stress have not yet been quantified. Still, they are likely an important part of a dolphin's thermal budget. As environments continue to change due to human influence, we can expect changes in temperature and activity budgets to influence the energy allotted to thermoregulation.

Concluding remarks

The wide range of thermal regimes that bottlenose dolphins inhabit due to their cosmopolitan distribution makes them an ideal species for studying thermoregulation. From warm, inshore habitats to colder, pelagic waters, bottlenose dolphins persist in temperatures ranging from 5 to 30°C, providing unique insight into the physiological and behavioral mechanisms that maintain homeostasis. Additionally, this broad habitat has made bottlenose dolphins one of the most accessible and widely studied marine mammal species globally. There is a breadth of knowledge about dolphin biology and physiology that is unparalleled in other cetaceans. Long-term monitoring programs, such as those in Sarasota Bay (Wells et al., 2004; https://sarasotadolphin.org/) and Shark Bay (Connor and Smolker, 1985; https://www.monkeymiadolphins.org/), have taken advantage of coastal populations to study bottlenose dolphins in their natural environmental regimes and collect longitudinal data on wild populations. Additionally, studies on captive dolphins have allowed us to collect crucial physiological data on important thermoregulatory features such as internal heat generation through basal metabolism and lower critical temperatures. Similar studies would not be possible for larger cetaceans. Technological advances in field studies have enhanced our knowledge of thermoregulation by measuring physiological variables relevant to thermoregulation (e.g., skin temperature and heat flux) in wild bottlenose dolphins that are freely swimming or diving (e.g., Westgate et al., 2007; Barbieri et al., 2010).

Although bottlenose dolphins have become the model species for thermoregulation in cetaceans, questions remain regarding how these animals withstand life in an aquatic environment. Offshore bottlenose dolphin populations living in colder, more pelagic waters are less accessible, thus limiting our knowledge of bottlenose dolphin thermoregulation in more extreme environments. Further, while the costs of heat generation through metabolism and activity are well-known for bottlenose dolphins and other cetacean species, the costs associated with heat dissipation and rapid offloading of heat have not been documented in any cetacean. Preventing hyperthermia plays an important role in the maintenance of homeostasis for cetaceans to prevent protein denaturation. Several studies have identified mechanisms for offloading heat in bottlenose dolphins (e.g., using their dorsal fin as a thermal window); however, the energetic costs associated with these mechanisms are unknown. Further research into these topics will complete our understanding of thermoregulation in a harsh, aquatic environment.

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