

Reproductive thermoregulation in marine mammals: mechanisms, adaptations and evolutionary implications

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Abstract

Marine mammals inhabit thermally challenging environments in which maintaining internal body temperature is essential for survival, metabolic function, and reproductive success. Unlike terrestrial mammals, many marine male species lack external reproductive structures (e.g. scrotum), raising questions about how reproductive temperatures are regulated in the absence of conventional cooling mechanisms. This review synthesizes current knowledge of reproductive thermoregulation in marine mammals, with a focus on cetaceans and pinnipeds, and highlights key anatomical and physiological adaptations. These include countercurrent heat exchange systems, specialized vascular networks surrounding reproductive organs, and behavioral strategies that facilitate localized cooling while conserving overall body heat. The review also addresses thermal protection of the developing fetus, illustrating how vascularization and insulation help maintain optimal intrauterine conditions. In addition, it examines evolutionary trade-offs associated with internal testes and streamlined body forms, ecological pressures imposed by aquatic environments, and the integration of thermoregulation with diving physiology. Finally, implications for conservation are discussed, particularly in the context of climate change, rising ocean temperatures and human-induced habitat disturbances. By integrating anatomical, physiological, ecological and evolutionary perspectives, this article underscores how marine mammals have evolved highly efficient thermoregulatory strategies, offering insights into reproductive biology and species resilience in dynamic aquatic ecosystems.

Keywords: Marine thermoregulation, reproductive adaptation, heat exchange, internal testes, aquatic ecology

Introduction

Thermoregulation is a fundamental physiological process that enables organisms to maintain internal temperature within a narrow range, despite external fluctuations.¹ In mammals, this regulatory capacity is especially critical because most species are endothermic, relying on internally generated heat to sustain metabolic processes.² Even slight deviations from optimal body temperature can disrupt cellular function, enzyme activity and overall homeostasis. Among the physiological systems most sensitive to temperature variation, reproduction is particularly vulnerable.³ Spermatogenesis, for instance, typically requires temperatures several degrees below core body temperature to proceed efficiently, whereas embryonic and fetal development depend on a stable and tightly regulated thermal environment.⁴ As a result, mammals have evolved a diverse array of specialized mechanisms to ensure that reproductive tissues are maintained within optimal temperature ranges.²

In terrestrial male mammals, these requirements are often met through anatomical adaptations, including the scrotum, that position the testes outside the abdominal cavity to facilitate cooling.⁵ This external placement promotes heat dissipation through convection and radiation, aided by reduced insulation and specialized vascular structures that regulate testicular blood temperature.⁶ Similarly, pregnant females can dissipate excess heat through the abdominal surface that functions as a thermal window to protect the developing fetus from overheating.^{7,8} These adaptations underscore the importance of localized temperature regulation within an otherwise tightly controlled internal thermal environment.

In contrast, marine mammals present a distinct thermoregulatory paradigm shaped by the aquatic environment. Unlike many terrestrial mammals, most marine mammals lack functional sweat glands, effectively eliminating evaporative cooling as a mechanism of heat loss. Consequently, heat dissipation relies

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primarily on vascular heat exchange systems, peripheral thermal windows and behavioral modulation rather than evaporative water loss. Thermoregulation in these species can be conceptualized as a classical homeostatic process governed by a sensor-integrator-effector framework, in which thermal inputs are detected by peripheral and central thermoreceptors, integrated within the hypothalamus, and translated into coordinated vascular and behavioral responses. The efficiency of these systems reflects thermodynamic constraints imposed by heat-transfer in high-conductivity aquatic environments.

Marine mammals, including cetaceans (whales, dolphins) and pinnipeds (seals, sea lions) also exhibit notable deviations in reproductive anatomy. Many species lack a scrotum and their testes are retained within the body cavity, embedded within insulating layers of blubber and muscle. However, this condition is not uniform across taxa: cetaceans possess fully internal testes retained within the abdominal cavity whereas pinnipeds typically exhibit abdominal or inguinal testicular positions without a true scrotum, with additional variations linked to species, reproductive state and environmental conditions.⁹⁻¹² Despite this seemingly thermally disadvantageous arrangement, these animals maintain normal reproductive function, raising important questions about how reproductive cooling is achieved under aquatic constraints.¹⁰⁻¹²

The aquatic environment imposes unique and often opposing thermal challenges compared to terrestrial habitats. Water conducts heat away from the body far more efficiently than air, increasing the risk of rapid heat loss and hypothermia. To counteract this, marine mammals have evolved thick layers of blubber, a specialized stratified hypodermal connective tissue composed of lipid-rich adipocytes embedded within a fibrous and vascular matrix that serves insulatory and metabolic functions.¹³ Importantly, blubber is not uniformly distributed across the body; regional variations in its thickness and vascularization contribute to functional thermal specialization. Although these adaptations are essential for conserving heat in cold water, they simultaneously constrain the capacity for localized heat dissipation, creating a physiological trade-off between systemic insulation and regional cooling of reproductive tissues.¹³⁻¹⁵ The thermoregulatory adaptations described herein exemplify the principle of complementarity, in which anatomical specialization underpins physiological function.

This review examines how marine mammals resolve competing thermoregulatory demands through integrated anatomical, physiological, and behavioral strategies that collectively enable reproductive success in thermally challenging aquatic environments. In particular, it focuses on specialized vascular structures (e.g. countercurrent heat exchange systems) that facilitate precise regulation of blood temperature and localized cooling of reproductive organs, thereby ensuring functional thermal homeostasis, despite the constraints imposed by an aquatic lifestyle. The review further explores the evolutionary pressures that have shaped these adaptations, including the transition from terrestrial to aquatic environments and the physiological constraints associated with diving (e.g. peripheral vasoconstriction) and need for oxygen conservation and episodic changes in perfusion patterns. By integrating comparative insights from anatomy, physiology and ecology, this synthesis provides a comprehensive framework for understanding reproductive thermoregulation in marine mammals and highlights its broader biological importance in relation to environmental adaptation and life-history evolution.

The primary objective of this review is to synthesize current knowledge on reproductive thermoregulation in marine mammals within a comparative and mechanistic framework. Specifically: 1. evaluate anatomical, physiological, and behavioral adaptations that support reproductive thermal balance across marine mammal taxa; 2. integrate thermoregulatory mechanisms with diving physiology and vascular heat exchange systems to understand their functional interdependence and 3. identify shared principles and taxon-specific differences that govern thermal regulation of reproductive tissues in aquatic environments. Collectively, these interspecific differences suggest that reproductive thermoregulatory strategies in marine mammals are best understood within a taxon-specific framework rather than as a uniform physiological condition. By consolidating evidence across physiology, anatomy and ecology, this review moves beyond isolated descriptive accounts to provide a unified mechanistic and evolutionary perspective on reproductive thermoregulation in marine mammals. Collectively, available evidence indicates that reproductive thermoregulation in marine mammals is not governed by a single uniform mechanism. Rather, marine mammals have evolved taxon-specific solutions to a common physiological challenge: reconciling systemic thermal conservation with the thermal requirements of reproduction. Countercurrent vascular heat exchange is particularly well characterized in cetaceans, whereas the relative contributions of vascular, anatomical, behavioral, and environmental mechanisms vary considerably among marine mammal lineages. Accordingly, this review adopts a comparative, taxon-specific framework to distinguish shared thermoregulatory principles from lineage-specific adaptations.

Thermal constraints on reproduction

Temperature sensitivity of spermatogenesis

Spermatogenesis is highly temperature-sensitive across mammalian species, making precise thermal regulation essential for male fertility. In most mammals, optimal sperm production occurs at temperatures $\sim 2-4^{\circ}\text{C}$ below core body temperature, a requirement that reflects the vulnerability of developing germ cells to heat stress.^{5,16} Even slight elevations in temperature can disrupt the process of sperm formation by impairing meiosis, damaging DNA integrity and altering the function of enzymes involved in cell division.^{17,18} As a result, elevated testicular temperatures are commonly associated with reduced sperm quality, decreased motility and in severe cases, temporary or permanent infertility.^{17,19} To meet these stringent thermal requirements, terrestrial mammals have evolved specialized anatomical adaptations, most notably the scrotum.^{20,21} This external structure positions testes outside the abdominal cavity, where they are exposed to a cooler environment.^{20,21} The scrotum facilitates heat dissipation through increased surface area, reduced insulation compared to internal tissues and countercurrent heat exchange system within the spermatic cord that helps regulate blood temperature before it reaches testes.^{20,21} These mechanisms work together to maintain an optimal thermal environment for spermatogenesis. In contrast, marine mammals present a physiological paradox. Lacking a scrotum, their testes remain within the abdominal cavity, surrounded by insulating layers of blubber and muscle that are essential for conserving heat in cold aquatic environments.⁹⁻¹² This arrangement would seemingly expose the testes to higher temperatures than are conducive to sperm production, raising the critical question of how these animals achieve sufficient cooling to sustain reproductive functions.

Thermal challenges during pregnancy

Pregnancy introduces additional thermal constraints that require precise physiological regulation in mammals.⁷ As fetal development progresses, metabolic heat is generated by the fetus while the mother's metabolic rate increases to support growth, nutrient transfer, and the overall energetic demands of pregnancy.²² In terrestrial mammals, excess heat can often be dissipated through the abdominal surface, which functions as a 'thermal window' that facilitates heat loss to the surrounding environment.^{22,23} In contrast, this process is substantially more constrained in marine mammals. Thick layers of blubber and underlying musculature (comprising a specialized, stratified hypodermal connective tissue composed of lipid-rich adipocytes embedded within a fibrous vascular matrix that serves insulatory and metabolic functions) are essential for maintaining core temperature in cold aquatic environments but markedly reduce opportunities for passive heat dissipation.^{12,24} Although this adaptation is critical for thermal insulation, it simultaneously limits the ability to offload excess metabolic heat generated during pregnancy, thereby increasing the potential risk of fetal overheating under certain physiological or environmental conditions. Consequently, male and female marine mammals must rely on specialized internal thermoregulatory mechanisms to regulate reproductive tissue temperatures in an environment that inherently favors heat conservation over heat loss.^{12,24}

Countercurrent heat exchange systems

The vascular and integumentary structures involved in heat exchange represent clear examples of structure-function complementarity, where morphological specialization directly enables physiological thermoregulation.

Basic principles

Countercurrent vascular heat exchange is among the best-characterized mechanisms of reproductive thermoregulation in several marine mammal taxa, particularly cetaceans. This mechanism is a highly efficient physiological system that enables precise control of tissue temperatures within a broader homeostatic framework.^{12,24} Within this system, countercurrent heat exchange functions as an effector-level mechanism that allows localized modulation of tissue temperature while simultaneously preserving systemic thermal stability. Mechanistically, it involves closely associated arteries and veins arranged in parallel, facilitating efficient heat-transfer between adjacent blood vessels. As warm arterial blood flows from the body core toward reproductive organs, it travels alongside cooler venous blood returning from peripheral regions such as flippers or fins, enabling heat to be transferred from the warmer arterial blood to the cooler venous blood.^{12,14} This exchange effectively lowers the temperature of blood before it reaches thermally sensitive tissues such as the testes or uterus, thereby protecting reproductive function from thermal stress. At the same time, the process conserves overall body heat by recycling thermal energy within the vascular network, making it particularly advantageous in cold aquatic environments where minimizing heat loss is essential for maintaining physiological homeostasis.^{12,14}

These processes operate within fundamental physical constraints governed by the second law of thermodynamics, whereby heat flows spontaneously from regions of higher to lower temperature along established gradients. Countercurrent

exchange exploits temperature gradients between adjacent arterial and venous blood streams. The close apposition and opposing flow of these vessels facilitate heat transfer while reducing unnecessary heat loss to the aquatic environment. Consequently, the organization of closely apposed arterial and venous networks in marine mammals represents an adaptive solution that enhances thermal conservation while simultaneously enabling fine-scale regulation of reproductive tissue temperatures under conditions that strongly favor heat dissipation.

Vascular architecture in marine mammals

Marine mammals possess specialized vascular structures known as retia mirabilia ('wonderful nets'), dense, intricately arranged networks of arteries and veins that facilitate efficient heat exchange. These structures are strategically positioned throughout the body to regulate temperature in critical regions, particularly within the reproductive system.^{14,24} In males, arterial blood traveling toward the testes passes through these vascular networks, where it is cooled by adjacent venous blood returning from peripheral areas such as the dorsal fins, flippers, or flukes, body regions that readily dissipate heat into the surrounding water. This process ensures that the testes are maintained at temperatures suitable for spermatogenesis despite their internal location.^{12,14} In females, comparable vascular arrangements surround the uterus and associated reproductive tissues. These vascular arrangements have been proposed to facilitate heat exchange within the reproductive tract and may contribute to regulation of the thermal environment surrounding the gravid uterus and developing fetus.^{7,14,24}

Functional outcomes

The result of these vascular adaptations is the ability to achieve precise, localized cooling of reproductive organs without markedly affecting overall body temperature. This selective regulation is essential for maintaining reproductive efficiency in challenging aquatic environments. By lowering the temperature of blood supplied to the testes, marine mammals can sustain optimal conditions for spermatogenesis, ensuring proper sperm development despite the absence of external cooling structures.^{9,15} Similarly, in females, these mechanisms help protect the developing fetus from thermal stress by preventing excessive heat accumulation within the uterus.^{7,25} At the same time, the countercurrent heat exchange system conserves metabolic heat by recycling thermal energy within the body, minimizing heat loss to the surrounding water. This balance between heat conservation and targeted cooling highlights the remarkable efficiency of marine mammal thermoregulatory adaptations.^{14,24,26}

Male reproductive thermoregulation

Internal testes and cooling mechanisms

Unlike terrestrial mammals, male cetaceans and many pinnipeds possess internalized testes that are retained within the body cavity rather than suspended externally. This anatomical arrangement would seemingly expose the testes to core body temperatures that exceed the optimal range required for spermatogenesis. Nevertheless, marine mammals have evolved highly specialized thermoregulatory adaptations that maintain testicular temperatures within the narrow physiological limits necessary for normal sperm production and reproductive function. Central to this regulation is a countercurrent

heat exchange system embedded within specialized vascular networks, in which arterial and venous vessels are arranged in an antiparallel orientation, enabling continuous heat-transfer along the length of closely associated vascular bundles. As warm arterial blood travels toward the testes, it is cooled by adjacent venous blood returning from cooler peripheral regions, thereby reducing the temperature of blood before it reaches thermally sensitive reproductive tissues.^{9,10} In addition, cooled venous blood originating from appendages such as flippers, fins, and tail flukes further enhances testicular cooling by exploiting peripheral regions capable of efficient heat dissipation.¹⁰ Dynamic redistribution of blood flow during diving, swimming, and periods of heightened activity also contributes to localized thermal regulation, illustrating a highly coordinated physiological system that balances reproductive cooling with overall thermal homeostasis, despite the internal location of the testes (Figure 1).^{9,10,26}

Role of peripheral structures

Peripheral structures (e.g. fins, flippers, flukes) have a critical role in the thermoregulatory strategies of marine mammals by acting as natural thermal radiators that facilitate controlled heat exchange with the surrounding environment,^{27,28} whereas blubber, a metabolically active and highly specialized connective tissue rather than a passive fat depot, is structurally organized into lipid-rich and fibrous layers that collectively provide effective thermal insulation and essential mechanical support.^{12,24} Regional variation in blubber architecture is pronounced, with thinner, more vascularized layers in appendages (e.g. fins, flippers, flukes) promoting heat dissipation whereas thicker trunk-associated depots enhance overall thermal insulation. These peripheral appendages are characterized by a high surface-area-to-volume ratio and relatively reduced insulation, enabling efficient dissipation of excess metabolic heat into the surrounding aquatic medium.^{29,30} As blood circulates through these structures, it is progressively cooled before returning to the body core, thereby functioning as a physiological temperature buffer. This cooled venous blood subsequently enters specialized vascular networks, including countercurrent heat exchange systems, where it contributes to

the regulation of temperature in thermally sensitive organs such as reproductive tissues.²⁷⁻³² By utilizing peripheral regions as controlled sites of heat exchange, marine mammals achieve fine-scale modulation of internal organ temperatures without compromising overall systemic thermal homeostasis. This integrated thermoregulatory strategy is particularly advantageous in aquatic environments, where the high thermal conductivity of water amplifies heat loss and heat gain risks, making peripheral heat exchange structures essential for maintaining reproductive and physiological stability.

Behavioral contributions

Behavioral strategies also contribute substantially to thermoregulation in marine mammals, complementing anatomical and physiological adaptations.² For instance, changes in swimming patterns can influence the distribution of blood flow, directing cooler or warmer blood to specific regions of the body as needed.^{26,33} Similarly, intentional exposure to water of varying temperatures can assist in dissipating excess heat or maintaining warmth, depending on environmental conditions.³³ Activity levels further modulate thermoregulation by altering metabolic heat production; periods of increased activity generate additional heat that must be managed, whereas rest or slower movements reduce metabolic output and help maintain thermal balance.^{2,34} Together, these behavioral adjustments provide a dynamic means of regulating body and reproductive organ temperatures, allowing marine mammals to fine-tune their thermal environment in response to internal physiological needs and fluctuating external conditions (Figure 2).

Female reproductive thermoregulation

Thermal protection of the fetus

The developing fetus is especially sensitive to temperature fluctuations, as even minor deviations from optimal thermal conditions can disrupt normal growth and developmental processes,^{8,10} with elevated temperatures impairing cellular

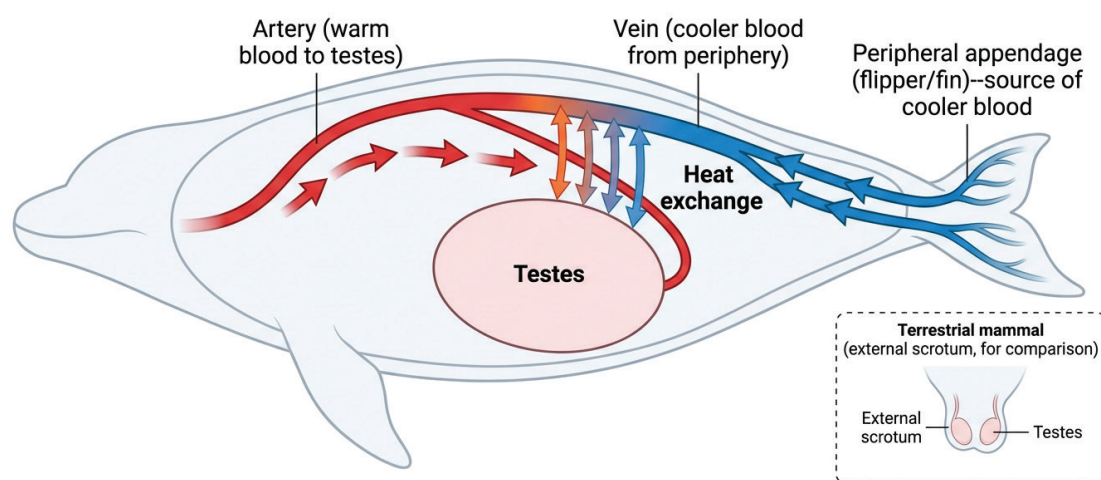


Figure 1. Schematic of countercurrent heat exchange in marine mammals. Warm arterial blood transfers heat to cooler venous blood returning from peripheral appendages, maintaining optimal reproductive organ temperature while conserving overall body heat. Heat-transfer follows a countercurrent gradient from warm arterial to cooler venous blood, resulting in localized testicular cooling. Arrows indicate directional blood flow (arterial versus venous), with color gradients representing relative temperature differences between incoming and outgoing blood streams

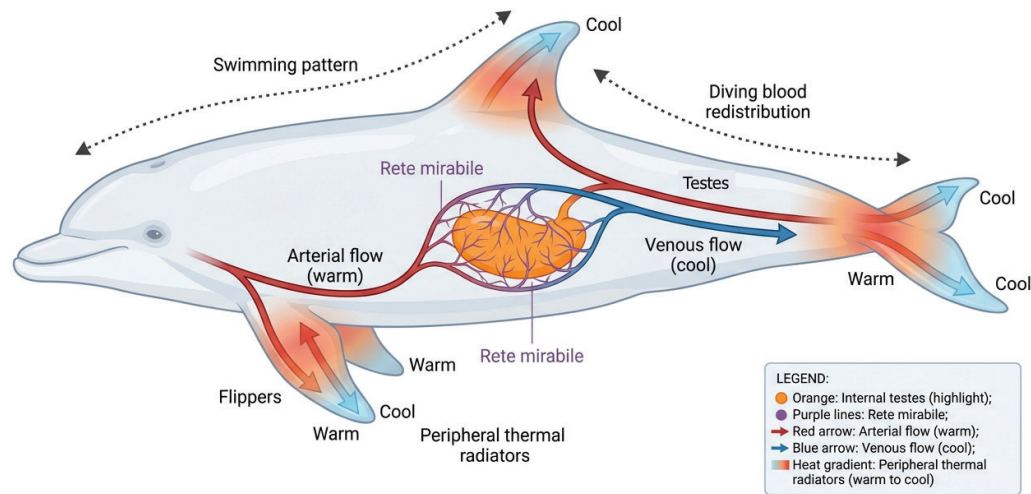


Figure 2. Integrated thermoregulatory adaptations in marine mammals. Anatomical, physiological mechanisms maintain optimal reproductive and core body temperature in aquatic environments. Thermal gradients across body regions reflect heterogeneity in blubber thickness and peripheral heat dissipation structures. Blubber distribution is regionally heterogeneous, contributing to localized heat exchange and insulation

function, increasing the risk of developmental abnormalities, and, in severe cases, leading to fetal loss. To mitigate these risks and ensure fetal survival in thermally challenging aquatic environments, marine mammals have evolved a suite of integrated physiological and structural adaptations that enable precise reproductive thermoregulation.^{10,26} Central among these are specialized vascular heat exchange systems surrounding the uterus, which facilitate selective cooling of arterial blood prior to its delivery to the fetus, thereby helping to maintain a stable intrauterine thermal environment.²⁵ In addition, dynamic regulation of blood flow to reproductive tissues allows further fine-tuning of heat distribution, ensuring that excess thermal energy can be redirected away from the uterus when necessary. Complementing these vascular mechanisms, marine mammals possess thick layers of blubber, a specialized stratified hypodermal connective tissue composed of lipid-rich adipocytes embedded within a fibrous and vascular matrix, which serves insulatory and metabolic functions. Together with the overlying blubber and surrounding musculature, this system provides robust thermal insulation that stabilizes internal physiological conditions, protects the mother and fetus from rapid external temperature fluctuations, and conserves metabolic heat in cold aquatic environments.^{28,35}

Uterine vascularization

The uterus in marine mammals is highly vascularized, containing extensive networks of arteries and veins that have a crucial role in regulating fetal temperature.^{10,25} These intricate vascular structures enable efficient heat exchange, allowing arterial blood to be cooled before it reaches the developing fetus. By lowering the temperature of incoming blood, the system helps maintain an optimal thermal environment essential for proper fetal development.³⁶ Additionally, the vascular networks facilitate the removal of excess heat generated by fetal metabolism, preventing overheating and protecting delicate tissues from thermal stress.^{25,36} This combination of cooling and heat removal ensures that the fetus remains within a narrow, stable temperature range, despite fluctuations in maternal body temperature or external water conditions.^{10,22} Overall, the uterine

vascular system exemplifies a sophisticated physiological adaptation that supports reproductive success in marine mammals (Figure 3).

Comparison with terrestrial mammals

In contrast to many terrestrial mammals, which rely on external heat dissipation through the abdominal surface and other exposed body regions, marine mammals depend far more heavily on internal vascular mechanisms to regulate reproductive and core body temperatures.^{10,37} In terrestrial environments, excess heat can be dissipated relatively efficiently because air possesses low thermal conductivity, allowing organs (e.g. testes, uterus) to maintain temperatures below core body temperature without extensive internal specialization.² In aquatic environments, however, water conducts heat away from the body ~ 25 times faster than air, creating simultaneous risks of excessive heat loss and thermal instability in temperature-sensitive tissues.¹⁰ Consequently, marine mammals have evolved intricate internal thermoregulatory systems, including countercurrent heat exchange systems and highly specialized vascular networks, that enable precise control of reproductive tissue temperatures while minimizing overall energetic heat loss.^{10,15} These mechanisms illustrate the profound influence of environmental thermal properties on the evolution of reproductive thermoregulation across mammalian lineages.

Marine mammals therefore face a fundamental thermophysiological conflict: they must conserve core body heat in cold aquatic environments while simultaneously maintaining cooler temperatures in specific reproductive organs (particularly the testes and to a lesser extent uterus) to sustain normal reproductive function. The strategies employed to resolve this conflict differ between males and females and vary considerably among taxonomic groups, including cetaceans (whales and dolphins) and phocids (true seals). Supplementary File compares and contrasts mechanisms of testicular and uterine thermoregulation across marine mammal taxa. Furthermore, marine mammals exhibit substantial diversity in reproductive anatomy and thermoregulatory organization, reflecting differences in evolutionary history, habitat use, diving behavior, and degree of aquatic specialization. Although internalized testes

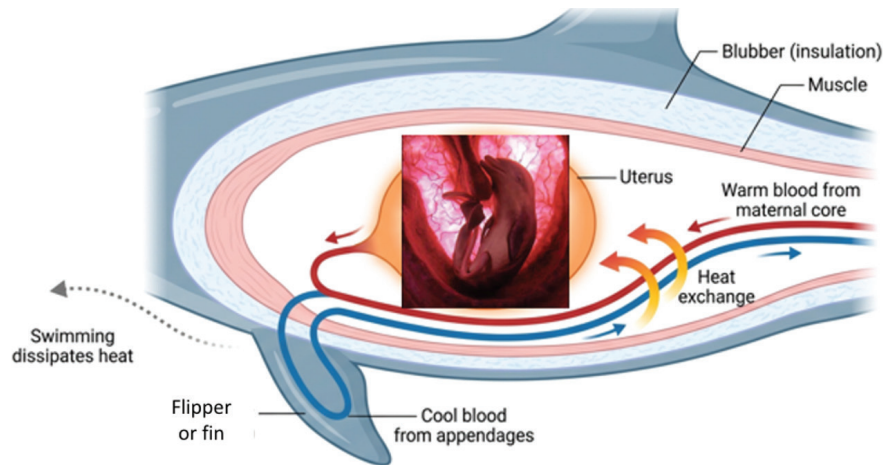


Figure 3. Conceptual schematic of proposed mechanisms contributing to uterine and fetal thermal regulation in marine mammals. Specialized vascular networks and countercurrent heat exchange maintain optimal intrauterine temperatures, protecting the developing fetus while conserving maternal core heat. Peripheral cooling and insulating layers support precise thermal regulation, with maternal behavior contributing to heat balance

and vascular heat exchange systems are common among fully aquatic species, these features are not universal across all marine mammals. Considerable interspecific variation exists in testicular position, blubber distribution and vascularization, peripheral heat exchange structures, and the integration of thermoregulation with diving physiology. To provide a comparative framework, major reproductive thermoregulatory characteristics across marine mammal groups, including testicular location, vascular specialization, mechanisms of heat exchange, and interactions among insulation, peripheral appendages, and reproductive cooling are summarized (Table). Collectively, these comparisons highlight shared adaptive principles and important taxon-specific differences in how marine mammals balance reproductive cooling with maintenance of core body temperature under thermally demanding aquatic conditions. Notably, cetaceans exhibit fully internal testes whereas pinnipeds display more intermediate patterns, with seasonal and functional modulation of testicular position and perfusion, particularly during haul-out periods. Thus, although marine mammals face a shared reproductive thermoregulatory challenge, the mechanisms used to resolve it differ substantially among lineages and should not be interpreted as a uniform marine mammal adaptation.

Integration of thermoregulation and diving physiology

Redistribution of blood flow

During diving, marine mammals experience profound physiological changes that are essential for conserving oxygen and supporting extended submersion, but these adjustments also have important implications for thermoregulation.²⁶ During diving, peripheral vasoconstriction redistributes cardiac output toward organs essential for maintaining aerobic function, particularly the brain and heart. These changes may secondarily alter perfusion of reproductive vascular networks and therefore modify reproductive heat exchange.²⁷⁻³¹ This redistribution ensures survival during periods of limited oxygen availability but simultaneously alters the dynamics of heat exchange, as cooled venous blood from peripheral regions becomes less available to regulate the temperature of internal organs. Additionally, overall circulation patterns shift, with blood being selectively directed to areas

where it is most needed, further influencing the efficiency of countercurrent heat-exchange systems and other vascular cooling mechanisms.^{31,32} Consequently, diving marine mammals must dynamically balance oxygen conservation with localized temperature control, demonstrating the intricate interplay between cardiovascular and thermoregulatory systems in these highly adapted aquatic species.

Balancing competing demands

Marine mammals face the complex challenge of simultaneously balancing multiple physiological demands.^{26,38} During dives, they must conserve oxygen by restricting blood flow to nonessential tissues, ensuring that vital organs receive adequate oxygen to sustain life underwater. At the same time, they must retain heat in cold aquatic environments, where water's high thermal conductivity can rapidly draw away body heat. Complicating this further, reproductive organs require localized cooling to maintain optimal temperatures for spermatogenesis and fetal development.^{4,10} Achieving all of these goals necessitates highly dynamic regulation of blood flow and precise control of vascular function, allowing marine mammals to fine-tune the distribution of heat and oxygen in response to environmental conditions and internal physiological needs.

Evolutionary perspectives

Loss of the scrotum

Lack of scrotum in many marine mammals is widely regarded as an evolutionary adaptation to life in aquatic environments. Retaining testes within the body cavity contributes to a streamlined body shape, which reduces drag and enhances swimming efficiency, an essential feature for animals that rely on speed and maneuverability for foraging, predator avoidance, and long-distance travel.³⁹ Additionally, internal placement of reproductive organs provides protection against the pressures and mechanical stresses associated with deep diving, where external structures could be vulnerable to compression or injury.³⁹ By integrating the testes within the torso, marine mammals maintain reproductive functionality while minimizing interference with hydrodynamics. This adaptation illustrates a

Table. Comparative reproductive thermoregulation strategies among marine mammal taxa

Taxonomic group	Testicular position	Scrotum presence	Primary male thermoregulatory mechanisms	Female reproductive thermoregulation	Blubber characteristics	Peripheral heat exchange structures	Degree of vascular specialization	Relationship with diving physiology	Representative examples
Cetaceans (whales, dolphins, porpoises)	Fully internal abdominal testes	Absent	Extensive counter-current heat exchange via retia mirabilia; cooling through venous return from dorsal fin, flukes, and flippers; dynamic blood flow redistribution	Uterine vascular countercurrent exchange systems protect fetal thermal stability and dissipate fetal metabolic heat	Thick, highly stratified blubber with strong insulatory properties; regional heterogeneity present	Dorsal fins, flukes, and flippers function as thermal windows with high vascularization and reduced insulation	Highly developed retia mirabilia and dense vascular plexuses surrounding reproductive organs	Strong integration with dive-induced vasoconstriction and oxygen conservation mechanisms	Dolphins, baleen whales, sperm whales
Phocid pinnipeds (true seals)	Primarily abdominal or inguinal; variable depending on reproductive state and season	True scrotum absent	Countercurrent vascular exchange; conductive cooling during haul-out; seasonal modulation of perfusion and testicular position	Vascular heat exchange supports fetal protection during prolonged fasting and aquatic exposure	Thick blubber layer adapted for prolonged cold-water immersion	Hind flippers and skin surfaces contribute to heat exchange during terrestrial haul-out	Moderate to highly developed vascular exchange systems	Diving-induced peripheral vasoconstriction influences reproductive perfusion and heat exchange	Elephant seals, harbor seals
Otariid pinnipeds (sea lions, fur seals)	Inguinal or near-abdominal testes with greater positional flexibility	Rudimentary or absent scrotal structures	Combination of vascular exchange and conductive cooling during terrestrial periods; environmental exposure contributes to thermal regulation	Uterine thermal regulation assisted by vascular perfusion and behavioral thermoregulation	Blubber generally thinner than in phocids but regionally variable	Flippers act as major heat dissipating surfaces during terrestrial activity	Moderate vascular specialization	Thermoregulatory balance influenced by alternating aquatic and terrestrial lifestyles	California sea lions, fur seals
Sirenians (manatees, dugongs)	Internal abdominal testes	Absent	Internal vascular cooling mechanisms; less specialized than cetaceans; reliance on stable, warm-water habitats	Vascular regulation of uterine temperature with lower thermal gradients due to warm environments	Thick but less regionally specialized blubber compared to cold-water taxa	Flippers contribute modestly to heat exchange	Moderate vascular specialization	Reduced thermal stress due to shallow warm-water habitats and limited diving capacity	Manatees, dugongs

(Continued)

Table. (Continued)

Taxonomic group	Testicular position	Scrotum presence	Primary male thermoregulatory mechanisms	Female reproductive thermoregulation	Blubber characteristics	Peripheral heat exchange structures	Degree of vascular specialization	Relationship with diving physiology	Representative examples
Sea otters	External or semi-external testes within scrotal region	Present	Thermoregulation more similar to terrestrial mammals; scrotal cooling supplemented by behavioral thermoregulation	Fetal thermal regulation supported primarily through metabolic and behavioral mechanisms	Minimal blubber; insulation primarily provided by dense fur	Limbs and extremities contribute to heat dissipation	Limited reproductive vascular specialization compared to fully aquatic mammals	High metabolic rate compensates for aquatic heat loss	Sea otters
Polar bears (semi-aquatic marine-associated mammals)	External scrotal testes	Present	Scrotal cooling mechanisms similar to terrestrial mammals; behavioral and vascular thermoregulation	Maternal insulation and denning behavior support fetal thermal stability	Thick adipose insulation beneath skin but not true marine blubber specialization	Paws and sparsely haired regions facilitate heat exchange	Limited specialized reproductive vascular exchange	Thermoregulation less tightly coupled to diving physiology	Polar bears

trade-off between traditional external cooling mechanisms, like a scrotum, and the physical demands of an aquatic lifestyle, highlighting the complex interplay among reproduction, thermoregulation, and locomotion in these species.^{40,41}

Emergence of vascular adaptations

The evolution of specialized vascular heat-exchange systems may have facilitated reproductive function following testicular internalization during adaptation to aquatic environments.^{9,12,14} These vascular networks provide precise control over localized temperatures, allowing sensitive reproductive organs to remain within optimal thermal ranges despite being retained internally. Beyond localized cooling, countercurrent systems are integrated with other physiological processes, including circulation, oxygen delivery, and metabolic heat management, enabling a coordinated response to environmental and internal demands.^{31,32} Furthermore, these adaptations enhance overall efficiency in cold aquatic environments by conserving metabolic heat while simultaneously preventing overheating of reproductive tissues.^{13,23} By balancing heat retention and targeted cooling, countercurrent heat exchange exemplifies an elegant evolutionary solution that supports reproductive success, survival, and energy efficiency in the thermally challenging habitats occupied by marine mammals.^{10,26}

Convergent evolution

Similar thermoregulatory strategies have independently evolved across diverse marine mammal lineages, providing a clear example of convergent evolution.^{28,31,42} Despite differences in ancestry, several species (e.g. cetaceans, pinnipeds, sirenians) have developed comparable adaptations, like internal testes, countercurrent heat exchange systems, and specialized vascular networks, to cope with the thermal challenges of aquatic environments.^{26,31,32,34} These shared features suggest that similar selective pressures, including cold water, high heat conductivity, and the need to maintain reproductive functions, have driven the evolution of analogous solutions.⁴¹ Convergent evolution in this context highlights how environmental demands can shape physiological systems in remarkably similar ways, even among species with distinct evolutionary histories.⁴³

Ecological and environmental implications

Climate change

Rising ocean temperatures pose substantial challenges to reproductive thermoregulation in marine mammals, potentially impacting male and female reproductive success.^{44,45} Elevated water temperatures can reduce the efficiency of heat dissipation mechanisms (e.g. countercurrent heat exchange systems, vascular cooling networks) making it more difficult for animals to maintain optimal temperatures in reproductive organs. This inefficiency may lead to localized overheating of testes or uterus, compromising spermatogenesis or fetal development.^{10,12,14} Additionally, warmer water can increase overall metabolic stress, forcing marine mammals to expend more energy on maintaining core body temperature and thermoregulatory balance.^{13,46,47} Over time, these physiological stresses may negatively affect reproductive output, reduce fertility, and impair population growth. Understanding how rising ocean temperatures influence these processes is therefore critical for assessing species resilience and informing conservation strategies in a warming climate. Although reproductive

consequences of marine heatwaves have been documented in some populations, direct evidence linking these effects to failure of reproductive-organ thermoregulation remains limited.

Human impacts

Human activities have profound indirect effects on thermoregulation in marine mammals, influencing their ability to maintain optimal body and reproductive temperatures. Pollution (e.g. chemical contaminants, plastics) can reduce the availability and quality of prey, forcing animals to expend additional energy searching for food.^{48,49} This increased energetic demand can elevate metabolic heat production that may challenge their internal cooling mechanisms, particularly for sensitive reproductive organs.^{10,41} Habitat disturbance from shipping, coastal development, and noise pollution can also increase stress levels, triggering physiological responses (e.g. elevated heart rate, blood pressure) that alter normal heat distribution and circulation.^{34,50-52} Furthermore, disruption of normal behavior (e.g. resting, diving, social interaction) can impair the animal's ability to use behavioral thermoregulation strategies effectively, including movement to cooler or warmer waters or adjusting swimming patterns.⁵³ Anthropogenic stressors may indirectly influence thermal balance through changes in activity, energetic expenditure, habitat use, diving behavior, and peripheral perfusion; however, direct evidence linking these stressors to reproductive-organ temperature remains scarce.

Conservation considerations

Understanding thermoregulatory mechanisms in marine mammals is essential for effectively predicting how species will respond to environmental changes, including climate warming, habitat alteration, and shifts in prey availability.⁵² By comprehending how animals maintain reproductive and core body temperatures under varying conditions, researchers can anticipate potential physiological stressors and vulnerabilities that may arise as ecosystems change. This knowledge is also critical for developing targeted conservation strategies, such as identifying critical habitats, designing protected areas, and mitigating human-induced disturbances that may disrupt thermoregulation.^{41,44,54} Additionally, insights into these mechanisms allow for better management of vulnerable populations by informing interventions that support reproductive success, maintain population stability, and enhance resilience. Overall, a detailed understanding of thermoregulatory processes provides a foundation for preserving marine mammal health and ensuring the long-term survival of species in increasingly dynamic and challenging aquatic environments.⁵⁵

Methodological approaches in research

Anatomical studies

Research on reproductive thermoregulation in marine mammals often relies on a combination of anatomical and post-mortem approaches, particularly given the challenges of studying these species in their natural aquatic environments.^{10,26,56,57} Examination of stranded or deceased animals provides invaluable opportunities to observe internal structures that are otherwise inaccessible, allowing researchers to gather detailed data on organ placement, vascular arrangements and overall morphology.^{58,59} Dissection and advanced imaging techniques (e.g. MRI, CT scans) enable precise visualization of specialized vascular networks, including countercurrent heat exchange systems and their relationship to

reproductive organs.⁵⁸⁻⁶¹ Histological analysis further enhances understanding by revealing tissue-level adaptations (e.g. density and structure of blood vessels) surrounding testes or uterus.^{36,62} Together, these methods provide critical insights into the mechanisms of reproductive thermoregulation, offering a foundation for comparative studies, evolutionary interpretations and the development of conservation strategies for marine mammal populations.

Physiological measurements

Studies of live marine mammals rely on noninvasive and minimally disruptive techniques to investigate reproductive thermoregulation while ensuring animal welfare. Researchers frequently employ noninvasive monitoring methods, such as infrared thermography or telemetry, to measure surface and internal temperatures without physically restraining the animals.⁶²⁻⁶⁴ Temperature sensors that can be attached externally or inserted temporarily provide real-time data on changes in body and organ temperatures under varying environmental and behavioral conditions.^{65,66} Additionally, blood flow measurements, obtained through Doppler ultrasonography or other imaging techniques, allow scientists to track the movement of cooled or warmed blood through vascular networks, including countercurrent heat exchange systems, and assess how circulation supports localized cooling of reproductive organs.¹⁰ Collectively, these approaches provide dynamic, high-resolution insights into thermoregulatory processes in living animals, complementing anatomical studies and enhancing understanding of physiological adaptations in natural and experimental contexts.

Ethical considerations

Given the conservation status of many marine mammal species, research on reproductive thermoregulation must be conducted with the highest ethical standards to minimize harm and disturbance.⁶⁷ Scientists prioritize noninvasive or minimally invasive methods whenever possible (e.g. remote monitoring, temperature sensors, imaging techniques) to collect accurate data without jeopardizing the animals' health or behavior.⁶⁸ Ensuring ethical treatment also involves careful planning of study design, adherence to regulatory guidelines, and consideration of the animals' natural behaviors and habitats.⁶⁹ By balancing scientific inquiry with conservation and welfare concerns, researchers can gather critical information while protecting vulnerable populations and supporting long-term species survival.

Future directions

Technological advances

Emerging technologies are poised to revolutionize the study of reproductive thermoregulation in marine mammals by providing more precise and dynamic insights than ever before.¹⁰ Advanced tools now allow real-time monitoring of internal temperatures, offering continuous data on how reproductive organs respond to environmental changes, diving behavior, or metabolic activity.⁶²⁻⁶⁶ Improved imaging techniques, including high-resolution MRI, CT scans and 3D vascular mapping, enable researchers to visualize intricate vascular networks such as countercurrent heat exchange systems with unprecedented clarity.⁵⁸⁻⁶¹ These technologies also facilitate a better understanding of dynamic physiological processes, including

blood flow redistribution, heat exchange efficiency, and the interplay between metabolic rate and temperature regulation. By integrating these technological advances, scientists can study live animals in more naturalistic conditions, enhancing our understanding of marine mammal thermoregulation and supporting conservation strategies in a changing climate.

Interdisciplinary research

Integrating multiple scientific disciplines (e.g. physiology, ecology, evolutionary biology) provides a comprehensive framework for understanding thermoregulation in marine mammals.^{15,26,34} Physiological studies reveal the mechanisms by which reproductive and core body temperatures are maintained, including vascular adaptations, countercurrent heat exchange systems and behavioral strategies.^{10,41} Ecology contextualizes these findings by examining how environmental factors, (e.g. water temperature, prey availability, habitat use) influence thermoregulatory demands and constraints.^{26,70} Evolutionary biology offers insights into how these adaptations have arisen over time, highlighting patterns of convergent evolution and the selective pressures that shaped internal and behavioral thermoregulatory strategies.^{71,72} By combining these perspectives, researchers can develop a holistic understanding of how marine mammals balance heat retention, reproductive cooling, and survival, leading to more accurate predictions about species' responses to environmental change and informing effective conservation and management strategies.

Applications to other species

Insights gained from studying thermoregulatory mechanisms in marine mammals have broad applications beyond marine biology.³⁰ Understanding how these animals maintain reproductive and core body temperatures in cold, high-conductivity aquatic environments can inform studies of other aquatic or semi-aquatic species, helping researchers identify similar physiological adaptations and evolutionary strategies.^{26,41} In biomedical research, these findings may provide models for human thermoregulation,⁷³ offering potential applications in treating reproductive disorders, managing hyperthermia, or designing therapies that mimic natural cooling systems. Additionally, marine mammal adaptations inspire engineering and bioinspired design, such as efficient heat exchange systems, thermal management technologies, and energy-conserving devices. By translating biological principles into applied contexts, research on marine mammal thermoregulation not only enhances our understanding of animal physiology but also contributes to technological innovation and practical solutions to challenges in medicine, conservation, and engineering.⁷⁴⁻⁷⁶

Knowledge gaps and research limitations

Despite substantial progress in understanding marine mammal thermoregulation, important knowledge gaps remain. Quantitative data on in vivo temperature gradients, vascular perfusion rates, and heat flux dynamics remain limited. Integration between thermoregulation and diving physiology is also incomplete, particularly under variable ecological conditions. Furthermore, female reproductive thermoregulation is less extensively studied than male systems, resulting in a male-biased knowledge framework. Environmental uncertainty, including spatial and temporal variability in ocean temperature, pollution impacts, and prey distribution shifts,

further limits predictive capacity. Addressing these gaps will be essential for improving mechanistic understanding and conservation applications.

Conclusion

Marine mammals have evolved diverse anatomical, vascular, physiological, and behavioral mechanisms that reconcile the competing demands of whole-body thermal conservation and reproductive function in aquatic environments. In cetaceans, specialized vascular arrangements and countercurrent heat exchange provide particularly strong evidence for regulation of internally located testes, whereas reproductive thermoregulatory mechanisms in pinnipeds, sirenians, and other marine-associated mammals are more variable and, in several cases, less completely characterized. Female reproductive thermoregulation remains especially understudied, and the functional significance of uterine vascular arrangements requires further in-vivo investigation. Future studies integrating direct temperature measurement, blood-flow assessment, biolaging, imaging, and environmental data will be essential to determine how reproductive thermal balance varies among taxa and responds to diving, reproductive state, and changing ocean conditions. Such information will clarify both the evolutionary physiology of marine mammals and their reproductive resilience in a warming environment.

Conflict of interest

Authors declare that there are no conflicts of interest related to this work.

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Authors' contributions and declaration

Authors contributed equally to this work; authors read and approved the final submission.

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