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Diving into the deep: The effects of vertical gradients on the diving behavior and ecophysiology of deep-diving marine megafauna

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DIVING INTO THE DEEP: THE EFFECTS OF VERTICAL GRADIENTS ON THE DIVING BEHAVIOR AND ECOPHYSIOLOGY OF DEEP-DIVING MARINE MEGAFAUNA

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Arina B. Favilla

September 2023

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Table of Contents

List of Tables

List of Figures

Abstract

Diving into the deep:
The effects of vertical gradients on the diving behavior and ecophysiology of deep-diving marine megafauna

by

Arina B. Favilla

Studying the movement ecology and ecophysiology of marine megafauna is critical for understanding how increased stressors will overlap with species distribution and affect species behavior, which will ultimately have ecological consequences. Warming water temperatures and ocean deoxygenation will likely alter habitat suitability for marine megafauna either directly through physiological impact or indirectly through shifting prey distributions. Previous studies have shown that the horizontal distribution of marine predators can be explained by the temperature-dependence of predation success and metabolism. However, temperature and oxygen vary drastically in the vertical dimension. These vertical gradients influence metabolism, behavior, and predation success but remain understudied despite advances in biotelemetry that permit investigating movement in four dimensions (i.e., 3D space and time). To address this gap, my dissertation investigates how physiological demands and environmental factors, specifically temperature and oxygen, influence the diving behavior and ecophysiology of marine megafauna.

First, we reviewed current knowledge on the thermoregulatory strategies of air-breathing marine vertebrates and synthesized the complementary contributions of lab and field studies (Chapter 1). We then focused on reviewing the dynamic role of blubber and peripheral perfusion for marine mammal thermoregulation and demonstrated the potential of physio-logging to advance our studies of thermoregulation in an ecologically relevant context (Chapter 2). Using northern elephant seals (*Mirounga angustirostris*) as a model species, we performed at-sea experiments with custom-made biologgers and examined novel physiological data showing fine-scale changes in thermal responses while diving (Chapter 3). Unlike water temperature, dissolved oxygen data is limited resulting in few efforts to understand how oxygen affects diverse marine megafauna, particularly the indirect effects on air-breathers. We investigated the diving and foraging behavior of an air-breathing mesopelagic predator in relation to dissolved oxygen and found that elephant seals primarily use the oxygen limited zone rather than the oxygen minimum zone as previously hypothesized (Chapter 4). Overall, this dissertation contributes a new ecologically relevant understanding of marine megafauna movement in three dimensions. Expanding and synthesizing such studies across various marine taxa is critical for understanding how changing ocean conditions (e.g., warming waters and ocean deoxygenation) will differentially affect marine species and ultimately ecosystem structure and function.

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Thank you to my advisor, Dan Costa, for accepting me into The Costa Lab straight from undergrad and giving me so many opportunities to grow as a scientist, both at home in Santa Cruz and around the world. I always thought I'd end up working with sea turtles or sharks for my PhD, but working with elephant seals has been amazing. Thank you for introducing me to the world of lower-case-p physiology—what we like to call ecophysiology. You taught me that if we find what we didn't expect in our data, it's often because something more interesting is going on than what we imagined. I look forward to continuing to collaborate with you.

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Arina

Statement of Contribution

The text of this dissertation includes reprints of the previously published material:

Chapter 1:

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Chapter 2:

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This manuscript was published open-access under the terms of the Creative Commons Attribution License (CC BY). This work was original creation of Arina Favilla (ABF) with contributions from co-authors. ABF carried out the literature review, conducted the research, and wrote the manuscript. MH assisted with dry lab work and data collection. DPC assisted in project conceptualization and design. MH and DPC edited the manuscript. All authors approved the submitted version before publication. Supplementary materials from Favilla et al. (2022) were included in Appendix A2.

Introduction

Broad Context

Movement ecology aims to understand why organisms move and what constrains their movement, which ultimately shapes their ecology (Hays et al., 2016; Nathan et al., 2008; T. A. Patterson et al., 2017). Animal movement occurs over a broad range of spatiotemporal scales and is driven by intrinsic and extrinsic factors. The relative importance of these factors and how they interact to influence animal behavior is key to understanding species' movement patterns and ecophysiology (Williams et al., 2019).

The marine environment provides a complex 3D space for animal movement (Hussey et al., 2015). While some terrestrial counterparts may exist (e.g., rain forest canopies), the lack of barriers and the extent of vertical stratification in the marine environment is noteworthy. While large-scale horizontal movement across ocean basins is ubiquitous (Block et al., 2011; Costa et al., 2012; Horton et al., 2017), vertical movement is physiologically constrained by steep environmental gradients. Of particular interest are temperature and oxygen because of their vital and interacting role in physiology and function (Pörtner & Farrell, 2008; Pörtner & Gutt, 2016). An aquatic environment imposes additional challenges associated with thermoregulation and oxygenation because water is 25 times more conductive than air and holds less than 3% of the oxygen compared to an equivalent volume of air (assuming 100% saturation). Whether endothermic or ectothermic, air-breathing or water-breathing, all marine megafauna share the same aquatic environment; however, the physiological challenges imposed by temperature and oxygen gradients differ in how they influence vertical movement and distribution of different species.

Due to the thermally challenging nature of the marine environment, marine megafauna have various adaptations to maintain thermal balance while encountering steep temperature gradients during vertical movement. Endothermic megafauna (i.e., marine mammals) have insulation that helps maintain their high core body temperature while immersed in cold water. Physiological adaptations also allow fine-scale control of heat distribution within the body and heat transfer across the body (Castellini, 2018; Davis, 2019). Similarly, some ectotherms have evolved unique anatomical structures that allow for regional endothermy (J. C. Patterson et al., 2011; Watanabe et al., 2015), but all ectotherms depend to some extent on behavioral thermoregulation where they exploit different temperature niches in the water column (Carey & Scharold, 1990; Coffey et al., 2017; Dewar et al., 2011, 2018; Graham & Dickson, 1981; Holland et al., 1992; Wallace et al., 2005).

The extent to which thermoregulation dictates a species' vertical distribution will also depend on the influences of other factors, such as oxygen. The vertical movement of air-breathers is constrained by their onboard oxygen supply, and their need to return to the surface to breathe results in discrete dives. The cardiovascular adjustments associated with the dive response in addition to enhanced oxygen storage capacities allows for impressive dive records in some species (Ponganis, 2015). On the other hand, water-breathers rely on dissolved oxygen in the water, which limits their vertical movement to waters with sufficient oxygen content. Species vary in their low oxygen tolerance, with some showing divergent adaptations that enable greater hypoxia tolerance compared to closely-related species (Lowe et al., 2000; Wootton et al., 2015). The amount of dissolved oxygen in the water and the rate of oxygen utilization are also affected by temperature, which leads to interacting effects of temperature and oxygen that influence vertical distributions as well as performance limits (Pörtner & Gutt, 2016). While both air-breathers and water-breathers may exceed their usual limits by performing anaerobically for short durations, this strategy is not sustainable in the long term (Brill, 1994; Costa & Favilla, accepted).

Since the primary reasons to dive seem to be for foraging followed by avoidance of predators (Aguilar de Soto et al., 2020; Beltran et al., 2021; Heithaus & Frid, 2003; Thompson & Fedak, 2001), the distribution of prey and predators is another extrinsic factor that interplays with the physiological constraints imposed by the environment to determine the vertical habitat niche of marine species. Vertical distributions of marine megafauna will determine interspecific overlap and the potential for trophic and competitive interactions (Hays, 2003; Heithaus & Frid, 2003; Vetter et al., 2008). Previous studies have shown that the horizontal distribution of marine predators can be explained by the temperature-dependence of predation success and metabolism (Cairns et al., 2008; Grady et al., 2019). However, the vertical dimension, where both temperature and oxygen will influence metabolism, behavior, and predation success, has yet to be integrated into our understanding of marine megafauna distributions and their ecological consequences (see Deutsch et al., 2015, 2020 for lower marine trophic levels).

Studying the ecophysiology of marine megafauna is critical for understanding how stressors, such as anthropogenic disturbance and changing ocean conditions, will affect species behavior and distribution, which will ultimately have ecological consequences. Both warming water temperatures and ocean deoxygenation will likely alter habitat suitability for marine megafauna either directly through physiological impact or indirectly through shifting prey distributions or ecosystem structure and function (Albouy et al., 2020; Doney et al., 2012; Gilly et al., 2013; Grose et al., 2020; Hazen et al., 2013; Prince & Goodyear, 2006; Simmonds & Isaac, 2007; Stramma et al., 2012; Worm et al., 2005). Of 328 studies reviewed by Melo-Merino et al. (2020) that used ecological niche models or species distribution models, 240 included temperature as an environmental descriptor variable whereas only 36 considered dissolved oxygen in their models. Moreover, despite the large gradients of these variables in the vertical dimension, most studies have focused on predicting how climate change will impact the horizontal distribution of marine megafauna, leaving changes to their vertical distribution relatively understudied (Melo-Merino et al., 2020; Santana-Falcón & Séférian, 2022).

Dissertation Summary

By analyzing vertical movement in relation to temperature and oxygen, this dissertation aims to investigate the interplay between physiological demands and environmental influences on the diving behavior of marine megafauna. First, we reviewed current knowledge on the thermoregulatory strategies of air-breathing marine vertebrates to synthesize what is understood about how temperature and thermal requirements interact with other physiological demands to affect the diving behavior of different taxa (Chapter 1). Air-breathers, unlike water-breathers, are limited in their ability to select and follow isotherms, and thus are faced with the challenge of maintaining thermal balance while encountering steep temperature gradients as they dive and forage. We then focused on marine mammal thermoregulation and reviewed the dynamic role of peripheral perfusion, which we highlighted is important to study in an ecologically relevant context (Chapter 2). To enhance our understanding of how air-breathing endotherms coordinate thermoregulation with the dive response, we performed at-sea experiments on one of the deepest diving marine mammals, the northern elephant seal (*Mirounga angustirostris*), to examine fine-scale changes in thermal responses while diving (Chapter 3).

The relative ease of obtaining water temperature data—via *in situ* measurements or modelled results—allows for such fine-scale analyses of diving behavior as well as broad-scale analyses of global species movement patterns and distribution relative to water temperature (e.g., Adamczak et al., 2020; Cairns et al., 2008; Grady et al., 2019; Kaschner et al., 2006; Worm et al., 2005). In contrast, the paucity of oxygen data has led to a comparably limited understanding of how oxygen affects diverse marine megafauna, particularly the indirect effects on air-breathing top predators, despite its potential to affect species movement and alter trophic interactions and ecosystem structure. We used oxygen data available from ocean databases to investigate the influence of oxygen on the diving and foraging behavior of an air-breathing top predator in the mesopelagic zone (Chapter 4).

Advances in biotelemetry have provided the opportunity to investigate movement in four dimensions (i.e., 3D space and time), vastly improving our understanding of marine megafauna movement ecology (Bograd et al., 2010; Evans et al., 2012; Williams et al., 2020). Additionally, animal-borne instruments with physiological and environmental sensors have revolutionized field physiology and given us a new ecophysiological perspective on animal movement (Chmura et al., 2018; Costa & Sinervo, 2004; Whitford & Klimley, 2019; Wilmers et al., 2015). Overall, this dissertation seeks to demonstrate the importance of integrating behavioral, physiological, and environmental variables in the vertical dimension to gain a more ecologically relevant understanding of marine megafauna movement patterns and distribution.

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Chapter 1

Thermoregulatory strategies of diving air-breathing marine vertebrates: A review

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1.1 Abstract

The aquatic habitat of marine “air-breathing” vertebrates provides a significant thermoregulatory challenge due to the high thermal conductivity of water. In addition to temperature changes across their range, air-breathing vertebrates experience temperature changes on the timescale of seconds to minutes as they perform dives to access two critical resources: air at the surface and food at depth. In response to these challenges, air-breathing vertebrates have developed morphological and physiological adaptations that align with their life histories and phylogenies and contribute to homeostasis. However, the physiological and behavioral mechanisms used to maintain thermal balance while diving is still poorly understood. The cardiovascular system is integral to the physiological responses associated with the dive response, exercise, digestion, and thermoregulation. The adjustments required to meet one physiological demand may not be compatible with another and can result in a potential conflict between the various physiological demands imposed on air-breathing divers. We reviewed the literature on thermoregulation while diving in an effort to synthesize our current understanding of the thermoregulatory strategies of diving air-breathing marine vertebrates. Studies have demonstrated that

thermoregulatory strategies can involve the temporal separation of two conflicting responses, a compromise in the performance of one response over another, or coordination of synergistic responses. We hope that a review and synthesis of both laboratory and field studies will stimulate future research efforts at the intersection of thermoregulation and diving physiology. Expanding the use of physiological biologgers, particularly to understudied species, will enhance our understanding of how these animals coordinate various physiological demands to maintain homeostasis in a thermally challenging environment.

1.2 Introduction

Marine vertebrates can be categorized as either “air-breathers” or “water-breathers”. While they all share the same aquatic environment and its associated challenges, air-breathers are faced with an additional challenge: the spatial separation of two critical resources, air and food (I. L. Boyd, 1997; Rosen et al., 2007; Whittow, 1987). Moreover, the implications for aquatic vertebrate thermal physiology are significant as heat transfers about 25 times faster in water than in air. Thus, the avenues of heat exchange that animals can use to control their thermal balance are more limited in water.

Multiple independent transitions from a terrestrial to marine life were made possible by developing a concomitant, often converging, suite of morphological, physiological, and behavioral adaptations that allow marine vertebrates to meet their thermoregulatory needs (Kelley & Pyenson, 2015; Pyenson et al., 2014; Reidenberg, 2007). In addition to spanning the endothermy-ectothermy spectrum, marine air-breathing vertebrates have different lifestyles that expose them to a wide range of thermal environments. While some have made the full transition to an aquatic lifestyle, others are tied to the land for reproduction and molting (Costa, 1991; Davenport, 1997; Schreiber & Burger, 2002), which exposes them to the contrasting thermal demands imposed by air and water. Some species, like the Galápagos fur seal, *Arctocephalus galapagoensis*, experience an extreme dichotomy in their thermal environments that requires different thermoregulatory strategies: dissipating excess heat while breeding on land in warm climates and conserving heat while foraging in cold waters (Chilvers, 2018; Costa & Maresh, 2018). Additionally, some migrate long distances from tropical breeding to polar foraging grounds where sea surface temperatures can vary from 30°C to -2°C (Corkeron & Connor, 1999; Guerrero & Rogers, 2019). While this large shift in their thermal environment occurs over weeks to months, marine vertebrates also experience significant temperature changes on the timescale of seconds to minutes while diving. The exceptions are shallow divers that remain in the mixed layer or polar species that are exposed to cold temperatures throughout the water column. Thus, recognizing the temporal and spatial range of thermal challenges faced by marine air-breathers is essential when considering the suitability of their thermal adaptations for maintaining homeostasis (Figure 1.1).

This review synthesizes our current understanding of the thermoregulatory strategies of marine air-breathing vertebrates in light of the physiological challenges imposed by diving. We have selected lab and field studies that provide critical insights into the diving and thermal capabilities of marine air-breathers and how they operate in a physiologically challenging environment. To encourage field research to confirm the ecological relevance of lab-based findings in natural settings (Costa & Sinervo, 2004; Rosen et al., 2017), we summarize the approaches currently available to study the thermal physiology of free-ranging divers and evaluate their applicability to different taxa. Finally, we highlight gaps in our knowledge to direct future efforts at the intersection of diving physiology and thermoregulation, which will hopefully lead to a deeper understanding of how air-breathing marine vertebrates maintain homeostasis.

1.3 Diverse Divers Face a Common Challenge

Marine “air-breathing” vertebrates—referred to as air-breathers or divers in this review—span three classes of tetrapods (i.e. Mammalia, Aves, and Reptilia), all of which reinvaded the marine environment at different times and thus have adapted to marine living within the constraints of their different phylogenies (Kelley & Pyenson, 2015; Pyenson et al., 2014). Given the perspective of this review, we chose a particular subset of marine air-breathers that are diving species and cover a broad range of thermal strategies and habitats (Figure 1.2). This group provides the opportunity to examine whether there is convergence in how the different ecologies and life histories shape physiology and behavior.

Within marine mammals, the most diverse and well-suited to marine life are the fully aquatic cetaceans. While both cetaceans and sirenians are fully aquatic, only cetaceans span tropical to polar waters, as sirenians are limited to tropical latitudes (Figure 1.2). Sirenians are the only herbivorous marine mammals, which has important implications for their thermoregulatory abilities. Their diet constrains them to low metabolism, which limits their capacity for thermogenesis and therefore increases their cold sensitivity (Domning, 2018; Gallivan et al., 1983; Gallivan & Best, 1980). Pinnipeds display a broad spectrum of morphologies for thermal adaptations that align with their amphibious lifestyle and different breeding strategies that dictate the frequency and duration of their foraging trips and the overall proportion of time they spend at sea (Berta, 2018; Chilvers, 2018; Hammill, 2018). Species of the other two extant taxonomic groups of marine mammals—mustelids and ursids—face some unique extreme challenges: sea otters, *Enhydra lutris*, are the smallest marine mammal and are found in cold temperate to subarctic waters (Kenyon, 1969) whereas polar bears, *Ursus maritimus*, spend most of their time on Arctic sea ice, a rapidly diminishing habitat (Rode & Stirling, 2018).

Seabirds are endothermic marine vertebrates that are all amphibious, a constraint likely associated with oviparity. Seabirds are defined as those species that feed in the marine environment and thus spend most of their lives above, on, or diving into the sea (Schreiber & Burger, 2002). However, in this review we only consider those species that dive, of which there are four avian orders: Sphenisciformes, Procellariiformes, Charadriiformes, and Pelecaniformes (Ponganis, 2015). Seabirds have diverse adaptations to the marine environment that suite their respective ecologies. They generally either use their wings or feet for propulsion and employ plunge or pursuit diving to feed (Ellis & Gabrielsen, 2002). Their relative efficiencies as flyers and divers are dictated by their anatomy and morphology, including body density, wing loading, as well as plumage wettability (Lovvorn & Jones, 1994). This trade-off in efficiency between the two modes of locomotion has thermal and ecological implications for their horizontal (i.e. distance from breeding colony) and vertical (i.e. diving depth) ranges (Figure 1.1). For example, the most efficient flyers, the albatrosses, soar long distances to reach productive waters to feed at the surface. In contrast, penguins have lost the ability to fly, but with paddle-like wings, some can dive down to 500 meters but have much more limited horizontal movements (Ellis & Gabrielsen, 2002; Prince et al., 1994).

In contrast to marine mammals and seabirds, marine lizards, sea snakes and sea turtles are ectotherms and mainly rely on behavior and habitat selection to regulate their body temperature. There is only one species of totally marine iguana, *Amblyrhunchus cristatus*, and it is in the family Iguanidae (Dawson et al., 1977). There are 70 species of sea snakes that are entirely marine as they are mostly ovoviviparous and are able to give birth at sea (J. C. Murphy, 2012). Due to their ectothermy and small size, sea snakes are limited to narrow thermal habitats, which constrains their thermoregulatory abilities. Furthermore, they employ cutaneous respiration while diving, which curtails the physiological restriction faced by strictly air-breathing divers and thus will not be considered further (Heatwole et al., 2012; Udyawer et al., 2016). As such, sea turtles will serve as the representative group of marine reptiles for this review.

All sea turtles are in the family Cheloniidae, except the leatherback turtle, *Dermochelys coriacea*, the only extant species of the family Dermochelyidae, which has many unique characteristics that set it apart from the hard-shelled turtles. Sea turtles are amphibious as they must nest on land, but only female sea turtles come ashore after mating at sea to bury a clutch of eggs, which are left unattended to hatch into precocial young (Davenport, 1997). Egg-laying commonly occurs at night and allows sea turtles to minimize time spent on land where they are more vulnerable to heat stress (Meek & Avery, 1988; Spotila & Standora, 1985). As reptiles, they have temperature-dependent sex determination, which could result in skewed sex ratios as temperatures on beaches are affected by rising global temperatures (Hamann et al., 2013).

1.3.1 Adaptations for diving with a finite oxygen supply

All air-breathing divers face the dilemma of needing to forage underwater, where they do not have access to an exogenous source of oxygen. Thus, the key to being an efficient diver is optimizing the utilization of their ‘on-board’ oxygen supply. This is accomplished by a suite of cardiovascular adjustments that characterize the dive response, which includes apnea, bradycardia, and peripheral vasoconstriction (for reviews on diving physiology, see Costa, 2007; Hochachka, 2000; Kooyman & Ponganis, 2017; Ponganis, 2015). The intensity of these cardiovascular adjustments depends on the circumstances of the dive, supporting the concept of a plastic rather than an all-or-none response (Butler & Jones, 1997; Elmegaard et al., 2016). Ultimately, differences in physiology and ecology dictate species-specific routine diving behavior and performance (Figure 1.3). Here, a brief overview of diving adaptations and energetics is presented with emphasis on key differences between marine mammals, seabirds, and sea turtles.

1.3.1.1 Not all oxygen stores are equal

Oxygen is stored in the lungs, blood, and muscle, as well as a small fraction in the brain (via neuroglobin; T. M. Williams et al., 2008). The diver's oxygen storage capacity is a function of the size of these principal compartments (i.e., lung volume, blood volume, and muscle mass) as well as the concentrations and characteristics of the oxygen-binding proteins in the blood and muscle (i.e., hemoglobin and myoglobin, respectively). The aerobic diving capacity is, therefore, dictated by the size of oxygen stores, which also scales with body mass, and its rate of utilization (Ponganis et al., 2011). The magnitude and distribution of these oxygen stores vary among species (Figure 1.4). For example, lung oxygen stores account for less than 30% of the total oxygen stores in marine mammals. In contrast, sea turtles rely heavily on their respiratory oxygen stores (Lutcavage & Lutz, 1991). Seabirds have lung oxygen stores roughly equal to their muscle and blood oxygen stores combined (Butler et al., 1984; Ponganis, 2015). Interesting outliers within their respective groups are: sea otters, with larger lung oxygen stores (45% of total); leatherback turtles, with larger muscle and blood oxygen stores due to relatively small lung volumes (Lutcavage et al., 1992); and penguins, with a smaller relative respiratory oxygen store due to increased oxygen affinity of hemoglobin, which allows them to carry more oxygen in their blood at lower partial pressures (Ponganis, 2015).

Increased reliance on respiratory oxygen stores has important implications for diving, including buoyancy and pulmonary gas exchange. The air in the respiratory system—or any other part of the body—will increase the diver's buoyancy at the surface and contribute to the high initial cost of descent, which decreases as air is compressed with depth. Some species—usually those less reliant on lung oxygen stores—minimize buoyancy by diving after exhalation (e.g., phocids, Figure 1.4; and some ducks, which were not included in this review). Some species of penguins, cormorants, and otariids that dive upon inhalation regulate their lung air volumes to match the oxygen requirements of the dive, showing some anticipatory pre-dive adjustments (Cook et al., 2010; McDonald & Ponganis, 2012; Sato et al., 2002; Wilson, 2003). On the other hand, sea turtles adjust their diving depth to achieve neutral buoyancy with the given lung air volume (Hays et al., 2004; Hochscheid et al., 2003; Minamikawa et al., 2000).

Regardless of their pre-dive respiratory pattern, many species undergo lung collapse past a certain depth, which reduces their risk of pressure-related complications, such as decompression sickness and nitrogen narcosis (Bostrom et al., 2008; Fahlman et al., 2009; Falke et al., 1985; Hooker et al., 2012; Kooyman et al., 1972; McDonald & Ponganis, 2012). Sea turtles undergo lung collapse during forced submergence (Berkson, 1967), but under natural conditions, intermittent perfusion of the lungs allows access to their primary oxygen supply (García-Párraga, Moore, et al., 2018; Hochscheid, McMahon, et al., 2007; Lutz & Bentley, 1985). Continuous gas exchange at depth would increase their susceptibility to decompression sickness by increasing nitrogen absorption in the blood, which would result in bubble formation on the ascent. However, body temperatures lower than those of endotherms by ~10°C increase the solubility of nitrogen in the blood and reduces the risk of bubble formation, ultimately counteracting the effects of gas exchange at depth (Fossette et al., 2010). Moreover, their ability to control pulmonary ventilation-perfusion mismatch minimizes nitrogen uptake while preferentially exchanging oxygen and carbon dioxide. Thus, sea turtles should be more tolerant of decompression sickness during normal diving than endothermic divers (Fossette et al., 2010; García-Párraga et al., 2014; García-Párraga, Lorenzo, et al., 2018; García-Párraga, Moore, et al., 2018). Besides pressure-related injuries, the primary role of blood to transport rather than store oxygen for sea turtles has direct implications for thermoregulation that will be discussed further below (section 2.2.3).

1.3.1.2 Quantifying how limited oxygen affects diving behavior

Quantifying the magnitude, distribution, and utilization of oxygen stores is a prerequisite for understanding the physiological basis of diving ability. The aerobic dive limit (ADL) is the dive duration associated with the threshold where metabolism becomes predominately anaerobic. The physiological basis for this metric is the depletion of muscle oxygen stores and a subsequent rise in blood lactate, a byproduct of anaerobic metabolism (Butler, 2006; Kooyman et al., 1980; Ponganis et al., 2011). While ADLs have only been determined empirically in a few species for which post-dive blood samples were feasible (Kooyman et al., 1980; Ponganis, Kooyman, Baranov, et al., 1997; Ponganis, Kooyman, Starke, et al., 1997; Shaffer et al., 1997; T.

M. Williams, Haun, et al., 1999), estimated ADLs are useful for ecological comparisons of diving abilities (I. L. Boyd & Croxall, 1996; Butler, 2006; Costa et al., 2004; Halsey et al., 2006; Watanuki & Burger, 1999). ADLs are generally calculated using lab measurements of oxygen stores and oxygen consumption rate. ADLs have also been determined behaviorally for wild animals equipped with time-depth recorders, where the majority (95-97%) of dive durations or those that precede routine surface intervals are considered within the ADL (Ponganis, 2015).

A comparison of ADLs to observed dive durations provides a proxy for investigating how often divers operate near their physiological limits in nature (Figure 1.5; I. L. Boyd & Croxall, 1996; Costa et al., 2001, 2004; Green et al., 2005). Because metabolic rates dictate the rate of oxygen utilization, ADL inherently integrates the energetic costs of all physiological demands during a dive, including thermoregulatory costs. However, a better understanding of the extent to which thermoregulatory demands might limit their diving behavior requires disentangling the complex interactions between these physiological responses occurring in a diving animal.

1.3.2 Adaptations for a thermally challenging environment

In addition to diving with a limited oxygen supply, air-breathers must maintain thermal homeostasis in their highly conductive aquatic environment. Even with the constraints of their different life-history strategies and phylogeny, marine vertebrates have converged upon similar thermoregulatory adaptations that include morphological, physiological, and behavioral traits (Reidenberg, 2007) with varying degrees of plasticity.

1.3.2.1 Thermal dynamics across and within an immersed body

Animals are exposed to the environment through their body surface, and heat transfer across the body surface dictates their thermal state. For a homeothermic endotherm, thermal equilibrium is maintained when internal heat production balances heat loss (Scholander, 1955). Endogenous heat production is limited in ectotherms and their ability to store heat and dampen their response to environmental fluctuations will depend on their size (Willmer et al., 2005). Thus, the implications of the body's surface area to volume ratio (SA:V) is relevant for the thermal physiology of both endothermic and ectothermic air-breathing divers.

A common solution to reduce heat loss in the marine environment is to have a small SA:V, which favors large-bodied animals (Gearty et al., 2018; Innes et al., 1990). The largest animals exemplify this trait in each of the taxonomic groups, which all encounter near-freezing water temperatures: blue whales, *Balaenoptera musculus*, emperor penguins, *Aptenodytes forsteri*, and leatherback turtles. Some consider leatherback turtles to be endothermic (Davenport et al., 1990; Goff & Stenson, 1988; Mrosovsky & Pritchard, 1971) while others suggest they use gigantothermy. However, most agree that the endothermic-like state is due to their large size, insulation, muscular thermogenesis, along with careful regulation of peripheral perfusion (Bradshaw et al., 2007; Davenport et al., 1990; Paladino et al., 1990).

While diving, the primary modes of heat transfer are conduction and convection. Both radiation (which is quickly absorbed by water) and respiratory evaporative heat loss are generally limited to when divers are at the surface. Some marine mammals, such as dolphins, exhibit significant cutaneous water loss, which is associated with osmoregulation rather than heat balance (Andersen & Nielsen, 1983; Hui, 1981). As eared seals are amphibious, they have retained functional sweat glands and sweat to regulate heat loss while on land (Khamas et al., 2012; Mauck et al., 2003; Rotherham et al., 2005).

In addition to heat retention or dissipation mechanisms, activity-oriented strategies—the heat increment of feeding (HIF) and exercise—can contribute to thermoregulatory homeostasis by increasing heat production. A prerequisite for either form of thermal substitution is that the ambient temperature must be below the lower critical temperature of the animal, which is not uncommon in the marine environment (Croll & McLaren, 1993; Hampton & Whittow, 1976; Humphries & Careau, 2011). HIF, also known as specific dynamic action (SDA), is the rise in metabolism associated with processing a meal, including digestion, absorption, and conversion of food to useful macromolecules and excretory products. Since divers are generally active for at least some portion of their dive, the heat generated from their locomotory muscles—where only 20% of energy is converted into useful power—can also contribute to thermal substitution. If the 80% of energy that becomes ‘wasted’ heat can be efficiently stored in the body, it can mitigate the need for increased metabolic heat production (Bostrom & Jones, 2007; Kaseloo & Lovvorn, 2006; Liwanag et al., 2009). Furthermore, these two forms of facultative thermogenesis could occur during dives, unlike shivering thermogenesis, which is inhibited by the dive response (Kvadsheim et al., 2005).

1.3.2.2 Fat, fur, feathers: Trade-offs between diving with internal versus external insulation

Increases in insulation reduces conductive heat transfer across the body surface by increasing the thermal resistance of the outer layer. Fur and feathers are located externally and are relatively static, whereas subcutaneous fat, or blubber, is internal and much more dynamic (Davis, 2019). These differences, as well as the quantity and quality of the insulation, have significant thermal consequences for divers.

Blubber is a subcutaneous layer of adipose tissue reinforced by connective tissue fibers (Parry, 1949). Its relatively low conductivity (1/10th that of water) limits heat transfer, which allows skin temperatures to drop close to water temperatures while the core body temperature remains elevated (Castellini, 2018). It also serves as an energy source, although more so for some species or age-classes than others (Dunkin et al., 2005; Kwan, 1994; Worthy & Edwards, 1990). This dual role inherently introduces a trade-off between energetics and thermoregulation (Bryden, 1968; Ryg et al., 1988; Stewart & Lavigne, 1980). The insulating quality of blubber varies with its thickness as well as its lipid content and composition and may provide some heat storage capacity similar to phase change materials (Davenport et al., 1990; Dunkin et al., 2005; Liwanag et al., 2012b; Pearson, 2015; Worthy & Edwards, 1990). Thermal habitat ranges and phylogenetic constraints across species results in differences in blubber quality and quantity (Figure 1.6). For example, some deep-diving toothed whales in tropical and temperate waters have a relatively thin blubber layer for their size. It is thought that the presence of wax esters—an uncommon lipid in mammals—reduces blubber conductivity and excess heat loss in deep cold waters (e.g., pygmy sperm whale, *Kogia breviceps,* and short-finned pilot whale, *Globicephala macrorhynchus*; Bagge et al., 2012).

While the blubber conductivity of smaller shallow diving porpoises and dolphins are similar to that of the larger deep-diving cetaceans, their mass-specific blubber thicknesses vary between species. The much smaller harbor porpoise, *Phocoena phocoena*, occupies a narrower and colder thermal range than the spotted dolphin, *Stenella attenuata*, and bottlenose dolphin, *Tursiops truncatus*, and thus has significantly higher mass-specific blubber thickness (Figure 1.6). Interestingly, brown adipose tissue is present in the inner blubber along the entire body of both the harbor porpoise and bottlenose dolphin, Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, and Dall's porpoise, *Phocoenoides dalli*. Known for its thermogenic properties, brown adipose tissue may enhance the function of their blubber layer—from modulating heat transfer to also generating heat—and allow these species to maintain thermal balance while inactive (Hashimoto et al., 2015).

Both fur and feathers are better insulators per unit quantity than blubber. Their effectiveness is due to the air layer that is trapped within the insulative layer as air has a very low thermal conductivity (0.025 $W\ m^{-1}\ °C^{-1}$). A few marine endotherms have developed specialized features, such as interlocking hairs and feather barbs, to prevent water penetration and enhance air-trapping—a prerequisite for relying on external insulation while submerged (Liwanag et al., 2012a; Lustick, 1984). While fur and feathers do not introduce energetic tradeoffs in the same manner as blubber, they are energetically more costly to maintain as they require grooming/preening and periodic molting (Lustick, 1984; M. E. Murphy, 1996). To compensate for its large SA:V, the sea otter has the densest fur (Figure 1.7) and spends up to 12% of its time grooming to maintain the fur's integrity (Loughlin, 1977), which is crucial for its survival in temperate habitats. As molting reduces the animal's insulation and requires perfusion of the skin that also increases heat loss, several species have found ways to reduce the physiological burden of molting. Many amphibious species return to land to molt (Boily, 1995; Walcott et al., 2020; Worthy et al., 1992), while others molt gradually and sometimes migrate to warmer waters (Boily, 1995; Pitman et al., 2019).

Blubber provides better insulation for deep divers despite its lower insulative capacity compared to fur or feathers (Figure 1.7), because the insulating layer of air compresses and may escape as the animal descends. The deeper the dive, the lower the insulative capacity of fur/feathers (until completely saturated), and the higher the thermoregulatory costs. Certain species can retain some air within their pelage or plumage at depth, but this entrapped air increases their buoyancy and adds to the energetic costs of diving (Fish et al., 2002). Some divers have sacrificed their insulation layer to reduce their buoyancy. For example, the deeper the diving seabird, the lower their mass-specific plumage air volume. Surface-feeders have the largest air volume, followed by plunge divers and, lastly, pursuit divers (Croll & McLaren, 1993; Lovvorn & Jones, 1994; Wilson, Hustler, et al., 1992).

While incompressible, blubber may also affect buoyancy regulation (Miller et al., 2004; Webb et al., 1998), albeit on a longer timescale as the thickness of the blubber layer changes seasonally in response to energetic demands (Figure 1.6; Meagher et al., 2008; Mellish et al., 2004; Rosen & Renouf, 1997; Slip et al., 1992). Additionally, a body free from fur or feathers is advantageous for moving through the water efficiently by reducing hydrodynamic drag (Fish, 2000). However, while streamlining is improved, a thicker layer of blubber is required to compensate for its poorer insulative capacity (Figure 1.8), which can, in turn, hinder maneuverability and flexibility. Therefore, small animals may be constrained to using fur or feathers, while large animals use blubber (Figure 1.7; Liwanag et al., 2012b).

In general, sea turtles are the only vertebrate group considered here that does not rely on substantial insulation. While the carapace and plastron are good insulators (Spotila & Standora, 1985), their fat reserves are primarily an energy store (Kwan, 1994). Leatherback turtles are the only sea turtle with a substantial fat layer containing both white and brown adipose tissue (Davenport et al., 1990, 2009; Goff & Stenson, 1988), which contributes to their homeothermic abilities. Interestingly, they are also the only sea turtle without a hard-shelled carapace.

The evolutionary transition from fur/feathers to blubber in highly-adapted divers is exhibited in the most extreme divers of each taxonomic group, e.g., elephant seals, emperor penguins, and leatherback turtles (Figure 1.7). Marine mammals, in particular, demonstrate how their evolutionary history explains this convergence upon insulation strategies: the first groups to reinvade the oceans (Cetaceans and Sirenians) have lost nearly all their hair and are fully aquatic, the most recent groups (sea otters and polar bears) rely on a dense coat of fur, and the pinnipeds as the intermediate group exemplify a gradient of strategies that best suits their breeding strategies (i.e., income versus capital breeding; (Costa, 1991) and diving behavior (Fish, 2000; Liwanag et al., 2012a; Uhen, 2007). Similarly, with penguins, feathers are advantageous for their amphibious lifestyle, particularly those in polar climates, where it makes an effective barrier to freezing wind chills (Chappell et al., 1989). Moreover, the larger quantity of blubber required to provide an equal amount of insulation as fur or feathers would be too heavy in the case of a flying seabird or too cumbersome for species, like penguins or a sea otter, that are amongst the smaller air-breathing divers (Costa & Kooyman, 1982).

1.3.2.3 Using blood flow to control heat flow

In addition to the role morphology (i.e., size and insulation) plays in modulating heat transfer to the animal's surroundings, key anatomical features present in the vasculature of air-breathers allow for more precise control of heat exchange by redistributing heat in the body. While heat conservation is a common challenge in the marine environment, there are occasions where excess heat must be dissipated to prevent hyperthermia, especially during bouts of activity associated with the active pursuit of prey. Thus, a level of physiological plasticity is required in these adaptations.

Counter-current heat exchangers (CCHEs) are generally found in peripheral body parts and help retain heat in the core body by rewarming cold venous blood returning from the periphery as it passes in proximity to outgoing, warm arterial blood (Willmer et al., 2005). This mechanism makes regional heterothermy possible. The positive correlation between the number of humeral arteries within the plexus of penguin wings and the surface area of the wing shows the importance of this mechanism across species. Larger penguins have more of these heat-retaining structures to compensate for their large wings, and makes it possible to have up to a 25°C temperature difference between their shoulder and tip of the wing (Thomas & Fordyce, 2012).

CCHEs are present in the flippers and flukes of marine mammals (Elsner, 1969; Pabst et al., 1999; Rommel & Caplan, 2003), tongues of large cetaceans (Heyning, 2001), legs, neck, and wings of seabirds (Frost et al., 1975; Midtgård, 1981; Thomas & Fordyce, 2012), and the limbs of leatherback turtles (Davenport et al., 2015; Greer et al., 1973). CCHEs also perform the opposite task of cooling temperature-sensitive organs, such as the brain (Odden et al., 1999; Pettit et al., 1981; Scholander et al., 1942; although see Porter & Witmer, 2016) and intra-abdominal testes (Pabst et al., 1995; Rommel et al., 1994, 1995). In these cases, cold blood from the periphery is directed towards a rete mirabile near the organ, providing a localized thermal gradient to cool the organ.

CCHEs require the circulation of blood to function and yet, peripheral vasoconstriction during the dive will limit the use of this mechanism. In short, shallow dives, CCHEs may still operate as the dive response is not as profound.

However, in longer, deeper dives, the function of CCHEs is likely to be limited by the dive response. Sea turtles may be the exception as they maintain some circulation during dives to access oxygen stores in the lung. Although well-developed CCHEs are only present in the flippers of leatherback turtles (Davenport et al., 2015), evidence of the thermoregulatory role of flippers in green turtles, *Chelonia mydas*, and loggerhead turtles, *Caretta caretta*, suggests adjacent arteries and veins can serve a similar function (Hochscheid et al., 2002; Mrosovsky, 1980).

Arteriovenous anastomoses (AVAs) provide another thermoregulatory adaptation that relies on regulating peripheral blood flow through vasomotor control. AVAs are highly-innervated vessels in the dermal layer and provide a conduit for blood to bypass capillaries, shunting directly from the arterial to the venous supply. These “shunt” vessels can be dilated or constricted to regulate blood flow to the skin, contributing to heat conservation or heat dissipation by shifting the location of the temperature gradient to either within the blubber layer or across the body surface, respectively (Figure 1.8). If, however, the skin is covered by dense fur, AVAs are not as effective because the temperature gradient within the fur serves as a barrier to heat transfer.

While present in all mammals, AVAs differ in density and distribution amongst taxonomic groups in part due to their relative fur densities. This is best demonstrated within the pinnipeds. Earless seals have equally high densities of AVAs—up to eight times that of other mammals—across their entire body surface (Molyneux & Bryden, 1978) that contribute to heat dissipation. Unlike earless seals, eared seals have higher densities of AVAs in their flippers than their bodies, but sea lions have deeper AVAs in their furred flippers, whereas fur seals have superficial AVAs in their bare-skinned flippers (Bryden & Molyneux, 1978). These anatomical differences allow fur seals to use their flippers as heat dissipators on land or at the water's surface (e.g., jughandling behavior; Liwanag, 2010), Meanwhile, AVAs within sea lion flippers are likely to be more effective when immersed due to the negligible amount of insulation their fur provides in water.

Seabirds also have AVAs located in their eyelids, feet webbing, and brood patch (Frost et al., 1975; Midtgård, 1981; Thomas & Fordyce, 2012). These vascular structures are essential for thermoregulation during flight and incubation, but it is unclear whether they contribute to thermoregulation in water. Seabirds also have a sizeable marginal vein in their wings that provides an alternate path to CCHE and allows the axilla to serve as a thermal window, i.e. a peripheral site that is readily perfused to dump excess heat (Frost et al., 1975).

1.3.2.4 Thermoregulatory effects of regulating metabolism

Central to the concept of heat balance is the regulation of metabolism. While endogenous heat production is limited in ectothermic divers, its regulation during diving is unclear in marine endotherms. Measurements of basal metabolic rates (BMR) of marine mammals suggest that they have higher BMRs than terrestrial mammals, but this is somewhat controversial due to inconsistencies in how BMR was measured (Castellini & Mellish, 2015). Nonetheless, the higher metabolic rate of marine endotherms appears to be associated with the thermoregulatory costs related to the marine environment (Costa & Maresh, 2018, p. 201; Costa & Williams, 1999; Ellis & Gabrielsen, 2002; Irving, 1973; Lustick, 1984; T. M. Williams, 1998; but see Innes & Lavigne, 1991; Lavigne et al., 1986; T. M. Williams et al., 2001). While measuring and comparing basal metabolic rate is valuable for understanding maintenance costs, a more ecologically relevant measure is field metabolic rate. However, comparing energetic costs of marine and terrestrial vertebrates is confounded by the effects of temperature and diving on the metabolic rate of ectotherms and marine vertebrates, respectively (Costa & Maresh, 2018; Davis, 2014; Hansen & Ricklefs, 2004). The extent to which the dive response regulates metabolism will determine the rate of endogenous heat production (Hurley & Costa, 2001; Rosen et al., 2017), and ultimately thermal balance while diving. Thus, the interaction between the dive response and thermoregulation is context-dependent and expanded upon in the next section.

1.4 Physiological Interactions During the Dive: Synergistic or Antagonistic?

Many authors have pointed out the paradoxical interactions between the physiological demands imposed on air-breathing divers (Castellini et al., 1985; Green et al., 2006; Lewden, Enstipp, Picard, et al., 2017; Mauck et al., 2003; D. P. Noren et al., 1999; Rosen et al., 2007; Sparling et al., 2007; Whittow, 1987; T. M. Williams, Haun, et al., 1999; T. M. Williams, Noren, et al., 1999). There is potential for conflict between the dive response, exercise response, digestion, and thermoregulation because cardiovascular adjustments are integral to these responses, and those required for one activity may not be compatible with another. Therefore, divers face the dilemma of either compromising performance or prioritizing one response over another. These conflicting demands are managed in different ways by different species due to the diversity of thermoregulatory adaptations and habitats (Figure 1.1).

1.4.1 The potential for thermal conflict is context-dependent

Thermoregulation is energetically demanding, which is exacerbated in the thermally challenging marine environment. The ability of marine divers to meet this challenge and maintain thermal homeostasis will depend on their energetic balance. For example, if they are in an energy-deficient state, those that rely on blubber will begin to deplete this layer as an energy source. Whereas when those that depend on fur or feathers become energy deficient, they may not be able to maintain the integrity of their insulation through preening, grooming, or molting (Croll & McLaren, 1993; Loughlin, 1977; Walcott et al., 2020). Reducing the effectiveness of the insulation will, in turn, increase thermoregulatory costs and create a feedback cycle that leads to deteriorating body conditions where the body is unable to maintain thermal balance or meet energetic requirements (Costa & Kooyman, 1982; Rosen et al., 2007; Worthy & Lavigne, 1987).

The following discussion about the interplay between the dive response, exercise response, digestion, and thermoregulation, illustrated in Figure 1.9, assumes that the diver can acquire sufficient energy while foraging. Placing these interacting physiological requirements into context will serve to demonstrate situations where thermal conflicts may arise, and others where responses are synergistic.

1.4.2 Consequences of the dive response on thermoregulation

The cardiovascular adjustments of the dive response, i.e. bradycardia and peripheral vasoconstriction (Figure 1.9, Box D), are generally associated with a reduced metabolism during diving, which is advantageous for increasing aerobic diving capacity due to decreased oxygen consumption. However, hypometabolism as a diving strategy also has implications for thermal physiology as a reduced metabolism results in less internal heat production. Diving into colder waters generally exacerbates the issue of heat conservation (Figure 1.9, bottom side panel); however, reducing the temperature gradient between the skin and water minimizes heat loss (Figure 1.9, Box E). This 'peripheral shell cooling' can be accomplished through active mechanisms (i.e., peripheral vasoconstriction) or passively as the high thermal conductivity of water and the temperature gradient experienced by divers will naturally promote heat loss and cooling of the skin.

Those species that rely on internal insulation allow their outer shell to cool while maintaining the temperature of the core. Whereas, divers with an air layer in their water-resistant pelage or plumage undergo less cooling of their periphery, allowing them to maintain higher skin temperature (Castellini & Mellish, 2015). For example, the skin temperatures of northern elephant seals, *Mirounga angustirostris*, can drop to within a few degrees of water temperature (Figure 1.8). In comparison, sea otters and emperor penguins keep their peripheral temperatures as high as ~20°C above water temperature (Costa & Kooyman, 1982; Ponganis et al., 2003). Regardless, marine endotherms maintain impressive thermal gradients between their core (generally ~37°C) and water, and even sea turtles have been shown to maintain body temperatures a few degrees up to 18°C above water temperature in the leatherback turtle (Frair et al., 1972). This enables leatherback turtles to expand their thermal niche into subpolar and deeper waters (Figure 1.1; James et al., 2006; McMahon & Hays, 2006).

In addition to changes in their insulation, vasomotor adjustments allow redistribution of heat, contributing to large temperature gradients—these result in regional heterothermia, or more specifically peripheral hypothermia. The severity of the dive response will determine the extent to which peripheral hypothermia extends into the core and causes core temperature to fall below normothermia. Even a slightly reduced core temperature is beneficial for the diver as hypothermia will reduce oxygen demands through metabolic depression (Blix et al., 2010; Scholander et al., 1942). Hypothermia may also relieve some of the thermoregulatory costs of maintaining a stable high core body temperature while diving. At the same time, it would be beneficial for conserving energy at times of reduced activity (Figure 1.9, Box G). However, these energetic savings during the dive must be repaid through increased activity (i.e., swimming, but also flying for seabirds) during post-dive surface intervals to reestablish homeostasis (Figure 1.9, Box A). Additionally, since the metabolic rate of ectotherms is intrinsically dependent on ambient temperatures, sea turtles may be more vulnerable to significant reductions in body temperature as it would hinder physiological functions. Therefore divers, and particularly ectotherms, must find a balance between the degree of body cooling and maintenance of minimum temperature for digestion or locomotion.

1.4.3 Exercise versus thermoregulation: Context-dependent interactions and strategies

A hypometabolic state seems paradoxical for animals that are actively diving, pursuing prey, or escaping predators. Generally, exercise will increase heart rate and thus cardiac output to supply exercising muscles with elevated levels of oxygen to meet metabolic demands. Increased cardiac output is accompanied by the dilation of vessels to maintain blood pressure as well as an increase in breathing frequency to increase oxygen uptake (C. R. Taylor et al., 1987). Breath-hold divers have a limited ability to make these adjustments as their oxygen stores are limited. Most divers seem to avoid the typical exercise response, and maintain low diving metabolic rates by swimming efficiently—through neutral buoyancy and stroke-and-glide patterns (Figure 1.9, Box G; Hochscheid et al., 2003; Lovvorn, 2001; Trassinelli, 2016; Watanuki et al., 2003; T. M. Williams et al., 2000)—and matching their workload with perfusion patterns (Fedak et al., 1988; McDonald et al., 2018; T. M. Williams et al., 1991, 2015; T. M. Williams, Haun, et al., 1999).

Moreover, divers routinely experiencing intense peripheral vasoconstriction compensate with greater myoglobin concentrations in their locomotory muscles. More myoglobin allows for continued muscle activity despite ischemia (Davis et al., 2004). Isolating the muscle from circulation could result in a rise of local temperatures as the exercising muscle produces heat. Excess heat could be lost to the environment, or, could be retained to offset thermoregulatory costs (Figure 1.9, Box C).

If, however, exercise results in excess heat production, the diver may need to dissipate heat to avoid hyperthermia. This need to dump heat during periods of activity can lead to a thermal conflict for animals that are well insulated for the cold. To prevent hyperthermia and counteract thermal inertia during exercise, they can dissipate heat by bypassing the blubber layer using AVAs to perfuse the skin. Still, peripheral vasoconstriction during the dive will generally prevent this mechanism (Figure 1.9, Box D) as overriding the dive response will decrease their diving ability. The alternative is to store the excess heat, allowing body temperature to potentially rise, until the end of the dive when the dive response is relaxed (Figure 1.9, Box A and B). In other words, the diver may employ either a graded or temporally-delayed thermoregulatory strategy depending on the severity of the heat load and particular dive conditions. However, if surface waters are comparably warm, delaying thermoregulation may exacerbate the challenge of dissipating the excess heat that has been stored (Figure 1.9, top side panel). Since heat dissipation will be less efficient in warmer surface waters, this strategy may inevitably reduce diving efficiency by requiring longer surface intervals for thermoregulation.

1.4.4 Ingestion and digestion of cold prey: A sink and source of heat

Another physiological requirement that may be incompatible with the dive response is digestion. Foraging is one of the primary functions of diving for air-breathers; yet, digestion requires some blood flow to the splanchnic organs, which are generally hypoperfused during the dive (Davis, 2014; Davis et al., 1983; Zapol et al., 1979). Digestion could be delayed to when maximizing dive duration is not a priority, such as after foraging bouts or time on land to prevent this conflict. While delaying digestion may enhance foraging efficiency (up until satiation), there will also be thermal consequences of employing such a strategy.

An important thermoregulatory consideration associated with foraging is the ingestion of cold prey. In addition to the external temperature gradient experienced while diving, the ingestion of cold prey will introduce an internal temperature gradient. Warming ingested prey will exacerbate the challenge of maintaining thermal balance in cold water, particularly for endotherms feeding on cold ectothermic prey (Hedd et al., 1996; Wilson, Cooper, et al., 1992). However, the energetic costs of digestion contribute to HIF, which can offset thermoregulatory costs. Therefore, the ingestion and digestion of cold prey can serve as a sink or source of heat, respectively (Figure 1.9, Box F; Croll & McLaren, 1993). Considering when these processes occur is essential for understanding how the diver's thermoregulatory strategy may affect its diving, and thus foraging behavior (Costa, 1988; T. M. Williams et al., 2004).

Mathematical models of how a breath-hold diver should optimize their energy intake have been developed and have made predictions that can be tested in the field (Charnov, 1976; Houston & Carbone, 1992; Kramer, 1988; Thompson & Fedak, 2001). However, the additional constraints imposed by digestion and thermoregulation have yet to be considered. Theoretical models that combine laboratory data on the thermoregulatory costs of foraging with field studies that identify when these processes occur in nature would provide insight into the intrinsic and extrinsic factors, besides oxygen stores and prey field, that may influence foraging efficiency.

1.5 A Thermal Balancing Act

The management of concurrent, and potentially conflicting demands requires that a diver coordinates its response in a manner that aligns with diving conditions and physiological priorities. Such strategies could involve temporally separating two responses that are in direct conflict, using their response for one demand to minimize the cost of another, or attending to both requirements simultaneously but at a compromised capacity. A certain degree of flexibility is required to account for the complexity of potential interactions, differences between dive functions, and seasonal changes in their environment and body condition. In the following section, we review the literature for studies that examined thermoregulation in animals in the water and while diving in nature.

1.5.1 Temporal separation of conflicting demands

1.5.1.1 Checks and balances of thermal budgets: exercise and water temperature

The conflicting demands of the dive response and thermoregulation were examined with trained bottlenose dolphins, *Tursiops truncatus*, swimming, and diving in warm tropical waters (D. P. Noren et al., 1999; T. M. Williams, Noren, et al., 1999). They found significant changes in heat flux across the body with diving, where diving attenuated heat flux even after an extended period of swimming at the surface. Heat flux only started to increase during the latter portion of the ascent—which coincides with the anticipatory tachycardia occurring at the end of the dive—and remained high during the post-dive surface interval. The authors concluded that dolphins delayed heat dissipation until after the dive instead of overriding the dive response to dissipate heat at depth. Interestingly, one of the dolphins that was vigorously active before diving showed elevated heat flux at the dorsal fin at depth, which suggests a momentary override of the dive response to dissipate heat through this thermal window. This scenario emphasizes the effects of exercise in determining the flexibility of their responses to account for their thermal demands, and also supports the claim that the dive response can be modulated by activity (Davis & Williams, 2012; McDonald et al., 2018; S. R. Noren et al., 2012; T. M. Williams et al., 2015).

Does a delay in heat dissipation compromise thermal balance, and if so, to what extent is thermal imbalance tolerated before the dive response is overridden to allow for some heat dissipation? An animal's heat tolerance will dictate the extent and time scale at which cellular consequences of hyperthermia, such as destabilization of proteins and changes in membrane fluidity, require prioritization of thermoregulation to regain homeostasis, or manifest as heat stress symptoms. Bottlenose dolphins exposed to increasingly warmer water temperatures were able to delay the onset of hyperthermia for an hour or longer. They did this by redistributing core body heat to their periphery, demonstrating their physiological ability to tolerate some heat stress (Heath & Ridgway, 1999). Although the physiological demands faced by the resting dolphins in this study are different than those for wild, active dolphins, such a short-term heat tolerance would explain how dolphins can manage the thermal challenge of moving from cold pelagic waters to warmer inshore waters. Therefore, in the case of smaller cetaceans, activity and water temperature are important factors for determining their thermal economy and the degree to which heat stress is tolerated during the dive. Furthermore, diving could increase their heat tolerance as hypometabolism, and colder waters at depth promote passive heat dissipation. How larger cetaceans face a similar challenge when migrating from the poles to the tropics, albeit on much longer timescales, is unknown.

Polar seals, such as the Antarctic Weddell seal, *Leptonychotes weddelli*, are unlikely to face the thermal conflict of dissipating heat while diving, even during intense activity. Yet, they also appear to regulate their thermal balance during the post-dive surface interval. Hill et al. (1987) measured aortic temperatures during the dive. They observed significant changes between dives rather than during dives, suggesting that this drop in aortic temperature (up to 2°C) before bouts of diving serves as a ‘preparatory’ thermoregulatory response to extend dive durations by reducing metabolism. Thus, dolphins and Weddell seals in drastically different thermal habitats resolved the conflicting demands of thermoregulation during diving by deferring active thermoregulation until surface intervals.

1.5.1.2 Dive first, digest later

A similar strategy of temporal separation has been observed in diving endotherms to mediate the thermal consequences of digestion. Amphibious species that haul out often have the option of completely separating digestion from diving. In contrast, those that perform long foraging trips or are fully aquatic must find an opportune time to digest while at sea when they are not concerned with maximizing their dive durations. For example, elephant seals appear to defer food processing to drift dives where the animal stops swimming and drifts thereby sparing oxygen that would otherwise be expended on locomotion for digestion (Crocker et al., 1997; Mitani et al., 2010). However, these 'food-processing' dives were occasionally associated with extended surface intervals (ESIs), suggesting oxygen stores may at times be insufficient to complete digestion at depth following extensive foraging bouts and may require additional time at the surface (Crocker et al., 1997). The thermoregulatory costs associated with warming, potentially large quantities of ingested prey, may also be a factor limiting their diving efficiency while foraging (Austin et al., 2006; Kuhn & Costa, 2006).

ESIs have also been observed in grey seals, *Halichoerus grypus*, and harbor seals, *Phoca vitulina*. By simulating natural foraging trips with grey seals in a laboratory setting, Sparling et al. (2007) demonstrated that grey seals delay digestion until ESIs, which may occur hours after the initial ingestion of prey. This strategy was flexible in that some digestion occurred during shallow dives, but not in deeper dives. A similar observation was made in Steller sea lions, *Eumetopias jubatus* (Hindle et al., 2010; Rosen et al., 2015). These ESIs were accompanied by significant peaks in metabolic rate, much higher than those reported for non-diving seals, likely as a result of HIF, as well as the added physiological demands of diving (Markussen et al., 1994; Rosen & Trites, 1997), and perhaps paying back the thermoregulatory costs of warming cold prey (T. M. Williams et al., 2004).

1.5.2 Thermoregulating smarter, not harder by coordinating synergistic activities

1.5.2.1 HIF: equivocal evidence for heat substitution

Whether HIF offsets thermoregulatory requirements has been investigated in several species with mixed results. Some studies have speculated the potential contribution of HIF towards maintaining thermal balance from lab experiments. For example, thick-billed murres, *Uria lomvia*, little penguins, *Eudyptula minor*, and double-crested cormorants, *Phalacrocorax auritus*, may benefit by deferring digestion until after dives while floating at the surface where HIF can contribute to the post-dive recovery of body temperatures (Enstipp et al., 2008; Green et al., 2006; Hawkins et al., 1997). Heat substitution from HIF would be of lesser importance for cormorants as the partial wettability of their pelage requires them to return to shore to dry their feathers where they could then digest their prey.

On the other hand, studies on other seabirds and Steller sea lions have concluded that HIF does not significantly contribute to reduced thermoregulatory costs (Rosen & Trites, 2003; Wilson & Culik, 1991). Specifically, Wilson and Culik (1991) found that the increased postprandial metabolic rate of adult Adélie penguins, *Pygoscelis adeliae*, is due to the cost of warming cold prey, rather than HIF (for comparison with chicks, see Janes & Chappell, 1995). However, these studies were all performed in the lab where direct measurements of metabolic rate were possible. Still, the effects of varying activity levels associated with different foraging strategies are challenging to incorporate. Wilson and Culik (1991) suggest that the active foraging strategy of Adélie penguins may allow them to mobilize muscular heat to aid in warming ingested prey and would in turn dictate foraging rates to maximize food heating efficiency.

Unlike the majority of foragers limited by their non-prehensile limbs, sea otters can delay both prey ingestion and digestion until they are back at the surface. In doing so, they avoid the initial thermal costs required to warm ingested prey while at depth and reap the thermal benefits of HIF while inactive at the surface (Costa & Kooyman, 1984). Due to their overall high metabolic rates and unfavorable SA:V, sea otters rely on synergistically coordinating heat substitution strategies for maintaining thermal balance, as observed by a corresponding increase in activity as HIF decreased over time (Costa & Kooyman, 1984). Sea otters and seabirds suggest that perhaps the ability to float at the surface to reduce heat loss to the water may facilitate maximizing the thermal benefits of HIF, particularly during inactive periods that are increasingly costly with decreasing water temperatures (Richman & Lovvorn, 2011). These examples demonstrate the importance of disentangling the cost of warming ingested prey from those associated with digestion to assess the net thermoregulatory consequences of foraging.

1.5.2.2 Muscular thermogenesis: using muscular inefficiency for thermoregulation

Another mechanism of thermal substitution is utilizing the 'wasted' heat produced by muscular activity. While this was mentioned in relation to foraging for sea otters and Adélie penguins, it also contributes to thermoregulation in the absence of foraging activity. Muscular thermogenesis as a thermoregulatory strategy is particularly useful for (1) species with a low heat-retaining capacity (i.e., large SA:V), (2) juveniles that may not have well-developed thermoregulatory capabilities in addition to having an unfavorable SA:V relative to adults, and (3) ectotherms that have a reduced capacity to increase their metabolic heat production.

Studies on captive animals have demonstrated how body size affects the relationship between activity and thermal homeostasis. For example, Hawaiian spinner dolphins, *Stenella longirostris*, a comparably small delphinid species, live in waters near their lower critical temperature, and their stenothermic body temperature is dependent on activity, demonstrating a synergistic interaction between exercise and thermoregulation (Hampton et al., 1971; Hampton & Whittow, 1976). In contrast, a larger delphinid species, the Pacific bottlenose dolphin, has been shown to experience a 2°C increase in body temperature after periods of vigorous activity (McGinnis et al., 1972). As juveniles are smaller, they have reduced thermal capabilities compared to adults. However, it is energetically cheaper for juvenile California sea lions, *Zalophus californianus*, to maintain moderate activity levels than to rest in water below their thermal neutral zone, and incur the increased cost of shivering (Liwanag et al., 2009).

The activity of ectothermic divers is primarily influenced by their thermal environment, often resulting in circadian patterns. In hawksbill turtles, *Eretmochelys imbricata*, Storch et al. (2005) found that the duration of night dives increased with decreasing water temperature below 28°C. In contrast, there was no pattern in dive duration and water temperature during the day. They related this pattern to the different behaviors carried out during day and night. During the day, animals are actively foraging, while at night, they are resting, and their temperature and metabolism would be lower, allowing longer dives. Muscular thermogenesis associated with active swimming has also been demonstrated in green turtles in lab experiments (Jackson & Prange, 1979; Standora et al., 1982) and has been hypothesized to occur in free-ranging loggerhead turtles (Sakamoto et al., 1990). While heat generated in the muscles likely serves to primarily enhance muscle performance, some heat may be distributed to the rest of the body via circulation, increasing core body temperatures beyond their usual 1-2°C above ambient water temperatures (Sakamoto et al., 1990; Standora et al., 1982).

1.5.3 Modifying diving behavior as a thermoregulatory strategy

Vertical stratification of the water column allows divers to behaviorally thermoregulate by varying the time spent in warmer, surface waters versus colder, deep waters. Although relatively rare, ESIs have been recorded in the diving behavior of loggerhead turtles in the Mediterranean Sea, with the majority of ESIs occurring during the day following dive bouts into deep waters up to 10°C colder than surface waters (Hochscheid et al., 2010). The positive correlation between body mass and ESI duration, along with extended surface time during sunlit hours, led the authors to hypothesize that ESIs serve a thermoregulatory function. In contrast, nocturnal ESIs occurred after dives that exceeded their calculated ADL where they were presumably foraging on patchy prey, indicating an alternative role of post-dive recovery for nocturnal ESIs. Core body temperature measurements would allow a test of the hypothesized functions for daytime and nocturnal ESIs.

Unlike loggerhead turtles in the Mediterranean Sea, leatherback turtles encounter a broader range in temperatures across their habitat—which spans both tropical to subpolar waters—and thus require greater flexibility in their thermoregulatory strategy. Wallace et al. (2005) suggested that leatherback turtles behaviorally regulate their body temperature by either increasing the time spent at colder depths while in tropical waters or performing shallower dives when in colder waters at the northern limits of their range. Additionally, in warm tropical waters leatherback turtles can use CCHEs in their hindlimbs to retain muscular heat locally to prevent core hyperthermia; whereas in colder waters they can transfer some of this heat to their core, where it is retained by their thermal inertia and insulation (Davenport et al., 2015).

Although behavioral thermoregulation is a more common strategy in ectotherms, adjusting diving behavior as a thermoregulatory strategy has also been documented in endothermic divers. Similar to the leatherback turtles, Magellanic penguins, *Spheniscus magellanicus*, occupy a relatively wide range of water temperatures on the Patagonian coast and adapt their diving behavior relative to water temperature and foraging activity. By comparing penguins from colonies at different latitudes and modeling the effects of environmental parameters on their thermal dynamics, Ciancio et al. (2016) found that penguins increased their swim speeds in colder waters while performing shallow transiting dives. Increased swim speeds will also increase convective heat loss. Still, they showed that the associated increase in heat production was disproportionately higher and compensated for convective heat loss, thus making this a suitable strategy to mitigate heat loss while diving shallowly in cold waters. However, when performing deep dives, heat loss is exacerbated by the reduced effectiveness of the external insulating layer with depth. This may explain why penguins reduced, rather than increased, swim speeds during the ascent and descent of deeper foraging dives. By shifting their strategy and prioritizing oxygen conservation instead of thermoregulation, penguins could maximize bottom time and thus foraging efficiency. This exemplifies how diving behavior is modified to balance the physiological demands of thermoregulation and foraging.

Little is known about behavioral thermoregulation in marine mammals while in water despite a plethora of studies that describe behavioral strategies of amphibious species while on land (Beentjes, 2006; Codde et al., 2016; Norris et al., 2010; Whittow et al., 1972). One well described at-sea behavior is jughandling in Northern fur seals, *Callorhinus ursinus,* which is commonly associated with sleep (Donohue et al., 2000). By exposing their flippers while floating at the surface, fur seals enhance the efficiency of AVAs in their flippers for either heat conservation by reducing heat loss to the water or heat dissipation by increasing convective heat loss in air. Jughandling increased with water temperature in pups, and although shivering was observed, there was no relationship with water temperature. Despite an initial increase in metabolism associated with this body position (likely due to changes in perfusion), fur seals—particularly pups in water below their lower critical temperature—can reduce thermoregulatory costs compared to resting by remaining in this position for ~30 minutes and thus extend their thermal neutral zone (Liwanag, 2010).

Manatees, *Trichechus manatus*, employ a longer-term behavioral strategy to avoid cold-stress. When Florida winter water temperatures reach below their lower critical temperature of 20°C, manatees may migrate to warm-water thermal refuges in inland natural springs or near power plants (Laist et al., 2013). There have been up to 282 manatee deaths due to cold-stress in a single year, and those most vulnerable are juveniles and sub-adults due to their inexperience of finding thermal refuges and high SA:V relative to adults (Erdsack et al., 2018). Still, even those that use these thermal refuges may face energetic trade-offs with foraging as it requires traveling further distances to feeding grounds, resulting in reduced foraging time (Haase et al., 2020). Conversely, winter water temperatures can reach 32°C, and during episodes of strenuous activity, albeit rare for this slow-moving mammal, heat may need to be dumped to prevent hyperthermia. Manatees do not possess AVAs, but a deep caudal vein has been proposed as a mechanism for bypassing the CCHE in their caudal fluke and contribute to heat dissipation (Rommel & Caplan, 2003). However, the deep location of this vein in comparison to AVAs in other species raises the question as to whether this strategy is efficient and sufficient to prevent hyperthermia.

1.5.4 Regional heterothermy versus hypothermy

The dive response and thermoregulation are intricately connected through common underlying physiological mechanisms, namely metabolic rate and peripheral perfusion. In the diving physiology literature, regional heterothermia has been hypothesized as a mechanism to reduce diving metabolism and thus extend aerobic dive duration (Niizuma et al., 2007; Ponganis et al., 2001, 2003). However, the use of this strategy for diving or thermoregulation is not mutually exclusive. Similarly, hypothermia-induced metabolic depression is an alternative hypothesis, and this strategy of lowering the set-point in body temperature has often been proposed in the literature to explain the impressive diving behavior of marine vertebrates, particularly seabirds (Bevan et al., 1997; Culik et al., 1996). The costs and benefits of employing regional heterothermy versus hypothermy will depend on concurrent physiological demands (e.g., foraging, migrating) and the suitability of their various adaptations (e.g. wettability of external insulation, vasomotor control).

Data from king penguins, *Aptenodytes patagonicus*, support a hypometabolic strategy as several studies have observed reductions of up to 11-13°C in abdominal and subcutaneous temperatures during dives with subsequent rewarming during the surface intervals returning to normothermic levels (Enstipp et al., 2017; Handrich et al., 1997; Schmidt et al., 2006). A reduction in metabolism afforded by lower body temperatures during the dive may explain their ability to routinely dive close to their ADL (Figure 1.5) and maximize foraging efficiency. Despite suffering increased heat loss, king penguins maintain peripheral perfusion while at the surface, particularly ESIs during the night, to either access or deposit fat into their subcutaneous layer depending on their foraging success and energy balance (Lewden, Enstipp, Bonnet, et al., 2017; Lewden, Enstipp, Picard, et al., 2017), thus demonstrating a trade-off between nutritional and thermoregulatory demands.

While a decline in the peripheral temperatures of emperor penguins and thick-billed murres have been observed, a marked reduction in core body temperature similar to the king penguins was absent (Niizuma et al., 2007; Ponganis et al., 2001, 2003). It is worth noting that Ponganis et al. (2001, 2003) observed a similar pattern to king penguins in the abdominal temperature of emperor penguins. Still, by comparing this site to several others in the body, they concluded that the abdominal temperature is not representative of the core body temperature for emperor penguins. Instead, deep venous temperatures that better represent core temperature did not drop below 37°C even during prolonged dives, while significant declines were observed in other peripheral sites. These findings do not support the concept of hypothermia or hypometabolism in emperor penguins but rather aligns with regional heterothermy.

Niizuma et al. (2007) reached a similar conclusion for thick-billed murres but also observed an overall decreasing trend in both core and peripheral temperatures throughout dive bouts. Superimposed on this trend is the opposing changes in core and peripheral temperatures during a dive. While the progressive decline in peripheral temperatures across dive bouts was driven by reductions that occurred during the dive, core temperatures remained relatively high during the dive but then decreased at greater magnitudes during surface intervals. This pattern of within-dive changes in core temperature contrasts with those observed in king penguins and led the authors to hypothesize that larger seabirds use different thermoregulatory strategies than smaller seabirds. While body size may be important, other factors, such as dive or trip duration, may explain why emperor penguins diving from an isolated ice hole seem to be more similar to the smaller murre than the larger, more closely related king penguins.

There are species-specific differences in thermoregulatory strategies within the Phalacrocoracidae (i.e., cormorants and shags). For example, both Great cormorants, *Phalacrocorax carbo carbo*, and European shags, *Phalacrocorax aristotelis*, maintain relatively stable core body temperatures (~41°C; measured via stomach temperature telemeters) while diving (Enstipp et al., 2005; Grémillet et al., 1998, 2001). In contrast with other cormorant species, such as bank cormorants, *Phalacrocorax neglectus* (Wilson & Grémillet, 1996), and South Georgian shags (Bevan et al., 1997), significant declines (~4°C) in body temperatures occurred (measured in the stomach and abdomen, respectively, reaching ~35°C) while diving. These differences were partly attributed to the thermal environments encountered by these closely related species. While they are all exposed to cold waters, bank cormorants can absorb the intense solar radiation from the South African sun to regain normothermia after decreases in core body temperature while diving. On the other hand, temporal hypothermia may be costlier than maintaining normothermia for European shags and Great cormorants diving near the Chausey Islands (Grémillet et al., 1998). South Georgian shags encounter colder waters around South Georgia (~5°C), where maintaining normothermia while diving appears to be too costly. Phalacrocoracidae (cormorants) living in polar climates reduce their time underwater by increasing their foraging efficiency providing more time to reestablish thermal balance between dives (Grémillet et al., 2001; although see Grémillet et al., 2005).

However, this does not explain the long foraging bouts of European shags diving near Scottish Islands when compared to conspecifics at the more southernly located Chausey Islands (~4 hours vs. ~1 hour near Chausey Islands; Daunt et al., 2007; Lewis et al., 2015). Furthermore, Greenland Great cormorants maintain normothermia despite diving in waters often less than 0°C (Grémillet et al., 2005). This is likely accomplished through intense thermogenesis to counteract heat loss to the water (Grémillet et al., 2001).

Compared to the seabird literature, there have been fewer studies on marine mammals that directly investigate hypometabolism and peripheral shell cooling. The ability to withstand hypothermia during forced submersion was demonstrated in some of the first sentinel studies of diving physiology on seals (Elsner, 1969; Irving et al., 1941; Scholander et al., 1942). However, it was not until reduced aortic temperatures were observed in Weddell seals diving voluntarily from an isolated ice-hole that hypothermia was suggested as a strategy employed by animals diving under natural conditions (Kooyman et al., 1980). While aortic temperatures were shown to decrease to 35°C during dives, the locomotory muscle temperature remained stable at 37°C instead of heating up as much as would be expected from the amount of work performed if it were completely ischemic (Hill et al., 1987; Kooyman et al., 1980; Ponganis et al., 1993). The lack of a temperature rise in the muscle likely indicates that either some perfusion is maintained or the muscle is hypometabolic while active. However, the muscle temperature could not be used to conclude the entire body's thermal conditions or metabolic rate (Ponganis et al., 1993). Andrews (1999) reached a similar conclusion about deep muscle temperature measurements in freely diving juvenile elephant seals. The muscle temperature dropped an average of only 1°C during dives, while peripheral temperatures (i.e. subcutaneous and blubber) decreased significantly supporting the strategy of peripheral hypothermia that may extend into the adjacent muscle tissue. In addition to these studies on phocids, regional heterothermy has also been observed in fur seals and dolphins (Barbieri et al., 2010; Heath & Ridgway, 1999; Ohata et al., 1977).

While confirming whether peripheral hypothermia is accomplished through active vasomotor control or passive mechanisms is more challenging, I. L. Boyd (2000) used a simple heat balance model in which peripheral circulation switched between complete and absent and demonstrated the model could predict the skin temperature changes observed in diving Antarctic fur seals, *Arctocephalus gazella*. However, he acknowledged that peripheral perfusion was modeled in an overly simplistic manner, and that it is likely to be more of a graded response. Nonetheless, the evidence of peripheral hypothermia in several endothermic divers emphasizes the importance of managing skin temperature for thermoregulation.

Unlike seabirds and most marine mammals, the majority of sea turtles do not have substantial insulation. Yet, their skin temperature is generally close to ambient water temperature while their core body temperature is maintained above water temperature. Their ability to maintain a high core body temperature is reduced when water temperatures reach <10°C (Foley et al., 2007; Schwartz, 1978). Although only described in a few sea turtle species, hypometabolism can reduce their energetic costs but is associated with a decrease in performance. Dives where turtles remain quiescent on the seafloor or in the water column (at the depth where neutral buoyancy is achieved) longer than their average dive duration have been described in green turtles (Felger et al., 1976; Godley et al., 2002; Southwood et al., 2003), hawksbill turtles (Storch et al., 2005), and loggerhead turtles (Carr et al., 1980; Hawkes et al., 2007; Hochscheid, Bentivegna, et al., 2007; Hochscheid et al., 2005). These dives are typically shallow and nocturnal, and occur during winter when the water is colder, which facilitates a temperature-induced depression of metabolism. By reducing their oxygen consumption, they can remain resting at depth for prolonged periods—as long as 10 hours was observed in a loggerhead turtle (Broderick et al., 2007). This behavioral thermoregulatory strategy has been referred to as hibernating, emphasizing the departure from homeostatic conditions that allows for minimal energy expenditure.

In addition to this behavioral strategy, there is evidence that sea turtles regulate their thermal balance. Laboratory studies have demonstrated that sea turtles have faster heating rates than cooling rates, suggesting physiological control over heat exchange (Heath & McGinnis, 1980; Smith et al., 1986). Although well-developed CCHEs, which provide an effective mechanism for controlling heat distribution, have only been identified in leatherback turtles (Davenport et al., 2015; Mrosovsky, 1980). Hochscheid et al. (2002) demonstrated changes in blood flow in response to changing ambient temperatures in the flippers of green and loggerhead turtles. Similarly, the relatively large size of green turtles, *Chelonia mydas*, and loggerhead turtles, *Caretta*

caretta, facilitates the retention of heat and has led to the use of other terms, including homeothermy and regional endothermy, to describe their thermoregulatory capabilities (Sato et al., 1994; Standora et al., 1982). Therefore, despite their intrinsic differences in physiology, sea turtles and diving endotherms have converged upon a similar thermoregulatory strategy of regional heterothermy, which is made possible by regulating their circulation to control heat distribution within the body and heat dissipation to the environment. As Irving and Hart (1957) eloquently summarized it: "…the homoiothermism of their bodies is sustained by the heterothermism of superficial tissues."

1.6 Methods for Studying the Thermal Physiology of Free-Ranging Divers

While laboratory investigations provide a fundamental understanding of thermoregulatory mechanisms, insight into conflicts between competing physiological processes associated during diving require field studies. Fortunately, technological advances have created new tools to study the movement patterns, behavioral and physiological ecology of air-breathing marine vertebrates. The incorporation of physiological sensors into biologging tags has made it possible to investigate how the physiological capabilities demonstrated in the lab are employed in the wild. The following section discusses the approaches that might be used to study the thermal physiology of free-ranging divers, with representative studies summarized in Table 1.1. These methods may not apply to all taxonomic groups, but a modification to procedures and approaches could expand our knowledge of understudied species.

1.6.1 Temperature

While handheld devices offer a snapshot of an animal's thermal state, continuous measurements at appropriate sampling rates can provide insight into the dynamic nature of an animal's physiological temperatures, which can vary drastically with activity and ambient conditions (J. C. Boyd & Sladen, 1971; Goldsmith & Sladen, 1961; E. N. Taylor et al., 2004). Thermistors and thermocouples have been used on many freely diving species, demonstrating the feasibility of using them for physiological studies. Given that continuous temperature measurements are likely to be taken at a few sites, these sites must be carefully chosen. Sensor placement can be guided by knowledge of the animal's anatomy, coupled with the specific research question of interest. The following section focus on temperature measurements in marine divers (for a thorough review of temperature measurements on free-ranging birds and mammals, see McCafferty et al., 2015).

Skin and subcutaneous temperatures have revealed the ability of several species of divers to cool their periphery and employ regional heterothermy (Irving et al., 1962; McGinnis, 1975; Ponganis et al., 2003; Schmidt et al., 2006). As blood flow measurements have only been done in laboratory setting (Bevan & Butler, 1992; Hochscheid et al., 2002; Zapol et al., 1979), fine-scale changes in peripheral temperatures can be used as a proxy for peripheral perfusion in free-ranging divers. On the other hand, changes in peripheral temperatures over long periods reflect changes in the insulation layer. For example, Enstipp et al. (2017) found minimum and maximum subcutaneous temperatures measured in juvenile king penguins occurred during diving and surface intervals, respectively, reflecting patterns of peripheral perfusion. They attributed a decline in the weekly average subcutaneous temperatures to increased insulation associated with a thicker fat layer accumulated over their year-long foraging trip during their dispersal phase. In contrast to pre-molt trips, periods of normothermic temperatures were longer and even occurred during some shallow dives during post-molt trips, underscoring the physiological need to restore their insulation layer after fasting for the duration of the molt on land (Enstipp et al., 2019). This example highlights the importance of considering how seasonal changes and varying energetic challenges across different life stages might influence thermoregulatory strategies.

While peripheral temperatures may provide insight into heterothermy and vasomotor control of heat dissipation, it is difficult to conclude whether an animal is effectively maintaining thermal balance without measuring their core body temperature. While rectal and cloacal temperatures are used to assess core body temperature, it is difficult to obtain long-term continuous measurements from this site. Probe placement is critical as unrepresentative cooler temperatures may be obtained that may lead to misinterpretations about true body temperature (e.g., too shallow or near the CCHE for animals with intra-abdominal testes; Mrosovsky & Pritchard, 1971; Rommel et al., 1994; Stahel & Nicol, 1982).

Therefore, field studies have relied on stomach temperature telemeters or thermistors inserted into the body to determine proxies for core body temperature.

Stomach temperature telemeters are less-invasive but may not work as well for animals that regurgitate or pass the sensor quickly through their gut. Some studies have modified the sensor housing to increase retention time (Austin et al., 2006; Kuhn & Costa, 2006; Sato et al., 1994; Wilson et al., 1998). When used for identifying core body temperatures, the temperature data must be analyzed appropriately to account for the temperature drop associated with the ingestion of cold prey or water (Grémillet et al., 1998; Wilson, Cooper, et al., 1992). While perhaps a nuisance for analyzing core body temperature, this temperature signal associated with ingestion has been useful for studying the thermal and metabolic effects of HIF in the lab as well as determining feeding events in the wild (Hedd et al., 1996; Heide-Jørgensen et al., 2014; Kato et al., 1996; Kuhn et al., 2009; Simmons et al., 2010; Vacquié-Garcia et al., 2015; Wilson et al., 1995, 2002).

A combination of simultaneous measurements of the core body and peripheral temperatures in free-ranging animals will be necessary to unravel the conflicting demands of diving behavior and ambient temperature on the spatial and temporal distribution of heat throughout the body (Andrews, 1999; Culik et al., 1996; Handrich et al., 1997; McGinnis, 1975; Niizuma et al., 2007; Ponganis et al., 2003). Whenever possible simultaneous measurements at multiple sites should be taken and will identify which locations accurately reflect core body temperature.

1.6.2 Heat flux

Most heat flux studies have been performed on captive animals using handheld devices (Erdsack et al., 2018; Hampton et al., 1971; Hampton & Whittow, 1976; Heath & Ridgway, 1999; McGinnis et al., 1972; D. P. Noren et al., 1999; T. M. Williams, Noren, et al., 1999). Willis and Horning (2005) and Westgate et al. (2007) measured heat flux in free-ranging Weddell seals and dolphins using packages specifically designed for their study species. Similar attachment methods used with sea turtles in the lab also show promise for field applications (Bostrom et al., 2010; Heath & McGinnis, 1980). However, heat flux measurements on animals with dense fur or feathers will be compromised if the area is shaved/plucked to ensure good contact between the sensor and skin. To circumvent this issue, I. L. Boyd (2000) avoided this problem by using two thermistors to measure the temperature gradient across the fur and modeled heat transfer in Antarctic fur seals.

Heat flux measurements have improved our understanding of the spatial variability of heat transfer across the body surface and how it is affected by changes in insulation, peripheral perfusion, behavior, and water temperature. By comparing heat flux at multiple body sites in relation to water temperature and activity level in the lab, thermal windows have been identified in various species: dorsal fin and flippers in dolphins (Hampton et al., 1971; Heath & Ridgway, 1999; McGinnis et al., 1972; Meagher et al., 2008; D. P. Noren et al., 1999; T. M. Williams, Noren, et al., 1999), fluke and flippers in manatees (Erdsack et al., 2018), flippers in seals (Kvadsheim & Folkow, 1997), and soft white skin areas in turtles (Heath & McGinnis, 1980; Standora et al., 1982). Unlike the dorsal fin of dolphins, heat flux sensors have not been attached to the highly maneuverable flippers of sea lions or fur seals and the wings of penguins to confirm the role of these appendages as thermal windows (Goldsmith & Sladen, 1961; Hindle et al., 2015).

1.6.3 Quantifying dynamic properties of insulation

Another important, but often overlooked, consideration is the dynamic changes that occur in insulation. Blubber varies in thickness and composition depending on nutritional requirements, whereas feathers and fur may vary in condition based on how recently they were molted or maintained. While these issues may only arise when collecting data over seasons, insulation will change during a dive for animals that rely on fur or feathers.

A fundamental property of insulation is its thermal conductivity, which has been determined for blubber and fur from sculp samples of various species (Figure 1.6; Bagge et al., 2012; Dunkin et al., 2005; Horgan et al., 2014; Kvadsheim et al., 1994, 1996; Liwanag et al., 2012a, 2012b). These studies provided a single, species-specific value for thermal conductivity, as is appropriate for *ex vivo* measurements. However, *in vivo* conductivity will vary during the dive due to changes in perfusion of the blubber layer or compression of fur/feathers at depth (Kvadsheim & Aarseth, 2002). Using *ex vivo* values in equations for modeling heat transfer of diving animals may result in inaccurate physiological conclusions.

The effects of hydrostatic pressure on the effectiveness of fur/feathers have been measured (Blix, Grav, et al., 1979; Blix, Miller, et al., 1979; Kooyman et al., 1976; Kvadsheim & Aarseth, 2002; Scholander et al., 1950; Sharma & Liwanag, 2017). The results were used to estimate the retention of an air layer and the external insulation layer upon submersion (Fish et al., 2002; Grémillet et al., 1998). While marine mammals do not have arrector pili muscles, pilomotor adjustments in seabirds may need additional consideration (Kooyman et al., 1976; Lovvorn & Jones, 1991).

On the other hand, the effects of peripheral perfusion on blubber conductivity have not been widely addressed, perhaps due to the difficulty of simulating conditions in the laboratory, as is possible with the compression of fur/feathers. The few instances where *in vivo* blubber conductivity was determined for an animal in the water revealed significantly higher values than excised blubber and varied with water temperature (Hart & Irving, 1959; Kanwisher & Sundnes, 1966). Similar approaches could be used to determine blubber conductivity in a free-ranging diver by obtaining three concurrent *in vivo* measurements: heat flux, subcutaneous temperature, and the temperature at the blubber-muscle interface (Figure 1.10). Measurements of *in vivo* blubber conductivity can serve as a proxy for peripheral perfusion as blubber conductivity will vary during the dive relative to the level of peripheral vasoconstriction.

1.6.4 Infrared thermography: An informative tool

There is a logistical and ethical limit to how many sensors are used and sites measured on an animal simultaneously. Infrared thermography (IRT) allows temperature across the entire body surface to be determined from an image, which makes it an extremely useful tool for studying the thermal physiology of animals on land (McCafferty, 2007; McCafferty et al., 2011; Speakman & Ward, 1998; Tattersall, 2016). Furthermore, IRT can be applied at the population level (e.g., aerial surveys, long-term monitoring and conservation efforts; Horton et al., 2017; Pabst et al., 2002;

Udevitz et al., 2008) to study the thermal ecology and habitat range of a species, which is crucial particularly in light of recent studies that highlight the differential vulnerability of marine species to climate change (Albouy et al., 2020; Hamann et al., 2013). Unfortunately, water absorbs infrared radiation precluding its use underwater, but IRT has been used to study thermoregulation of amphibious marine vertebrates while on land (Figure 1.11; Chaise et al., 2019; McCafferty et al., 2013; Mellish et al., 2015; Nienaber et al., 2010; Willis et al., 2005), as well as some divers while at the surface (Barbieri et al., 2010; Cuyler et al., 1992; Pabst et al., 2002; Perryman et al., 1999).

While limited in its applicability to freely diving animals, this technology can serve to examine how anatomy influences heat transfer and better inform the placement of sensors. IRT images of seals after exiting the water (Erdsack et al., 2012; Mauck et al., 2003) or during moments of heat stress (Codde et al., 2016; Norris et al., 2010) have revealed the dynamics of thermal windows while on land, verifying the role of broadly distributed AVAs to control heat exchange. Hindle et al. (2015) used IRT on Weddell seals to determine the placement of heat flux sensors that best represented heat flux across the entire body and then extrapolated these measurements to estimate whole-body thermal dynamics. Similarly, IRT of dolphin dorsal fins revealed different surface temperatures that correspond to the underlying vasculature (Pabst et al., 2002). By comparing heat flux from sensors placed directly over or away from superficial veins, Meagher et al. (2002) found heat flux values were influenced by the underlying vasculature, particularly when taken underwater, demonstrating the importance of sensor location.

1.6.5 Other valuable concurrent measurements

A suite of other measurements can contribute to an integrated understanding of physiology, energetics, and environmental factors. For example, a time-depth and temperature recorder can provide in-situ water temperature measurements at the scale and resolution of the animal's behavior and are essential for contextualizing physiological responses relative to diving behavior and the thermal challenge imposed by the environment. Metabolic rate is an important factor for determining the rate of heat production, but because direct measurement through respirometry is challenging on free-ranging animals, field metabolic rate can be estimated using the doubly-labeled water method and heart rate (for an assessment of the methods, see Butler et al., 2004; Costa, 1988; Sparling et al., 2008; Speakman & Hambly, 2016).

Heart rate is a useful measure of the dive response (Hindle et al., 2010; Irving et al., 1941; Murdaugh et al., 1961; Thompson & Fedak, 1993). While the onset and intensity of bradycardia only provide limited information on circulatory adjustments, measurements of blood flow have been made on captive animals using intravascular sensors as well as noninvasive Doppler flow sensors (Bevan & Butler, 1992; Hochscheid et al., 2002; Jobsis et al., 2001; West et al., 1992), and more recently, near-infrared spectroscopy (McKnight et al., 2019; C. L. Williams et al., 2011). Incorporating these noninvasive sensors into biologgers for deployment on free-ranging animals to directly measure circulatory changes would provide key insights into how diving animals coordinate their responses to meet thermoregulatory demands. Finally, sensors that measure variables related to locomotion (e.g. swim speed sensor, accelerometer, gyroscope, magnetometer) can help link the contribution of swimming activity to thermal substitution (Davis et al., 2003; Mitani et al., 2010).

1.6.6 Future directions for methodologies

The disparity among the number of studies of different taxonomic groups, and even species, underscores the challenges of studying freely diving animals, particularly their physiology (Andrews & Enstipp, 2016). The development of novel attachment methods will be critical to apply new sensor technologies to measure physiological variables. Most currently available devices require the temporary restraint of animals to allow sensor and datalogger attachment. Unfortunately, this has limited their use on large cetaceans, but recent developments have enabled studies of their diving behavior and kinematics (Baird, 1998; Goldbogen et al., 2017; Szesciorka et al., 2016). Sensors are typically been attached with suction cup tags or darts with little control over their placement. Despite these challenges, a recent study obtained the first heart rate measurements from a blue whale using a suction cup biologger, demonstrating the possibility of incorporating physiological sensors into existing tag designs (Goldbogen et al., 2019).

Nevertheless, it is still unknown how large cetaceans maintain thermal balance in their tropical breeding grounds while they are adapted to conserve heat in their polar foraging grounds (Brodie & Paasche, 1985; Kasting et al., 1989; Lavigne et al., 1990). The interplay between thermoregulation and the energetics of lunge feeding also provides an exciting area of research. Because so little is known about how they manage these thermal challenges given their large size, it would be valuable to develop tags that measure other physiological variables relevant to thermal physiology. For example, introducing thermistors into the tips of dart tags to measure blubber temperature, or integrating a heat flux sensor into large suction cups—similar to the integration of the ECG electrodes (Goldbogen et al., 2019)—could provide novel insight into their thermoregulatory strategies.

1.7 Concluding Remarks

The value of laboratory studies for studying physiology and aiding the interpretation of physiological data from field studies—where the natural environment introduces many confounding variables—cannot be understated. However, if we want to know how animals manage the thermal challenges of their environments, it is necessary to study their physiology in the wild (Costa & Sinervo, 2004).

The following questions highlight some important gaps in our understanding of the thermoregulation of marine air-breathers.

(1) To what extent is the dive response modulated by thermoregulation? Some laboratory studies have shown that under heat stress conditions—such as during intense exercise or heating of the hypothalamic region of the brain during a forced submersion—some degree of vasodilation is maintained, suggesting thermoregulatory responses are capable of overriding the dive response under extreme conditions (Hammel et al., 1977; T. M. Williams,

Noren, et al., 1999). Such a response would require a relaxation of peripheral vasoconstriction, resulting in increased oxygen consumption and thus decreased aerobic diving capacity. Field studies would provide the opportunity to address whether such situations occur in nature where overriding the dive response, and incurring the associated costs, to avoid thermal imbalance would be beneficial.

(2) When are thermal responses actively regulated, and when are they passive? Previous research studies have suggested that vascular changes are active thermoregulatory mechanisms (Hampton & Whittow, 1976; Hart & Irving, 1959; Heath & McGinnis, 1980; Schmidt et al., 2006). Passive responses are those that occur secondary to the dive response, ambient water temperatures, size or morphological adaptations (Sato, 2014). Although strategies fall along a continuum, Lovvorn (2007) suggested that the timescales at which the effects of active and passive mechanisms are observed differ and could therefore be used as a way to distinguish between the two, given appropriate sampling rates. Furthermore, understanding what factors dictate whether thermal responses are active or passive under natural conditions is critical for assessing thermoregulatory costs and the effects on overall energetic balance (Lovvorn, 2007).

(3) At what timescale is thermal balance maintained and how does it compare across taxonomic groups, age classes and sex? Since physiological time is

dependent on metabolism which in turn depends on size (Schmidt-Nielsen, 1984), it is reasonable to predict that the timescale at which thermal balance is maintained will differ between divers and result in varying levels of thermal resilience. The smallest and largest animals in each taxonomic group exhibit the extremes in terms of thermal inertia and stability. Small animals and juveniles, who may also not have well-developed thermal capabilities, are likely to experience larger fluctuations in their temperature. In contrast, large animals have the advantage of relying on thermal inertia to conserve heat, which can be particularly beneficial for deep divers. However, their relatively small SA:V could also increase their vulnerability to heat stress when exposed to warmer environments. It would be interesting to know if they have control over the timescales at which they maintain thermal balance. Such a strategy would be similar in concept to animals that strategically deviate from homeostasis at times for either energetic savings (e.g. facultative hypometabolic states) or enhanced performance of certain activities at the cost of others (e.g. temporal separation of diving and/or foraging and thermoregulation; Costa & Kooyman, 1984; D. P. Noren et al., 1999; T. M. Williams, Noren, et al., 1999; Wilson & Culik, 1991). When physiological limits are reached, active regulatory mechanisms may serve to induce faster changes in their heat balance than would passive mechanisms and restore homeostasis. Assessing when deviations from thermal homeostasis occur requires first defining normothermia and understanding how diving activity might shift the body temperature set-point (J. C. Boyd & Sladen, 1971; Stahel & Nicol, 1982).

(4) How is thermoregulation affected by tagging, handling and disturbance? Because stress responses often lead to changes in physiological temperature, it is important to consider how our interactions with the animals affect their thermoregulation. The implications of such activities could range from obtaining data that is unrepresentative of the animal in its natural state to population level consequences of disturbance. Despite our incomplete understanding of how they manage potentially conflicting demands, it is clear that marine air-breathers are well-adapted for the physiological challenges presented in the marine environment. However, it is unclear whether additional anthropogenic stressors would exacerbate currently manageable thermal conflicts and lead to physiological imbalance. Various stress responses have been observed in diving animals, including an unanticipated prolongation of the dive (i.e., dive inversion) and an up-regulation of the dive response despite increased activity levels associated with an escape response (Fregosi et al., 2016; T. M. Williams et al., 2017). The effects of these responses on an animal's thermal balance has yet to be investigated. For example, several studies have found evidence for pressure-related injuries in whales from mass-strandings that coincided with military exercises using sonar (Bernaldo de Quirós et al.,

2019). Yet, the observation that these strandings have occurred in warmwater regions warrants further investigation into whether thermal imbalance could have exacerbated an already precarious condition and contributed to the strandings (Filadelfo et al., 2009; Weise, 2009). A better understanding of the plasticity of their physiological adaptations under natural conditions would inform the analysis and mitigation of biologically significant responses to anthropogenic disturbances and changing environmental conditions.

This list is by no means exclusive and only serves to direct future research efforts towards topics that will ultimately advance our understanding of how marine air-breathers function and maintain homeostasis in a challenging environment. The current state and possible advances of physiological biologgers suggest a bright future for the study of thermal physiology of air-breathing marine divers.

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Table 1.1 Summary of studies and their approaches used in field thermal physiological studies for (A) sea turtles (B) seabirds, and (C) marine mammals. We included studies that performed field measurements of a thermal physiological variable(s) on free-ranging, diving animals. Two forms of remote measurement are possible on free-ranging animals. For thermal physiological measurements, telemeters that transmit summarized data include STT/STP = Stomach temperature telemeter or transmitter/pill. Otherwise, data is stored onboard data loggers or recorders: STL = Stomach temperature logger, TTR = Time temperature recorder, TDTR = Time depth temperature recorder, HTR = Heart temperature recorder, HRDL = Heart rate data logger. Symbols are used to denote the following: *used as proxy for core body temperature, ^{X}part of the study was performed in the lab, $^{\Delta}$measurement performed at the surface or while handling animal, ^{M}methodology paper, $^{+}$dissertation research.

	Species	*Study*	*Thermal Physiological Measurement(s)*	*Instrumentation*	*Other Measurement(s)*	*Derived Quantities*
SEA TURTLES	Green turtle	Heath and McGinnis, 1980^{X}	T_{stomach}* $T_{\text{peripheral}}$ – carapace & subcarapace HF^{x} – carapace, plastron, neck, flippers	external logger & STT	T_{water} – surface and benthic	$\Delta T_{\text{core-water}}$ from heating & cooling experiments^{X}, Thermal conductance^{X}
		Standora et al., 1982	T_{deep}* – near liver/pectoral muscle $T_{\text{peripheral}}$ – carapace, subcarapace, plastron, subplastron	sonic transmitter		Cooling-curve experiments^{X}
		Sato et al., 1998^{X}	T_{stomach}*	STL	In-situ T_{water}, diving depth	
	Leatherback turtle	Southwood et al., 2005	T_{stomach}* $T_{\text{peripheral}}$ – subcarapace	HTR/STT TDTR	In-situ T_{water}, diving depth, swim speed	
		Casey et al., 2014	T_{stomach}*	STP	In-situ T_{water}, diving depth	Metabolic rate (ΔT)
	Loggerhead turtle	Sakamoto et al., 1990	T_{stomach}*	TTR	In-situ T_{water}, diving depth	

		Sato et al., 1994, 1995, 1998	$T_{stomach}$*	TTR	Diving depth	
		Sato et al., 2014	$T_{stomach}$*	TTR	In-situ T_{water}, diving depth	Heat transfer model

	Species	*Study*	*Thermal Physiological Measurement(s)*	*Instrumentation*	*Other Measurement(s)*	*Derived Quantities*
SEABIRDS	Cormorants and shags	Wilson and Grémillet, 1996 Bank cormorants	$T_{stomach}$*	STL	Diving depth	Heat balance model
		Kato et al., 1996^{M} King cormorants	$T_{stomach}$*	STL	Diving depth	
		Bevan et al., 1997^{X} South Georgian shags	$T_{peripheral}$* – abdominal	HRDL	HR, diving depth	O_2 consumption (respirometry)^{X}
		Grémillet et al., 1998 Great cormorants & European shags	$T_{stomach}$*	STL	Diving depth	Heat loss model
		Grémillet et al., 2005 Great cormorants	$T_{peripheral}$* – abdominal	HRDL	HR, diving depth Body composition^{X}	Thermal conductance (based on Storch et al., 1999^{X}), fasting endurance, energetics model, heat loss calculations

Thick-billed murre	Niizuma et al., 2007	T_{deep}* – under liver near heart/lung/pectoral muscle $T_{peripheral}$ – muscle-skin interface	implantable logger	Diving depth	
African penguin	Wilson and Grémillet, 1996	$T_{stomach}$*	STL	Diving depth, swim speed	Heat balance model
Emperor penguin	Ponganis et al., 2001	T_{blood}* – inferior vena caval $T_{peripheral}$ – abdominal	external logger	Diving depth	
	Ponganis et al., 2003	T_{muscle} – pectoral T_{blood} – femoral, axillary, brachial, foot veins $T_{peripheral}$ – subcutaneous & subfeather $T_{stomach}$	external logger & STP	Diving depth, behavior via video recording	
King penguin	Culik et al., 1996	T_{deep} – heart, liver, sternum	implantable logger	Light levels	
	Handrich et al., 1997	$T_{stomach}$ $T_{peripheral}$ – top & bottom abdominal	TTR	Diving depth	
	Schmidt et al., 2006	T_{muscle} – pectoral $T_{peripheral}$ – brood patch	external logger	In-situ T_{water}, diving depth	
	Enstipp et al., 2017, 2019	$T_{peripheral}$ – flank	implantable logger	Diving depth	Heat loss model
Macaroni penguin	Green et al., 2003	$T_{peripheral}$ – abdominal temperature	HRDL	HR, diving depth	O_2 consumption (HR)

	Species	Study	Thermal Physiological Measurement(s)	Instrumentation	Other Measurement(s)	Derived Quantities
MARINE MAMMALS	Antarctic fur seal	Boyd, 2000	$T_{peripheral}$ – flank T_{skin} – flank	external logger	In-situ T_{water}	Heat balance model
	California sea lion	Villegas-Antmann et al., 2012	$T_{stomach}$*	STT with HTR		Total body O_2 stores
	Northern elephant seal	Andrews, 1999[+]	$T_{peripheral}$ – subcutaneous blubber, blubber-muscle interface T_{muscle}* (see text in 4.4)	external logger	HR, diving depth, swim speed	Field metabolic rate (DLW)
		Meir & Ponganis, 2010	T_{blood}* – arterial and venous	external logger	Blood P_{O2}, diving depth	
	Weddell seal	Hill et al., 1987	T_{blood}* – aortic	thermistor-tipped catheter	HR, blood samples	
		Ponganis et al., 1993	T_{muscle} – muscle	external logger	Swim velocity	
		Willis & Horning, 2005	HF – hips, flank, shoulders, axilla T_{skin} – hips, flank, shoulders, axilla IRT[Δ]	external logger with HF sensors, FLIR ThermaCam PM 695		Metabolic rate (HF)
		Hindle et al., 2015	HF – head, neck, axilla, flank T_{skin} – head, neck, axilla, flank $T_{stomach}$* (STP) IRT[¤] (FLIR P25 or P640)	external logger with HF sensors	Diving depth, acceleration	Total body heat dissipation
	Dolphins	Pabst et al., 2002 Spotted[a] & Spinner[b]	HF[a] – dorsal fin T_{deep}*[Δ] – colonic[a] IRT[bΔ]	20 cm deep, thermocouple, FLIR Agema 570	T_{water}, diving depth, swim velocity	
		Barbieri et al., 2010 Bottlenose	IRT[Δ]	FLIR Agema 570	T_{water}	$\Delta T_{fin-water}$

		Westgate et al., 2007[XM] Bottlenose & Spotted	HF – dorsal fin T_{skin} – dorsal fin	HF disks	In-situ T_{water}, diving depth, swim velocity	Trial test – Bottlenose[X]

Figure 1.1 A schematic comparing the variation in temperature experienced by air-breathing marine vertebrates while on land (**A**) and diving at-sea (**B**). The horizontal axis considers the temperature range experienced by horizontal movement across their home range, whereas the vertical axis considers temperature variability due to climate (on land) and water temperature at depth (at-sea). Unlike fully aquatic species (black), amphibious species (green and blue) partition their time between air and water, which have vastly different thermal properties. The extent of their habitat range (i.e., horizontal and vertical) dictates the thermal variability encountered in each environment. For example, the Galápagos fur seal has a limited home range and is exposed to a relatively constant tropical climate (**A**). Yet, the cold upwelling waters off the Galápagos Islands introduces a large temperature gradient for diving animals (**B**). The wandering albatross is on the opposite side of the continuum as it covers large distances while flying (**A**), but remains in the temperate latitudes and feeds in shallow waters (**B**). In contrast, blue whales migrate from polar foraging grounds to tropical breeding grounds, experiencing a large temperature range horizontally, as well as vertically during deep dives, although less so when diving in polar waters that are homogenously cold throughout the water column (**B**).

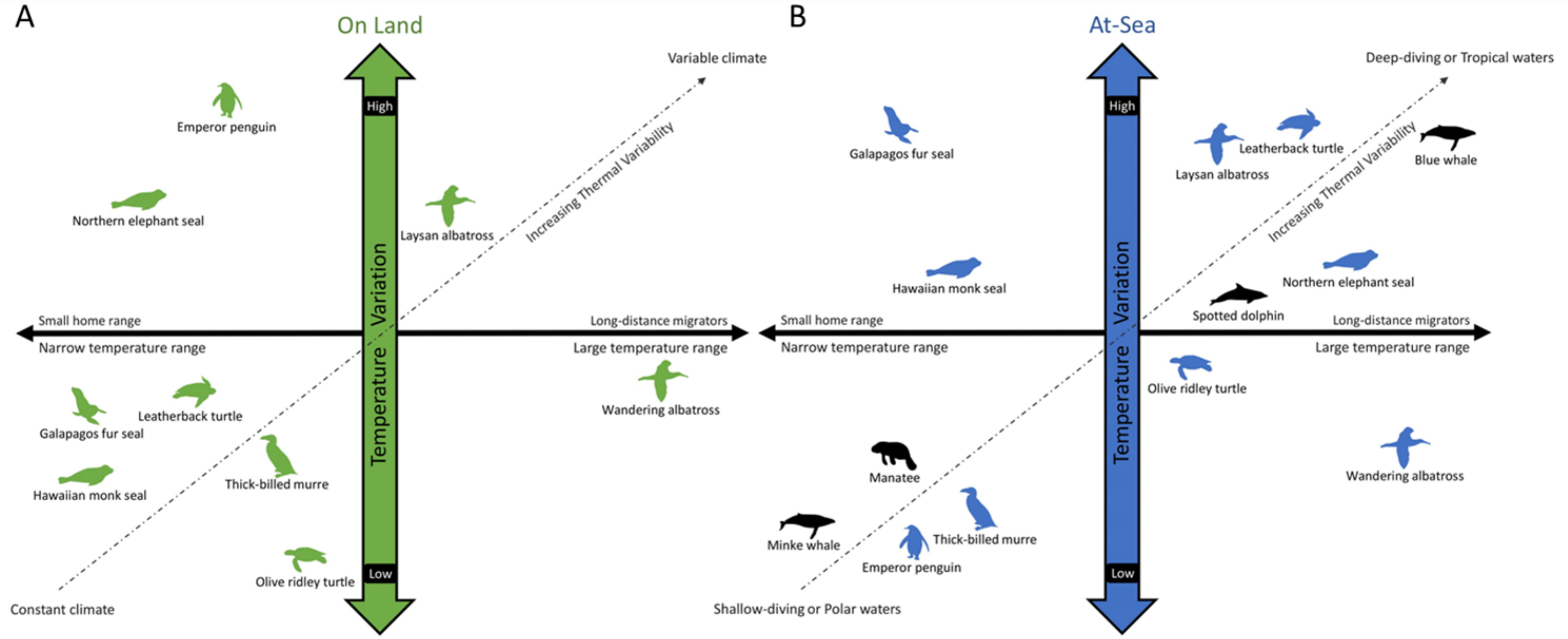

A
On Land
Variable climate
Increasing Thermal Variability
High
Low
Temperature Variation
Emperor penguin
Northern elephant seal
Laysan albatross
Small home range
Narrow temperature range
Long-distance migrators
Large temperature range
Wandering albatross
Galapagos fur seal
Leatherback turtle
Hawaiian monk seal
Thick-billed murre
Olive ridley turtle
Constant climate
B
At-Sea
Deep-diving or Tropical waters
Increasing Thermal Variability
High
Low
Temperature Variation
Galapagos fur seal
Leatherback turtle
Laysan albatross
Blue whale
Hawaiian monk seal
Northern elephant seal
Spotted dolphin
Small home range
Narrow temperature range
Long-distance migrators
Large temperature range
Olive ridley turtle
Manatee
Wandering albatross
Minke whale
Thick-billed murre
Emperor penguin
Shallow-diving or Polar waters

Figure 1.2 Marine air-breathing vertebrates are comprised of the following groups: marine mammals, seabirds, and marine reptiles. The table includes the common name used in the remainder of the review for each taxonomic group (representative bolded species are used for seabird orders that do not have an all-encompassing common name).The number of species and mass range for each taxonomic group are provided and include species considered to be true air-breathing divers (full list of species and mass references in Table A1.1), all of which are included in the bar graph, with the exception of Elapidae. Refer to the text in section 2 for further explanation about which groups are discussed in the review. The bar graph in the lower right shows the distribution of species grouped by taxa across absolute latitude using 5° bins. The habitat range classifications (Tropical, Subtropical, Temperate, Polar, and Subpolar) are defined based on the following absolute latitudes (0-25°, 25-35°, 35-55°, 55-65°, 65-90°) and denoted by dashed lines. Air and water temperature ranges are provided for polar (including subpolar), temperate, and tropical (including subtropical) habitat ranges. The greatest number of diving air-breathers are found at mid-latitudes (i.e., temperate, subtropical, and subpolar), where temperatures are more moderate compared to equatorial and high latitudes. Monthly mean air and sea surface temperature data were obtained from ICOADS data products provided by the NOAA/OAR/ESRL Physical Sciences Laboratory (https://psl.noaa.gov/data/gridded/data.coads.1deg.html). Temperatures in the winter and summer months (e.g., summer months: January, February, March in the Northern Hemisphere and July, August, September in the Southern Hemisphere) were used to estimate minimum and maximum average temperatures in each region. Distribution maps for 264 species were used: 13 Mysticeti, 65 Odontoceti, 4 Sirenia, 18 Phocidae, 16 Otariidae, 1 Odobenidae, 2 Mustelidae, 1 Ursidae, 18 Sphenisciformes, 52 Procellariiformes, 42 Pelecaniformes, 24 Charadriiformes, 6 Cheloniidae, 1 Dermochelyidae, and 1 Iguanidae. Distribution maps obtained from https://www.iucnredlist.org.

MARINE MAMMALS

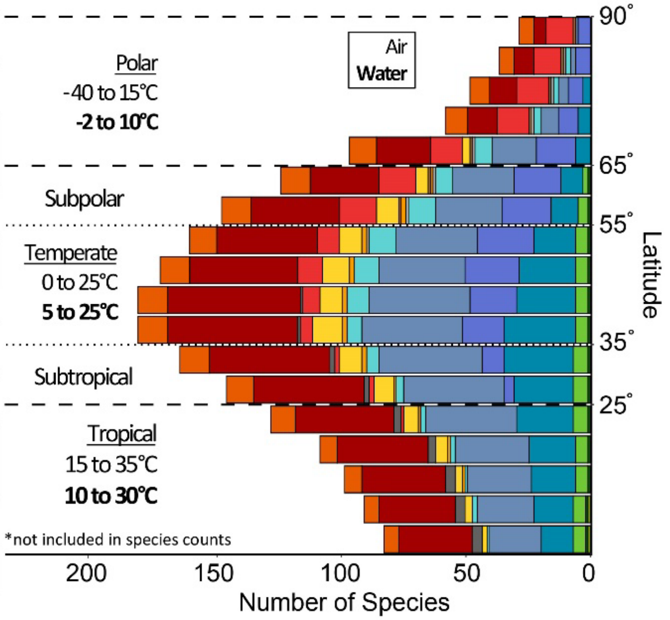
Cetaceans		Sirenians	Pinnipeds			Mustelids	Ursids
Baleen Whales	Toothed Whales	Manatees & Dugongs	Earless Seals	Eared Seals	Walrus	Marine & Sea Otters	Polar Bear
13 species	65 species	4 species	18 species	16 species	1 specie	2 species	1 specie
10^3 – 10^5 kg	20 - 10^4 kg	400 – 900 kg	45 – 2200 kg	30 – 1000 kg	600 – 1500 kg	5 – 30 kg	200 – 600 kg

DIVING SEABIRDS

Sphenisciformes	Procellariiformes	Pelecaniformes	Charadriiformes
Penguins	e.g. Petrels, **Albatross**	e.g. Boobies, **Cormorants**	e.g. **Alcids**
18 species	52 species	42 species	24 species
1 – 45 kg	0.2 – 12 kg	1 – 5 kg	0.08 – 1.5 kg

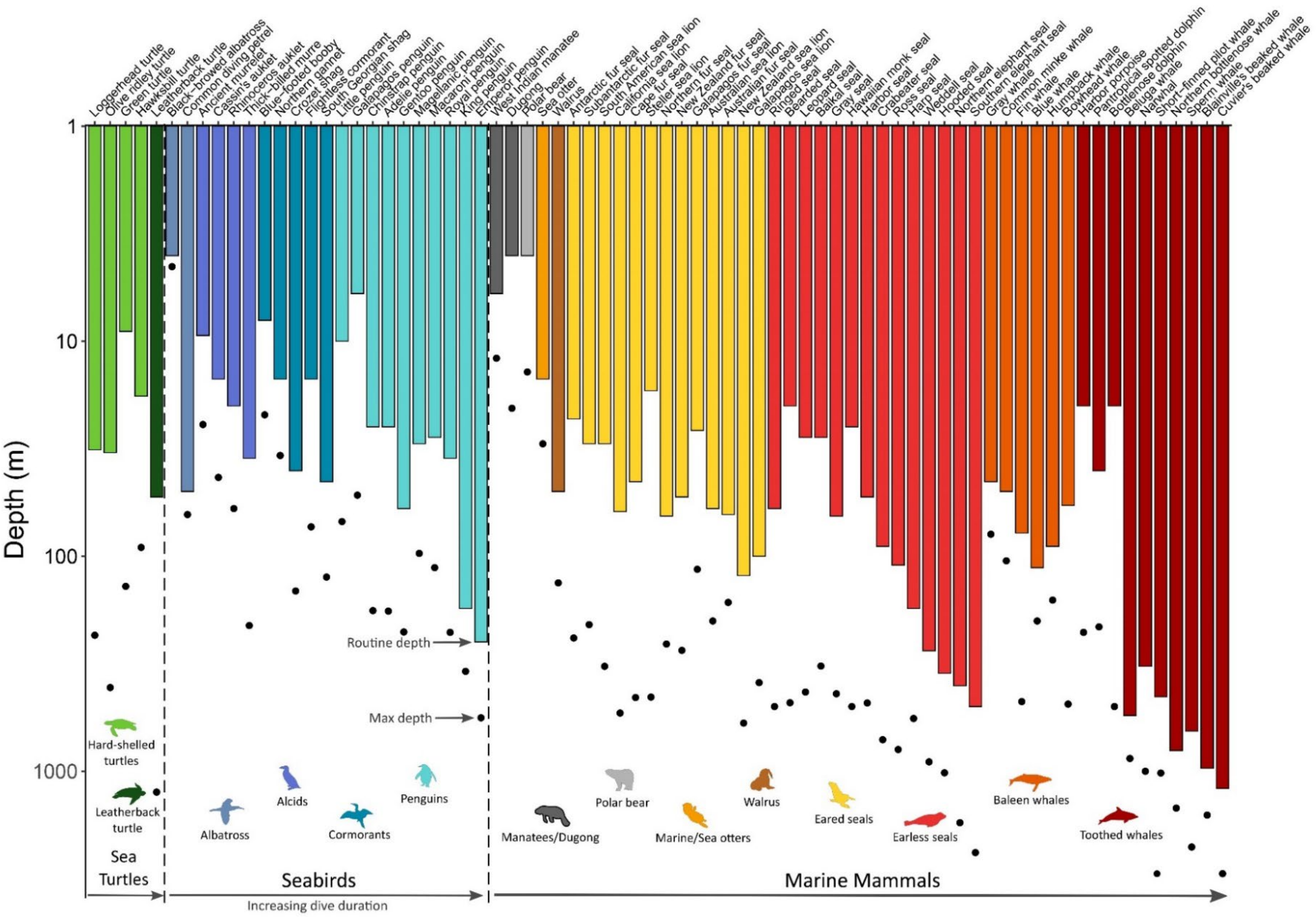
MARINE REPTILES

Cheloniidae	Dermochelyidae	Iguanidae	Elapidae*
Hard-shelled Turtles	Leatherback Turtle	Marine Iguana	Sea Snakes
6 species	1 specie	1 specie	70 species
30 – 200 kg	300 – 700 kg	0.9 – 12 kg	0.07 – 0.56 kg



*not included in species counts

Figure 1.3 Routine and maximum dive depths across marine air-breathers. Within the three taxonomic groups (sea turtles, seabirds, and marine mammals), species are grouped by order/family as indicated by the common names associated with the colored animal icons and then ordered by increasing routine dive duration. Species for which routine diving behavior data are available from time-depth recorders were included to demonstrate the physiological plasticity within a species (i.e., routine versus maximum depth) and the range of diving abilities within each order/family and across taxonomic groups. Refer to Table A1.3 for data sources.


Loggerhead turtle
Olive ridley turtle
Green turtle
Hawksbill turtle
Leatherback turtle
Black–browed albatross
Common diving petrel
Ancient murrelet
Cassin's auklet
Rhinoceros auklet
Thick–billed murre
Blue–footed booby
Northern gannet
Crozet shag
Flightless cormorant
South Georgian shag
Little penguin
Galapagos penguin
Chinstrap penguin
Adelie penguin
Gentoo penguin
Magellanic penguin
Macaroni penguin
Royal penguin
King penguin
Emperor penguin
West Indian manatee
Dugong
Polar bear
Sea otter
Walrus
Antarctic fur seal
Subantarctic fur seal
South American sea lion
California sea lion
Cape fur seal
Steller sea lion
Northern fur seal
New Zealand fur seal
Galapagos fur seal
Australian sea lion
Australian fur seal
New Zealand sea lion
Galapagos sea lion
Ringed seal
Bearded seal
Leopard seal
Baikal seal
Gray seal
Hawaiian monk seal
Harbor seal
Crabeater seal
Ross seal
Harp seal
Weddell seal
Hooded seal
Northern elephant seal
Southern elephant seal
Gray whale
Common minke whale
Fin whale
Blue whale
Humpback whale
Bowhead whale
Harbor porpoise
Pantropical spotted dolphin
Bottlenose dolphin
Beluga whale
Narwhal
Short–finned pilot whale
Northern bottlenose whale
Sperm whale
Blainville's beaked whale
Cuvier's beaked whale
Depth (m)
1
10
100
1000
Routine depth
Max depth
Hard-shelled turtles
Leatherback turtle
Albatross
Alcids
Cormorants
Penguins
Manatees/Dugong
Polar bear
Marine/Sea otters
Walrus
Eared seals
Earless seals
Baleen whales
Toothed whales
Sea Turtles
Seabirds
Increasing dive duration
Marine Mammals

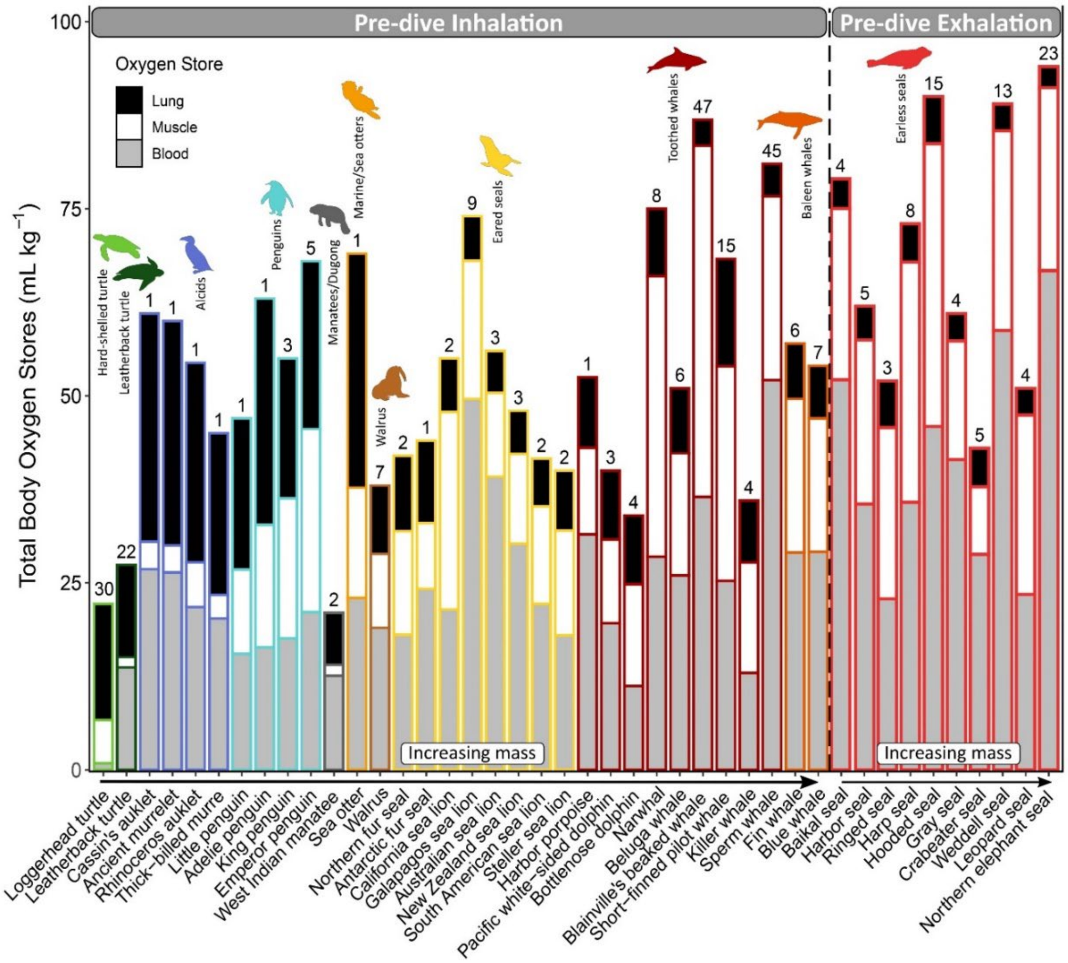
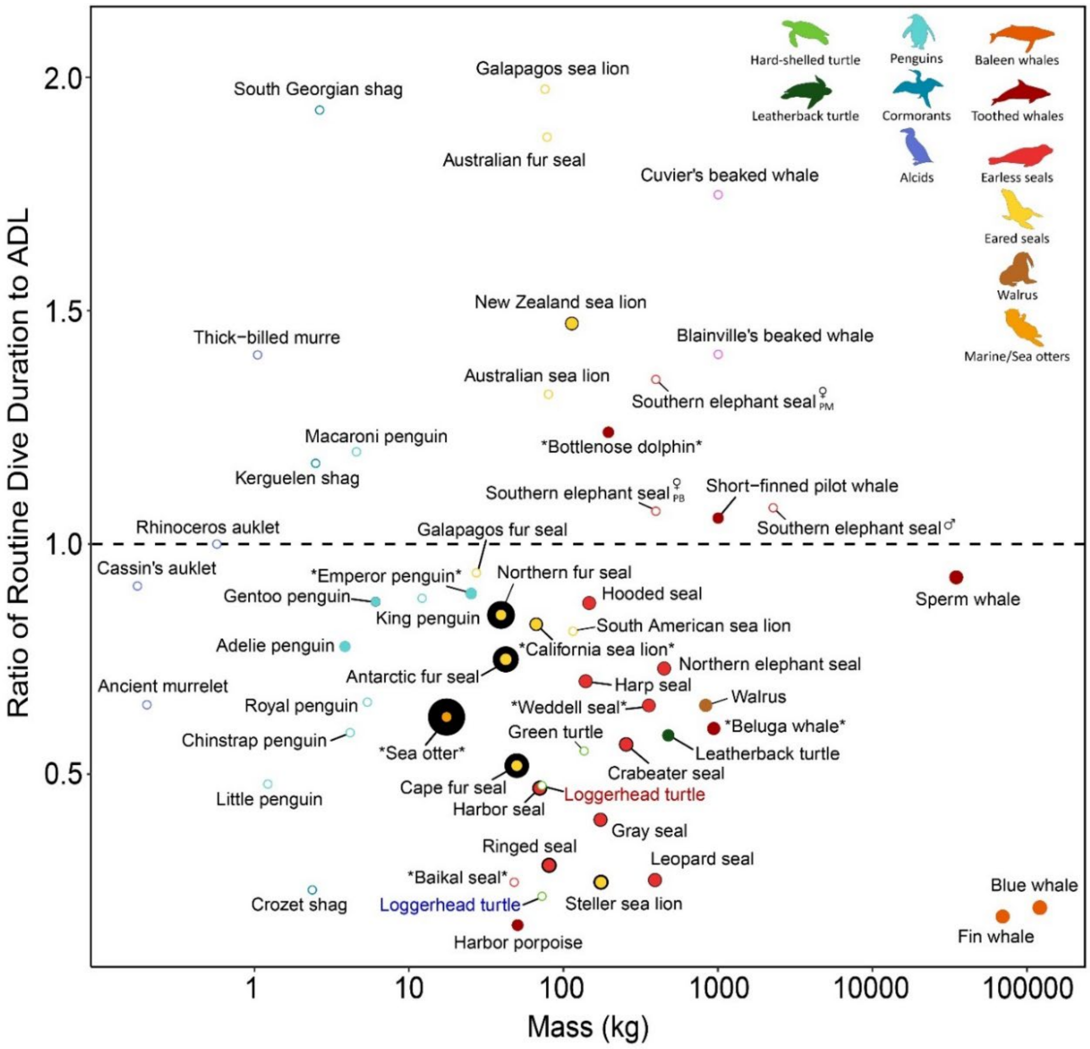


Figure 1.4 Magnitude and distribution of mass-specific total body oxygen stores and the relative contributions of each oxygen-storing compartment: lung (black), muscle (white) and blood (gray). Divers are grouped by those that inhale or exhale upon descent and ordered within each common name group by increasing body mass. Routine dive duration (minutes) is indicated above the bar for each species. All species of sea turtles, seabirds, and marine mammals for which this data is available to the best of our knowledge were included. Refer to Table A1.3 for data sources.

Figure 1.5 The relative amount of insulation across divers with varying dive performance. Dive performance here is defined as the ratio of routine dive duration to aerobic dive limit (ADL). A ratio greater than 1 indicates diving behavior exceeds what is expected based on ADL and diving performance may be close to physiological limits. Species denoted by asterisks have ADLs determined by lactate measurements; all other species' ADLs are estimated from oxygen stores and oxygen consumption rates (cADL) or behaviorally (bADL). Please refer to Table S3 for the various methods used to estimate ADL when interpreting the figure. The relative size of the colored points indicates blubber thickness and the black border around the colored points represents fur/feather density. Open points are species for which blubber thickness and/or fur/feather density are not available to the best of our knowledge, but are included for interspecific comparison. In addition to variation introduced by how ADL is estimated (see method for each species in Table A1.3), ADLs may vary across seasons and between sexes (especially for sexually dimorphic species, e.g., southern elephant seal; PM = post-molt foraging trip, PB = post-breeding foraging trip). The ADL of ectotherms will differ in cold versus warm water (e.g., blue versus red labeled loggerhead turtle) due to the temperature sensitivity of their metabolism. Generally, most species dive within their ADL, including earless seals and baleen whales, and reliance on blubber rather than fur is common among the larger divers. Other species, such as the Australian fur seal and South Georgian shag, routinely exceed their ADL. In addition to ecological factors (e.g., benthic foraging), increased thermoregulatory costs associated with a reduced air layer in the fur/feathers at depth may contribute to the need of performing near physiological limits for these relatively smaller divers. Refer to Table A1.3 for data sources.



Ratio of Routine Dive Duration to ADL
Mass (kg)
2.0
1.5
1.0
0.5
1
10
100
1000
10000
100000
Hard-shelled turtle
Penguins
Baleen whales
Leatherback turtle
Cormorants
Toothed whales
Alcids
Earless seals
Eared seals
Walrus
Marine/Sea otters
South Georgian shag
Galapagos sea lion
Australian fur seal
Cuvier's beaked whale
New Zealand sea lion
Thick−billed murre
Blainville's beaked whale
Australian sea lion
Southern elephant seal ♀ PM
Macaroni penguin
Bottlenose dolphin
Kerguelen shag
Southern elephant seal ♀ PB
Short−finned pilot whale
Rhinoceros auklet
Southern elephant seal ♂
Galapagos fur seal
Cassin's auklet
Emperor penguin
Northern fur seal
Gentoo penguin
Hooded seal
Sperm whale
King penguin
South American sea lion
Adelie penguin
California sea lion
Antarctic fur seal
Northern elephant seal
Ancient murrelet
Harp seal
Royal penguin
Weddell seal
Walrus
Beluga whale
Chinstrap penguin
Green turtle
Sea otter
Leatherback turtle
Crabeater seal
Cape fur seal
Little penguin
Loggerhead turtle
Harbor seal
Gray seal
Ringed seal
Leopard seal
Baikal seal
Blue whale
Crozet shag
Loggerhead turtle
Steller sea lion
Fin whale
Harbor porpoise

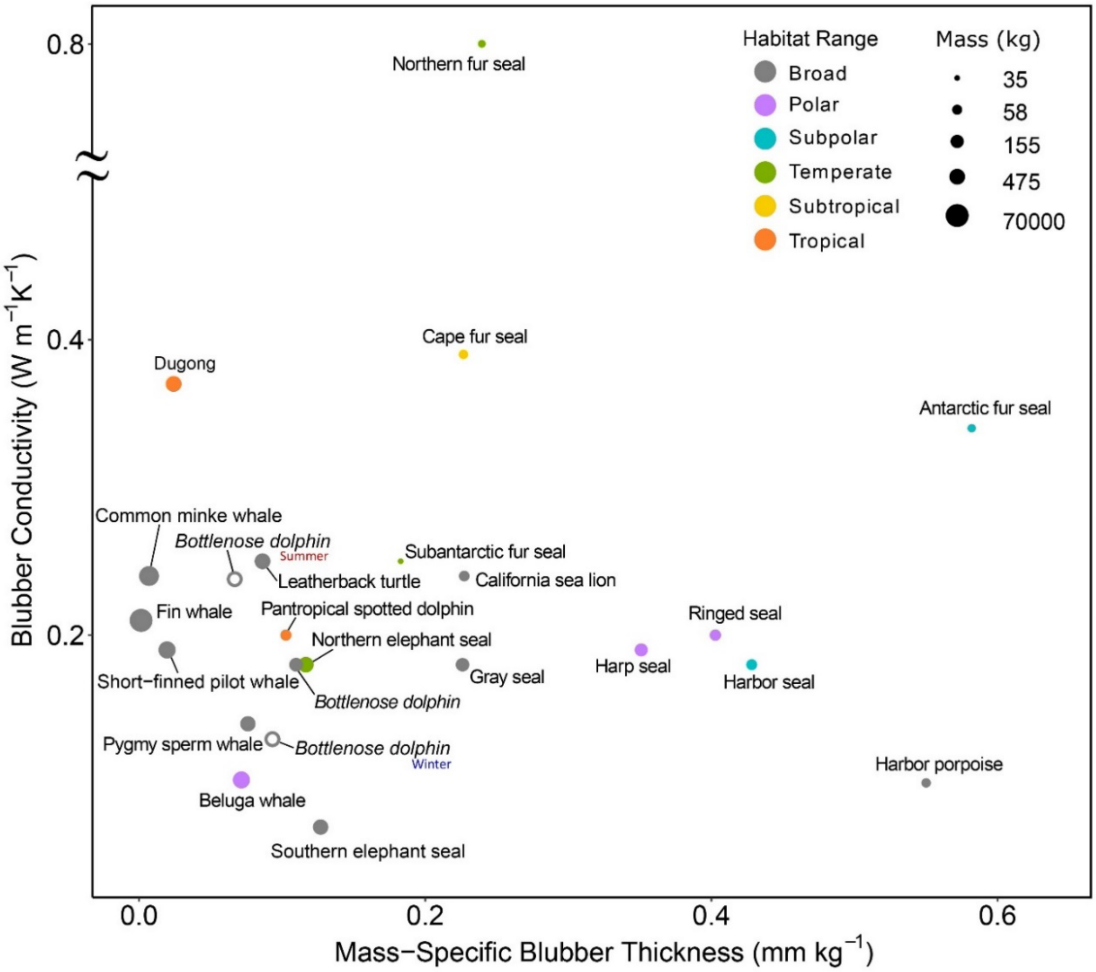
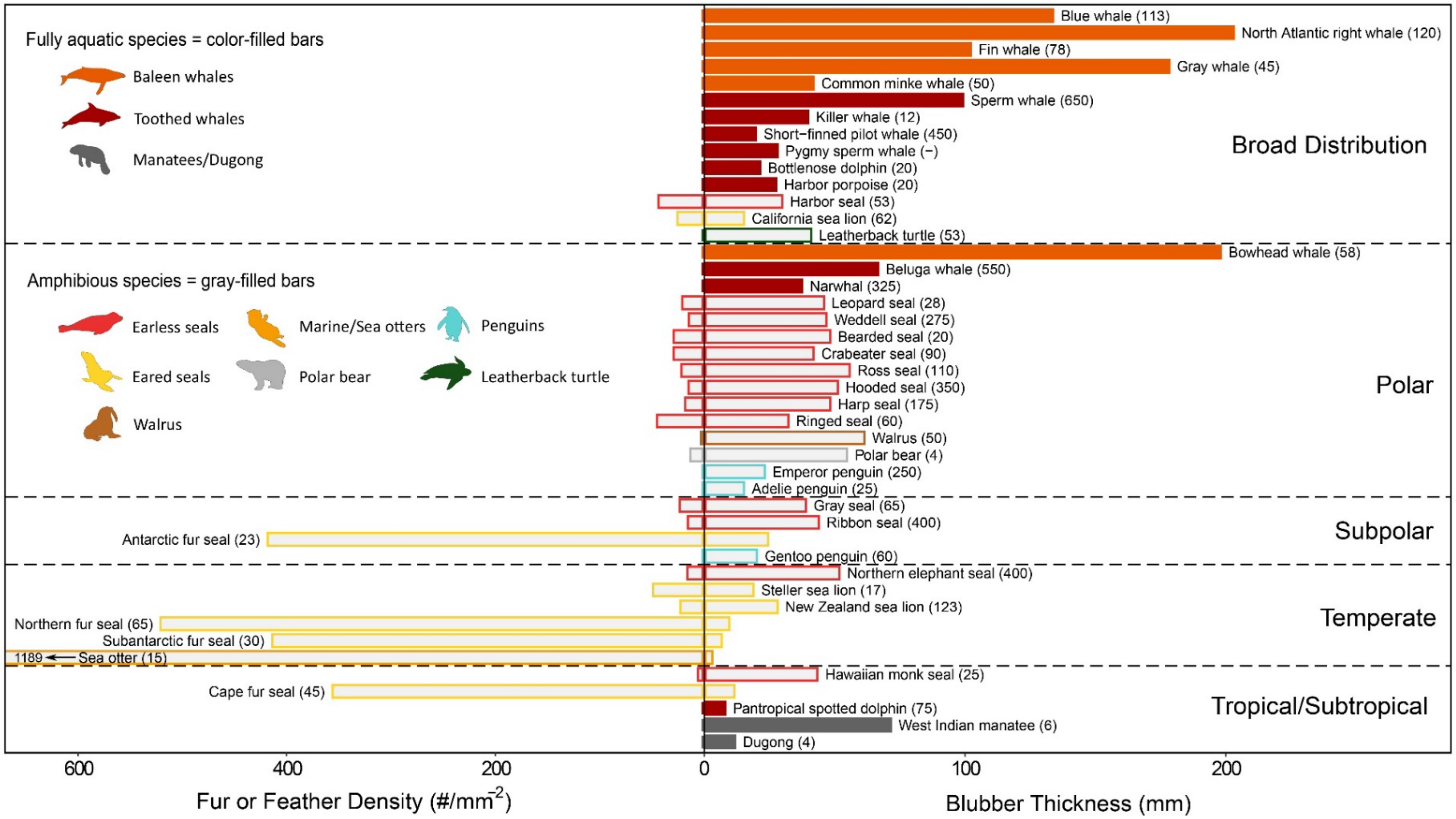


Figure 1.6 *Ex vivo* blubber conductivity versus mass-specific blubber thickness demonstrates the variability between species occupying different thermal habitat ranges in balancing the trade-offs between quality and quantity of blubber. Blubber quality here is represented by conductivity, where lower values mean less heat transfer and thus better-quality insulation. Larger whales and broadly distributed species have relatively little, but high-quality blubber. The poor-quality blubber of the Northern fur seal is compensated by its thick fur; in contrast, dugongs have poor insulation and thus a narrow thermal niche. Blubber conductivity was determined using the method indicated in Table A1.3 on excised samples. The only exceptions are the two additional bottlenose dolphins plotted as open points that use data from live animals in winter and summer months to demonstrate the seasonal effects of temperature on insulation. Refer to Table A1.1 for absolute latitudes used for determining habitat range (broad indicates the species span more than one habitat range) and Table A1.3 for blubber and mass data sources.

Figure 1.7 A comparison of the quantity of external and internal insulation among marine divers that occupy different habitat ranges. Species were included for which both fur/feather density (number of hairs/feathers per mm^{-2}) and blubber thickness (mm) are known (values represent whole-body averages, i.e. not site-specific). It was assumed that cetaceans and sirenians have lost all insulating hair. Within each habitat range, species are grouped by family and ordered by increasing mass along the vertical axis. Routine dive depth (meters) is indicated in parentheses for each species. Fully aquatic species (color-filled bars) rely exclusively on blubber, whereas amphibious species (gray-filled bars) that retain both forms of insulation vary in which layer is most effective. The primary insulation layer for the species is indicated by whether the species common name is written on the fur/feather or blubber side of the graph. Amphibious species with broad distributions (i.e., species that span more than one habitat range) use blubber as their primary insulation layer. With the exception of the Antarctic and Cape fur seals, those that rely on fur as their primary insulation are found in temperate zones, but a gradient of morphological adaptations is seen in this region. Few data exist on feather densities, which are orders of magnitude smaller when compared to fur densities. Moreover, while contour feather density is generally reported, plumule feathers provide greater insulation and are present at higher densities. Refer to Table A1.1 for absolute latitudes used for determining habitat range and Table A1.3 for insulation layer properties data sources.


Fully aquatic species = color-filled bars
Baleen whales
Toothed whales
Manatees/Dugong
Amphibious species = gray-filled bars
Earless seals
Marine/Sea otters
Penguins
Eared seals
Polar bear
Leatherback turtle
Walrus
Blue whale (113)
North Atlantic right whale (120)
Fin whale (78)
Gray whale (45)
Common minke whale (50)
Sperm whale (650)
Killer whale (12)
Short−finned pilot whale (450)
Pygmy sperm whale (−)
Bottlenose dolphin (20)
Harbor porpoise (20)
Harbor seal (53)
California sea lion (62)
Leatherback turtle (53)
Broad Distribution
Bowhead whale (58)
Beluga whale (550)
Narwhal (325)
Leopard seal (28)
Weddell seal (275)
Bearded seal (20)
Crabeater seal (90)
Ross seal (110)
Hooded seal (350)
Harp seal (175)
Ringed seal (60)
Walrus (50)
Polar bear (4)
Emperor penguin (250)
Adelie penguin (25)
Polar
Gray seal (65)
Ribbon seal (400)
Antarctic fur seal (23)
Gentoo penguin (60)
Subpolar
Northern elephant seal (400)
Steller sea lion (17)
New Zealand sea lion (123)
Northern fur seal (65)
Subantarctic fur seal (30)
1189 ← Sea otter (15)
Temperate
Hawaiian monk seal (25)
Cape fur seal (45)
Pantropical spotted dolphin (75)
West Indian manatee (6)
Dugong (4)
Tropical/Subtropical
600
400
200
0
100
200
Fur or Feather Density (#/mm^{-2})
Blubber Thickness (mm)

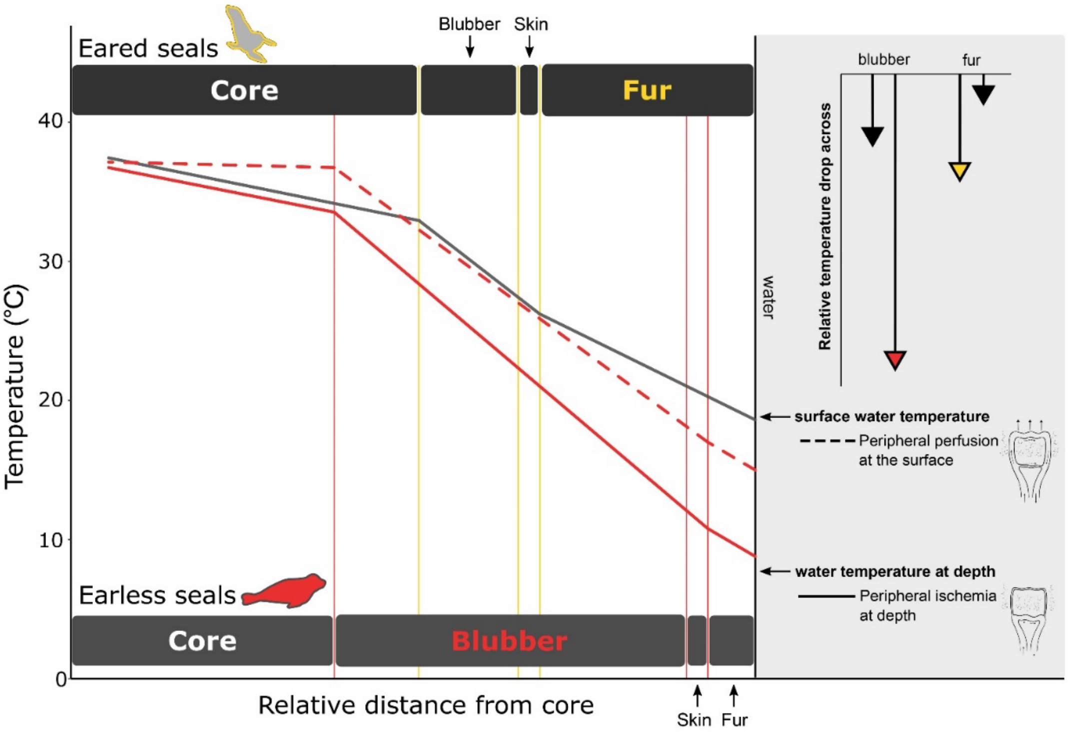
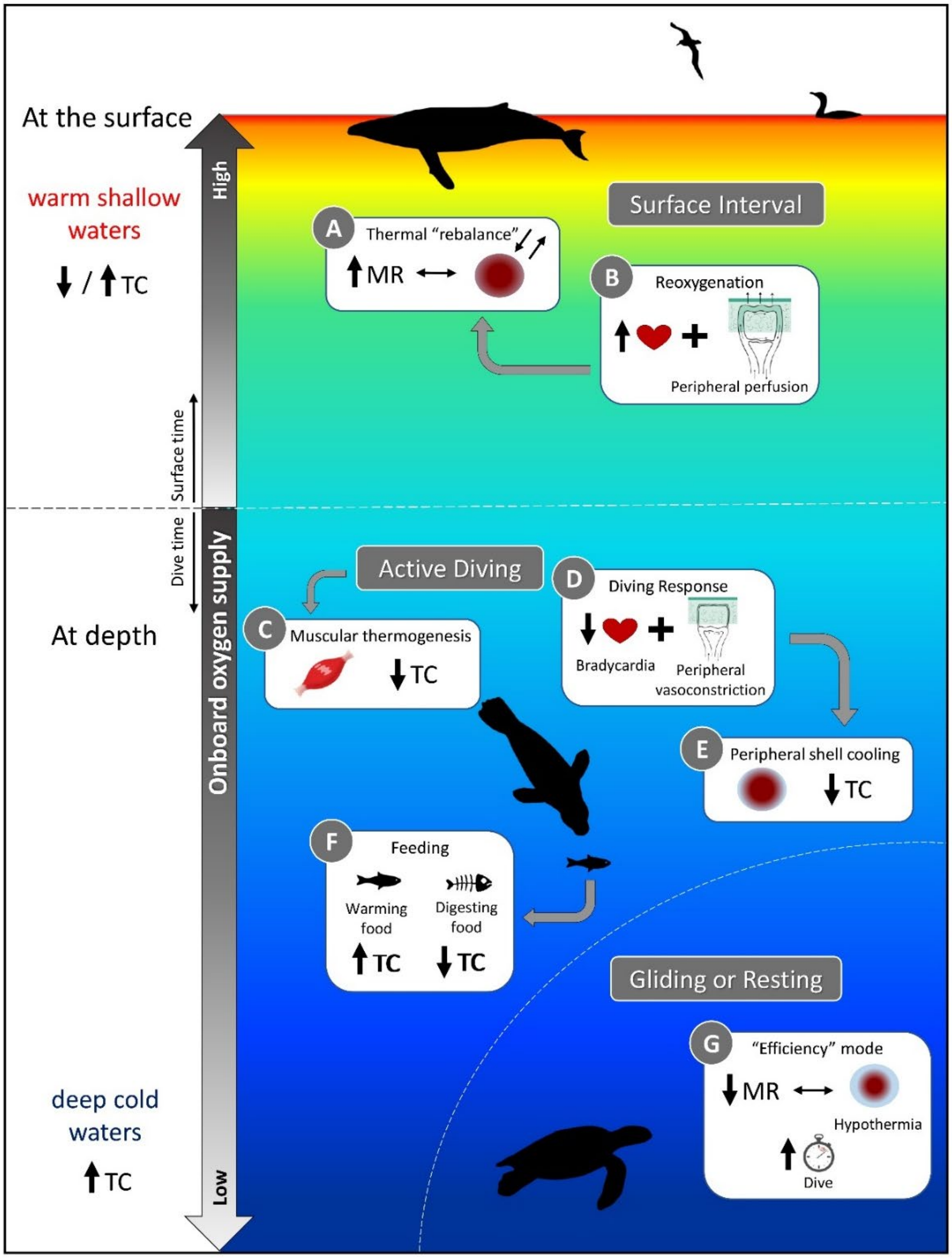


Figure 1.8 A comparison of the temperature gradients within the fur and blubber layer for eared (gray line) and earless seals (red line) that primarily depend on fur and blubber, respectively, for insulation. The relative thicknesses of the insulation layers are scaled based on the thickness of the primary insulation needed to provide equal insulation for each species. While diving (solid lines), peripheral vasoconstriction reduces blood flow to the periphery. For earless seals, this mitigates heat loss by keeping the skin within a few degrees of water temperature. For eared seals, the air layer in the fur provides an insulative barrier and prevents such a drastic reduction in peripheral temperature. The lengths of the arrows in the upper right depict the extent to which temperature decreases in the primary (colored arrowhead) versus secondary (black arrowhead) insulation layer when at depth. Larger temperature drops are observed in the primary insulative layer—fur for the eared seal and blubber for the earless seal—due to its lower conductivity when compared to that of the other species: pelt conductivity of the eared seal (0.11 W m^{-1} $°C^{-1}$) < earless seal (0.16 W m^{-1} $°C^{-1}$) whereas blubber conductivity of the earless seal (0.19 W m^{-1} $°C^{-1}$) < eared seal (0.28 W m^{-1} $°C^{-1}$). At the surface, peripheral perfusion reduces the temperature gradient within the core and blubber layer (dashed line), resulting in warmer skin temperatures. Data sources: Northern fur seal, *Callorhinus ursinus* (Scheffer, 1961; Ohata et al., 1977; Liwanag, 2008; Sharma and Liwanag, 2017); Northern elephant seal, *Mirounga angustirostris* (Kuhn & Costa, 2006; Favilla, unpublished data)

Figure 1.9 A schematic representation of the various physiological demands faced by air-breathing divers and how thermoregulatory costs (TC) are affected. While some activities, such as digestion (Box F) and muscular heat production (Box C) may reduce TC through substitution, diving into cold waters will increase TC (bottom side panel), unless mechanisms to mitigate heat loss are used (Box E & G; e.g., long, resting dives of sea turtles in which metabolic rate (MR) is reduced). A relaxation of the dive response at the surface (Box B, vs. Box D at depth) may facilitate regaining thermal balance (Box A), but the relative amount of time spent at the surface to achieve homeostasis may also be dictated by gas exchange in addition to thermoregulatory functions. If TC increases because surface waters are too warm to dump sufficient heat to compensate for increased activity, thermal inertia, etc. (top side panel), then diving activity may be altered to account for increased thermoregulatory needs. Refer to sections 3.2 – 3.4 of the text for further explanation.


At the surface
warm shallow waters
↓ / ↑ TC
High
Surface Interval
A Thermal "rebalance"
↑MR ↔
B Reoxygenation
↑ +
Peripheral perfusion
Surface time
Dive time
Onboard oxygen supply
Active Diving
At depth
C Muscular thermogenesis
↓TC
D Diving Response
↓ +
Bradycardia
Peripheral vasoconstriction
E Peripheral shell cooling
↓TC
F Feeding
Warming food
Digesting food
↑TC ↓TC
Gliding or Resting
G "Efficiency" mode
↓MR ↔
Hypothermia
↑ Dive
deep cold waters
↑TC
Low

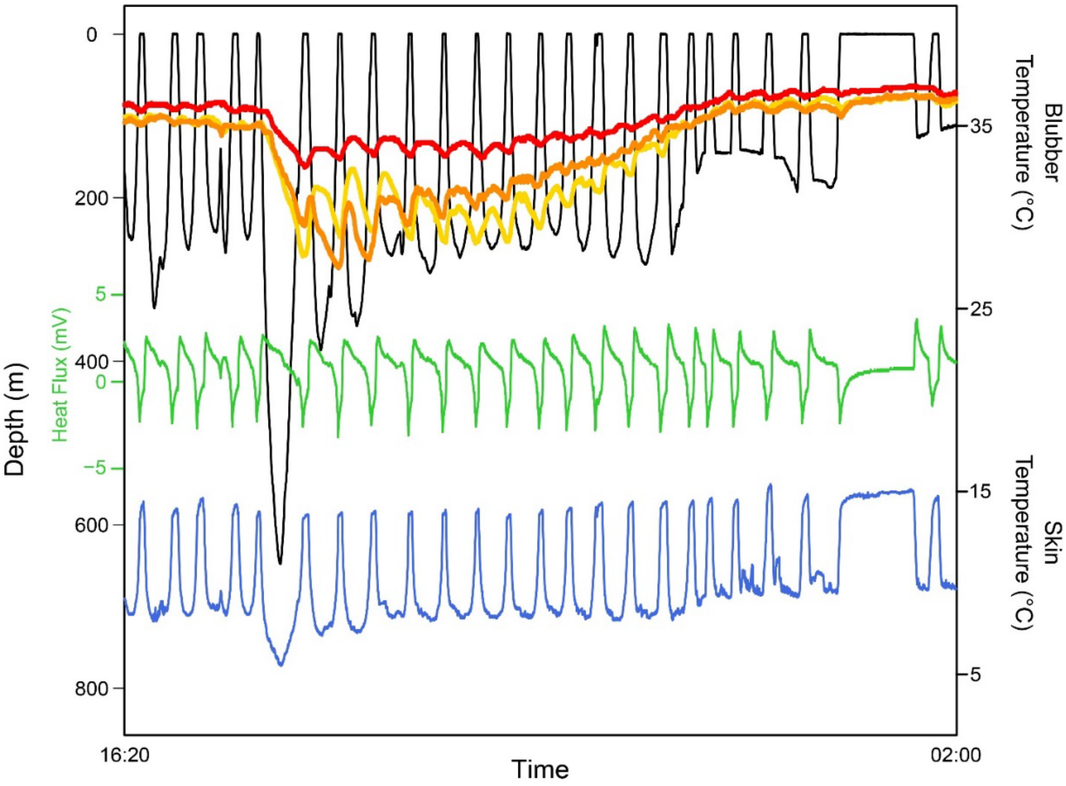


Figure 1.10 An example of time series data from a freely diving juvenile Northern elephant seal, *Mirounga angustirostris*, over a short at-sea trip equipped with physiological biologgers that measure heat flux and body temperatures. The dive profile (black) shows a deep dive to >600 m followed by an extended surface interval many hours later. The heat flux profile (green)—shown in raw voltage units—indicates whether the seal is gaining (>0 mV) or losing heat (<0 mV). Skin temperature (blue) measured by a thermistor imbedded in the heat flux sensor remained near water temperature (not shown; measured by a thermistor on the satellite tag mounted on the seal's head). Three thermistors inserted into the blubber layer (red=deep, orange=mid, yellow=shallow) show how the blubber temperature gradient changes with diving behavior, suggesting changes in peripheral perfusion (Favilla, unpublished).

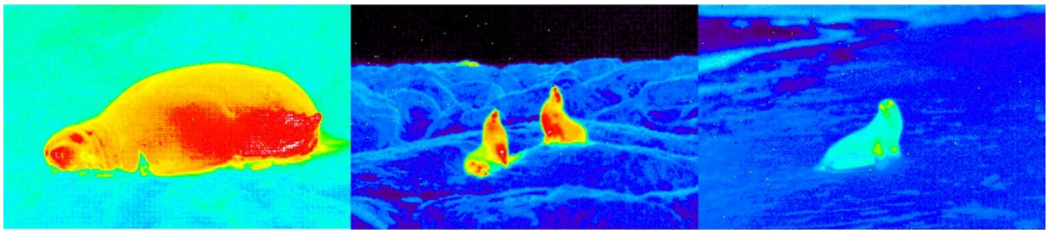


Figure 1.11 Infrared thermographic images of Australian sea lions, *Neophoca cinerea,* on Kangaroo Island, South Australia where areas with warmer colors indicate higher temperatures and thus greater heat loss. Left image, A female sea lion hauled out on the beach. The greatest heat loss is through the eyes, nose and flippers. Middle image, two sea lions appear considerably warmer than the surrounding habitat. Notice that the flippers are significant thermal windows. Right image, a female sea lion is just coming out of the water. Although the animal has significantly lower heat loss than the previous two images where the animals had been out of the water for some time, the female is still losing some heat from the eyes and the base of the fore flippers. Photos by Heather Liwanag.

Chapter 2

Advances in thermal physiology of diving marine mammals: The dual role of peripheral perfusion

Arina B. Favilla, Markus Horning, Daniel P. Costa

2.1 Abstract

The ability to maintain a high core body temperature is a defining characteristic of all mammals, yet their diverse habitats present disparate thermal challenges that have led to specialized adaptations. Marine mammals inhabit a highly conductive environment. Their thermoregulatory capabilities far exceed our own despite having limited avenues of heat transfer. Additionally, marine mammals must balance their thermoregulatory demands with those associated with diving (i.e., oxygen conservation), both of which rely on cardiovascular adjustments. This review presents the progress and novel efforts in investigating marine mammal thermoregulation, with a particular focus on the role of peripheral perfusion. Early studies in marine mammal thermal physiology were primarily performed in the laboratory and provided foundational knowledge through *in vivo* experiments and *ex vivo* measurements. However, the ecological relevance of these findings remains unknown because comparable efforts on free-ranging animals have been limited. We demonstrate the utility of biologgers for studying their thermal adaptations in the context in which they evolved. Our preliminary results from freely diving northern elephant seals (*Mirounga angustirostris*) reveal blubber's dynamic nature and the

complex interaction between thermoregulation and the dive response due to the dual role of peripheral perfusion. Further exploring the potential use of biologgers for measuring physiological variables relevant to thermal physiology in other marine mammal species will enhance our understanding of the relative importance of morphology, physiology, and behavior for thermoregulation and overall homeostasis.

2.2 Introduction

Few endothermic organisms live at ambient temperatures at or near body temperature. The marine environment is particularly challenging for thermoregulation due to the high thermal conductivity of water (Dejours, 1987). Marine endotherms must maintain thermal balance while immersed in a medium that conducts heat roughly 25 times faster than air (Pendergast & Lundgren, 2009). Additionally, the marine environment provides limited thermal refugia except perhaps in the vertical dimension or when hauling out. This thermally challenging environment has provided intense evolutionary pressure as endothermic tetrapods transitioned from terrestrial to aquatic living on multiple occasions (Pyenson et al., 2014; Reidenberg, 2007). While the underlying physiological mechanisms of marine mammals resemble those of humans, their thermoregulatory capabilities far exceed our own.

2.2.1 Technological innovations enable physio-logging of marine mammals

Marine mammals display many extreme adaptations suitable for investigations aligned with the Krogh Principle[1]. The increased thermal challenges often translate to

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[1] The Krogh Principle states that “for a large number of problems there will be some animal of choice or a few such animals on which it can be most conveniently studied” (Krogh, 1929). We consider

greater signal-to-noise ratio that may facilitate mechanistic studies linking cause and effect, especially through the application of biologging devices. However, challenging logistics, limited animal access, and animal welfare issues may limit such studies in addition to technological challenges associated with high-pressure cycles in a corrosive environment (Sikes & Gannon, 2011). As a result, most physiology research was carried out on dead (and/or excised tissue samples) or captive marine mammals. Field research, on the other hand, consisted primarily of observational studies of marine mammals on land (Figure 2.1).

Recent biologging innovations are now revealing novel insights into the behavior and physiology of these difficult-to-study species (Figure 2.1). The application of biologging to study physiology remotely, a.k.a. physio-logging (Fahlman et al., 2021), has also enabled the extension of earlier, traditional controlled-access laboratory experiments (e.g., Boily & Lavigne, 1996; Gallivan et al., 1983; Hansen & Lavigne, 1997; Hart & Irving, 1959; Morrison et al., 1974) and modeling efforts (e.g., Boily et al., 2000; Hokkanen, 1990; Kvadsheim et al., 1997; Watts et al., 1993) with field studies on free-ranging animals that are critical for determining the ecological relevance of findings derived from laboratory studies and modeling efforts (Fig. 2). To demonstrate this, we present preliminary results from our research on the thermal physiology of freely diving elephant seals. By capturing fine-scale changes in their thermal responses while diving, our findings provide novel

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marine mammals to be ‘Krogh organisms’ for studying thermal physiology because they have noteworthy, or even extreme, thermal adaptations (e.g., morphological traits and physiological mechanisms) (Green et al., 2018).

evidence of blubber’s dynamic nature and the complex interaction between thermoregulation and the dive response due to the dual role of peripheral perfusion.

2.3 Marine mammals: Masters of endothermy in water

2.3.1 An evolutionary perspective of their thermal adaptations

Extant marine tetrapods display diverse adaptations spanning morphology, physiology, and behavior that allow them to thrive in challenging thermal habitats. Species with longer evolutionary histories spend a greater proportion of time in the water. This has led to a convergence of morphological adaptations (Kelley & Pyenson, 2015; Reidenberg, 2007), including those pertinent to thermal physiology, such as a large size (i.e., small surface-area-to-volume ratio) and little to no hair (Ridgway, 1972). Over time, the loss of hair or fur was possible due to an evolutionary transition to blubber as the primary insulation (Liwanag et al., 2012b, 2012a). While mammals typically have subcutaneous fat, most marine mammals have a specialized blubber layer composed of adipose tissue reinforced by collagen and elastin (Pabst et al., 1999; Parry, 1949). The fully aquatic marine mammals, such as whales and dolphins (i.e., cetaceans), are the prime example of transitioning to this morphological adaptation (Wang et al., 2015). They rely solely on blubber for insulation.

In contrast, amphibious marine mammals have retained fur in addition to having a blubber layer because of the unique challenge of dealing with the contrasting thermal properties of air and water. These species include seals and sea lions (i.e., pinnipeds) that forage at sea but must return to land to breed or molt. The relative importance of their insulation layers depends on the frequency and duration of time at sea. Some species can strategically partition their time between land and water to meet their thermal demands (Khamas et al., 2012; Tarasoff & Fisher, 1970). Other species are constrained by long seasonal periods in either environment. They must therefore be able to maintain thermal balance in both (Codde et al., 2016; Gentry, 1973).

In water, blubber is advantageous due to its hydrodynamic qualities and greater functional resistance to pressure compared to fur. For this reason, deep divers do not rely on their fur for insulation while at depth. The pinnipeds' broad spectrum of diving capabilities is reflected in their relative blubber thicknesses and fur densities (Favilla & Costa, 2020). These species provide interesting case studies for comparing and understanding the role of blubber in their thermal flexibility (Ladds et al., 2017; Rutishauser et al., 2004).

What makes blubber the ideal insulator also makes it challenging for *in vivo* studies. Blubber is internal, which allows for blood to bypass this insulation when needed (Figure 2.3A). A complex microvasculature network exists within the skin and blubber of marine mammals (Bryden & Molyneux, 1978; Khamas et al., 2012; McClelland et al., 2012; Molyneux & Bryden, 1978; Tarasoff & Fisher, 1970). Superficial vessels are associated with arteriovenous anastomoses. These structures allow fine-scale adjustment to blubber's insulative and transmissive properties by either constricting or dilating to regulate peripheral perfusion. By effectively modifying their conductance, marine mammals control the characteristics of the thermal gradient (Figure 2.3B) and can maintain a high core body temperature while immersed in water (Boyd, 2000; Irving & Hart, 1957). Therefore, understanding the thermoregulatory strategies of diving marine mammals requires examining the physiological mechanisms that influence heat transfer at their periphery.

2.3.2 Modes and spatial heterogeneity of heat transfer

Marine mammals experience fewer avenues of heat transfer in water: there is no evaporative heat loss, and radiation is minimal as it is quickly absorbed by water. Thus, conduction and convection, both of which depend on the temperature differential, are the principal mechanisms through which heat transfer occurs. The temperature gradient and the thickness of the blubber layer determine the conductive heat transfer through the blubber and ultimately how much core body heat reaches the skin. Convective heat transfer causes the heat at the skin's surface to dissipate to the surrounding water. Unlike the thermal conductivity of blubber, which is a single readily measured property, the convective heat transfer coefficient depends on several factors, including fluid properties and type of fluid flow (Massoud, 2005). However, often neglected is the variability introduced by internal forced convection, which occurs due to active transfer of heat through the circulation of blood (Gallivan & Ronald, 1979; Kvadsheim & Folkow, 1997; Xu & Tikuisis, 2014).

Many studies have referred to conduction through the blubber layer when both conductive and convective mechanisms were considered. To account for this, the blubber conductivity, which describes how readily heat transfers through a material, was adjusted using a correction ('perfusion') factor (e.g., Brodie, 1975; Hokkanen, 1990). The values of marine mammal blubber conductivity are typically measured from excised blubber and genuinely reflect its intrinsic property. In live blubber, variable peripheral perfusion will contribute to heat transfer through active transport resulting in a different heat transfer rate than would be expected by conduction alone. Circulating blood thus sensibly changes the conductivity of the blubber layer (Ducharme & Tikuisis, 1991; Kanwisher & Sundnes, 1966; Meagher et al., 2008). Analyzing convective heat transfer is more complex than conduction. By incorporating a variable blubber conductivity relative to peripheral perfusion, the biophysical problem is simplified.

Kvadsheim and Folkow (1997) measured the total heat transfer (conductive and convective) with heat flux sensors in harp seals (*Pagophilus groenlandicus*) resting in the water to determine the circulatory effects of heat transfer through the blubber. This was compared to the calculated conductive heat transfer based on the blubber temperature gradient measured with thermistors placed in the deep blubber and subcutaneously. Convective heat transfer was minimal in cold water, and heat loss was mainly from the trunk. An increasing proportion of convective heat loss from the flippers as water temperatures increased to ~23-24°C documented the role of flippers as heat dissipators when seals were heat-stressed. This has also been demonstrated for the flippers and flukes of cetaceans (Meagher et al., 2008; Scholander & Schevill, 1955) and the hands and feet of humans (Taylor et al., 2014). The lack of insulation in these appendages and their large surface-area-to-volume ratio make these sites ideal as thermal windows, where rapid changes in heat transfer are induced through physiological mechanisms (i.e., regulating blood flow; Andrade, 2015; Romanovsky, 2014; Taylor et al., 2014).

This experiment demonstrated how ambient temperatures influence vasomotor control in seals, albeit to varying degrees across the body, which aligns with the expansive literature on the effects of temperature on vasoconstriction and vasodilation in humans (Kellogg, 2006; Low et al., 2020; Savage & Brengelmann, 1996; Walløe, 2016; Wong & Hollowed, 2017). While equivalent mechanisms underlie peripheral perfusion, marine mammals may have greater thermal capabilities than humans, in part, due to a greater density and distribution of arteriovenous anastomoses. Arteriovenous anastomoses are primarily found in the glabrous skin of humans and play a significant role in regulating body temperature with minimal energy expenditure within the thermoneutral zone (Romanovsky, 2014; Walløe, 2016). In contrast, marine mammals have arteriovenous anastomoses along their body surface—although some more than others (Bryden & Molyneux, 1978; Molyneux & Bryden, 1978)—which allows the well-insulated trunk to substantially contribute to total body heat flux (Kvadsheim & Folkow, 1997; Mauck et al., 2003; Øritsland, 1968). The different thermal responses of glabrous (i.e., non-hairy) and hairy skin regions of humans are analogous to the different roles of flippers or fins and the body trunk of marine mammals (Romanovsky, 2014). However, the importance of skin temperature as a feedback signal in marine mammals is unclear especially since water dampens the variation in temperature across the skin compared to in air (Guerrero et al., 2021; Hampton et al., 1971; Kastelein et al., 1997; Mauck et al., 2003; Meagher et al., 2008; Nienaber et al., 2010; Norris et al., 2010; Willis et al., 2005; Worthy, 1991). Given the limited modes of heat transfer in water and the additional constraints that diving imposes on regulating their body temperature (Figure 2.4), marine mammals are likely to rely on arteriovenous anastomoses and adjustments in peripheral perfusion as a primary mechanism for thermoregulation.

2.3.3 Perspectives from the field of diving physiology

In addition to the challenges mentioned above faced by endotherms in the marine environment, free-ranging marine mammals must balance the physiological demands of thermoregulation with exercise and diving. The cardiovascular system is integral to the physiological responses associated with the dive response, exercise, and thermoregulation. These responses could either be in sync or conflict, requiring marine mammals to coordinate their activities or compromise their performance (Favilla & Costa, 2020). The dive response involves a suite of cardiovascular adjustments, including apnea, bradycardia, and peripheral vasoconstriction. Together they reduce blood flow and oxygen consumption of non-essential tissues to conserve their 'on-board' oxygen supply for vital organs, such as the heart and brain (Costa, 2007). Therefore, blood flow regulation is essential for the redistribution of oxygen and heat within the body. While endotherms are generally considered homeotherms, homeothermy may not be the most efficient strategy for marine mammals due to the physiological demands of diving (Levesque et al., 2016). Any regional or systemic drop in body temperature would reduce tissue’s metabolic requirements (i.e., oxygen consumption) due to the temperature dependence of metabolic energy production (quantified by the Q_{10} temperature coefficient). This would extend the aerobic dive limit by decreasing the rate at which on-board oxygen stores are depleted. Hypothermia-induced metabolic suppression and regional heterothermy have been posited as separate hypotheses to explain how marine mammals increase their aerobic dive capacity (Butler, 2004; Scholander et al., 1942). The role of hypothermia and peripheral cooling has been primarily discussed in the diving physiology literature (Butler, 2004; Meir & Ponganis, 2010; Ponganis et al., 2003; Scholander et al., 1942). Still, the thermoregulatory implications of these diving strategies have not been adequately investigated. By integrating and building on knowledge gained in the separate considerations of diving physiology and thermal physiology, current research is advancing our understanding of the complex interactions between the dive response and thermoregulation.

2.4 Insights from *ex vivo* and *in vivo* lab studies

Unlike research in diving physiology that has embraced physio-logging to simultaneously record dive profiles along with physiological responses (e.g., heart rate and blood oxygen saturation) in freely diving species (McDonald & Ponganis, 2013; Meir et al., 2009, 2013; Meir & Ponganis, 2010; Ponganis, 2007, 2021; Ponganis et al., 1997; Tift et al., 2017; C. L. Williams & Ponganis, 2021), progress in thermal physiology has heavily relied on *ex vivo* studies (e.g., Bryden & Molyneux, 1978; Koopman, 2007; Molyneux & Bryden, 1978; Rommel et al., 1992; Tarasoff &

Fisher, 1970; Worthy & Edwards, 1990) or those on captive animals in the laboratory (e.g., Gallivan & Ronald, 1979; Hansen & Lavigne, 1997; McGinnis et al., 1972; Miller & Irving, 1975; Rosen & Renouf, 1997) (Figure 2.1). Similar to the differences between studying nude humans in the lab and humans in their routine states (e.g., clothed and working; Rutishauser et al., 2004), these laboratory findings demonstrated the maximum capabilities of marine mammals. Although these studies could not address whether or how often animals reached these maximum capabilities in their natural environments, they have, nonetheless, provided key insights that would not have been possible through field studies.

2.4.1 Structure meets function in blubber

Ex vivo studies have enhanced our understanding of the role of blubber by investigating the physical (e.g., adipocyte morphology, thickness, thermal conductivity; Ball et al., 2015; Dunkin et al., 2005; Horgan et al., 2014; Montie et al., 2008; Singleton et al., 2017) and biochemical (e.g., lipid content, fatty acid composition, and stratification; Bagge et al., 2012; Koopman, 2007; Liwanag et al., 2012b; Pearson, 2015; Samuel & Worthy, 2004) properties of blubber (Figure 2.2) . These have shown that most marine mammals have stratified blubber layers. The outer layer primarily functions as insulation where lipids with lower melting points confer flexibility particularly at lower temperatures. In contrast, the composition of the inner layer makes it more readily metabolized and thus primarily serves as an energy store (Figure 2.3B). The relative importance of either function is also dependent on age and season (Ball et al., 2015; Dunkin et al., 2005; S. R. Noren &

Wells, 2009), as well as species-specific thermal habitats and life-history strategies (McClelland et al., 2012; Worthy & Edwards, 1990). For example, blubber as an energy store may be more important for older animals during the breeding fast (especially for capital breeders) (Castellini et al., 2009; Cornick et al., 2016; Mellish et al., 2007). In contrast, blubber as an insulator may be more important for younger, smaller animals that have a greater body surface-area-to-volume ratio and/or are nutritionally dependent (Donohue et al., 2000; Dunkin et al., 2005; Hansen & Lavigne, 1997; Pearson et al., 2014).

The tradeoffs between blubber's dual role as insulation and an energy store are directly influenced by its relative thickness. Many studies using captive species have described the topographical distribution of the blubber layer and its significance (Beck & Smith, 1995; Cornick et al., 2016; Koopman, 1998; Mellish et al., 2007; Rosen & Renouf, 1997; Ryg et al., 1988; Samuel & Worthy, 2004; Tighe et al., 2016). In addition to seasonal and ontogenetic changes in blubber thickness, other changes in the blubber layer occur on much shorter time scales due to the physiological responses associated with diving, particularly the regulation of peripheral perfusion. Blubber is considered a dynamic insulator (Davis, 2019; Iverson & Koopman, 2018), and understanding its context-dependent roles can only be addressed *in vivo*.

2.4.2 A dynamic insulator used as a buffer zone

Many early studies investigated the thermoregulatory capabilities and whole-body thermal dynamics of marine mammals in laboratory settings (Figure 2.2). As early as the 1950s, experiments were performed *in vivo* to define a species's lower critical temperatures and whether an elevated metabolic rate is required to maintain thermal balance in an aquatic environment (Donohue et al., 2000; Gallivan & Ronald, 1979; Hampton & Whittow, 1976; Hart & Irving, 1959; Irving & Hart, 1957; Kasting et al., 1989; Kvadsheim et al., 2005; McGinnis et al., 1972; Morrison et al., 1974; D. P. Noren, 2002; Rutishauser et al., 2004; Worthy, 1991). Irving and Hart (1957) found differences in the blubber gradient explained how seals exhibited similar metabolic rates in air and water of the same temperature despite the greater cooling effects of water (Figure 2.5). They concluded that peripheral cooling is essential to allow homeothermy in aquatic 'bare-skinned' mammals. Such labile control of insulation through changes in vascular heat transfer would be advantageous over the static insulation provided by thick fur.

Fewer studies have investigated the upper critical temperatures of marine mammals while immersed. This is partly because they cannot respond to heat stress in water with evaporative cooling (Commission, 2001; Kvadsheim et al., 1997) (Figure 2.4). Without such an early warning indicator, there is the risk of surpassing their thermal tolerance limit, resulting in severe heat injury or death. Still, an experiment on captive bottlenose dolphins (*Tursiops truncatus*) resting in water examined how dolphins avoid hyperthermia when moving from cooler pelagic waters to warmer coastal waters (Heath & Ridgway, 1999). Water temperature was progressively increased and then maintained above skin temperature to prevent heat loss from the body. Heat flux values showed the rate of heat gain decreasing over time. Simultaneously, rectal temperatures declined up to 1.3°C of baseline temperature.

This reduction is surprising given the anticipated increase of 1.6°C based on basal metabolic heat production. These results imply that dolphins can redistribute core body heat to their periphery via increased peripheral blood flow. By using their blubber layer as a buffer zone to store heat, dolphins can achieve short-term heat tolerance (~1 hr) in coastal waters. Subcutaneous thermistors, alongside experiments investigating the phase change properties of blubber, could provide further evidence of blubber's dynamic role and its influence on peripheral heat flow and metabolic rates.

While similar experiments with large cetaceans would be challenging, modeling indicates that the regulation of peripheral perfusion is critical for long-term thermal homeostasis. Models based solely on the insulative properties of the blubber layer suggest that large whales are over-insulated for their size and metabolism (Hokkanen, 1990). While blood flow and metabolism were estimated, models that included peripheral circulation provided reasonable predictions of *in situ* temperature profiles of freshly harpooned fin and sei whales in the mid-1900s (Brodie & Paasche, 1985). These results suggest that whales must maintain some blood flow to the skin, even in the coldest waters they encounter, to maintain thermal balance. In warmer waters, the level of blood flow would increase exponentially.

These studies have provided key insights into the physiological responses to water temperature and thermal limits of species spanning three orders of magnitude in size and adapted to vastly different thermal habitats. However, the ecological relevance is limited since few marine mammals remain stationary in water for prolonged periods. Thus, an essential extension of these studies will require investigating how exercise and diving affect thermal dynamics.

2.4.3 Thermal effects of exercise and diving

The paradoxical interaction between the physiological demands of diving and exercise has interested many researchers (Castellini et al., 1985; D. P. Noren et al., 1999; S. R. Noren et al., 2012; Whittow, 1987; T. M. Williams et al., 1999). Studies have found that diving mammals seem to avoid the classic exercise response (Looney et al., 2019; Pendergast & Lundgren, 2009) and are rather well-adapted for exercise while breath-holding. A reduction in heart rate associated with the dive response reduces metabolism and conserves oxygen but is contrary to the expected elevated heart rate during exercise (Davis, 2019; Sparling & Fedak, 2004; T. M. Williams et al., 2000). Additionally, peripheral vasoconstriction reduces blood flow to the periphery during the dive, thus reducing oxygen supply to locomotory muscles (Scholander et al., 1942). To meet their exercising muscles' oxygen demands during breath-hold dives, marine mammals swim efficiently and utilize their larger muscle myoglobin oxygen stores (S. R. Noren & Williams, 2000; Ponganis et al., 2011). Studies have shown that the dive response is modulated by exercise (Davis & Williams, 2012; McDonald et al., 2018; S. R. Noren et al., 2012; T. M. Williams et al., 2015). Yet, whether the dive response is modulated by thermoregulatory demands and the associated consequences of exercise and diving on thermal homeostasis is unknown.

To investigate the thermal effects of exercise, the spatial patterns of heat flux in Steller sea lions (*Eumetopias jubatus*) were examined while stationary in the water, swimming naturally in a swim flume, and swimming under increased load (Willis et al., 2005). Areas with less insulation (hips and shoulders) had the highest heat flux values compared to other more insulated areas (middle and axillary girths) regardless of the level of physical exertion. It was concluded that the exercising Steller sea lions were not under thermal stress. Additionally, they used certain areas to preferentially dissipate heat (which parallels findings from Savastano et al., 2009). Studies of captive dolphins have shown that the dorsal fin serves as a flexible site for heat dissipation (Barbieri et al., 2010; Hampton & Whittow, 1976; McGinnis et al., 1972; Meagher et al., 2008), similar to the lesser insulated body surface areas of the Steller sea lions.

In addition to activity level, other factors influencing the use of thermal windows to control thermal balance are body size and water temperature. For example, Hawaiian spinner dolphins (*Stenella longirostris*) rely on activity-induced thermogenesis to maintain their body temperature in waters near their lower critical temperature, which are not uncommon in their habitat range (Hampton & Whittow, 1976; McGinnis et al., 1972). On the other hand, a larger delphinid species, the Pacific bottlenose dolphin, experienced elevated core temperatures after intense exercise, leading to a broader range in body temperatures than the stenothermic Hawaiian spinner dolphins (McGinnis et al., 1972). Despite these differences, the authors concluded that blood flow to the dorsal fin is independent of that to the body trunk for both species. Thus, the interacting effects of exercise and thermoregulation are species- and context-specific based on thermoneutral zones and capacities for thermogenesis.

Unlike studying exercise in a swim flume or large pool, using animals in a captive setting limits our ability to investigate how much the dive response modulates thermal responses because pools are shallow compared to the depths commonly reached by diving marine mammals (Favilla & Costa, 2020). D. P. Noren et al. (1999) took advantage of trained animals in a channel connected to the open ocean and recorded heat flux during dives using hand-held devices. Reduced heat flux at depth (15 m) compared to the surface suggests that heat dissipation is limited until the end of the dive where anticipatory tachycardia occurs. In an exceptional situation, elevated heat flux values at the dorsal fin were observed at depth on a dolphin that had been vigorously active prior to the dive. This indicates there was a momentary override of the dive response to dissipate heat through a thermal window. These findings beg the questions: how often is thermoregulation prioritized during natural diving conditions, and how much volitional control is involved in coordinating these potentially conflicting demands? Translating research with trained dolphins to the natural context can provide a sense of how close they operate to their thermal limits and their physiological capacity to adapt when faced with additional stressors (Figure 2.2).

2.4.4 Psychological influences of physiological responses

Researchers have used animals trained or forced to dive or haul out to investigate how anticipatory behavior and psychological influences modulate physiological responses (Figure 2.2). A diving physiology study compared the dive response in trained versus naïve harbor seals (*Phoca vitulina*) under forced submersions to investigate the effects of anticipation (Jobsis et al., 2001). Compared to naïve seals, trained seals accustomed to 3-minute forced submersions had significantly higher heart rates. They thus maintained greater blood flow to the muscle (measured using laser Doppler flowmetry). In one instance, the submersion was prolonged to 5 minutes without any cues. The heart rate and muscle blood flow profiles show abrupt reductions occurred at precisely 3 minutes into the submersion and were maintained at levels comparable to naïve seals until the end of the submersion (Figure 2.6). Although forced submersion is far from seals' natural diving behavior, this and other studies (e.g., Elmegaard et al., 2016; Hammel et al., 1977; Scholander et al., 1942; Zapol et al., 1979) demonstrated that animals can modify their physiological response when the need arises.

To investigate the degree of control seals exert over heat dissipation through thermal windows, Erdsack et al. (2012) used infrared thermography on trained harbor seals. Seals that hauled out voluntarily remained out of the water for several hours and developed thermal windows within minutes regardless of the environmental conditions. Significant amounts of heat dissipation occurred through these thermal windows, which could take several minutes to close once the animal returned to the water resulting in large energy losses. In contrast, when seals hauled out on command during training sessions, they anticipated transitioning between water and land several times. None developed thermal windows, which may be explained by the influence of their psychological state on the autonomic nervous system that regulates peripheral perfusion (Ootsuka & Tanaka, 2015). By suppressing the formation of thermal windows, amphibious marine mammals minimize excessive heat loss upon returning to water, and thus overall thermoregulatory costs. In addition to demonstrating how physiological demands are balanced to minimize energetic costs, these examples exemplify the value of laboratory studies because sometimes there are not simple parallel approaches in the field.

2.5 Thermal responses during natural diving behavior

Unlike captive studies where animal behavior is manipulated or limited to some extent, wild animals exert control over their activities. During normal, undisturbed diving, it is reasonable to assume that marine mammals that do not frequently haul out are ultimately capable of maintaining thermal balance. Investigating the mechanisms that underlie their physiological thermoregulation requires using remote methods, i.e. biologgers with physiological sensors (Figure 2.2).

2.5.1 Temperature regulation as a diving strategy

Studies in diving physiology have used state-of-the-art biologgers to record the impressive breath-hold dives of phocids (true seals) (Andrews, 1999; Hill et al., 1987; Hochachka, 2000; Ponganis et al., 1993). The addition of physiological sensors to time-depth recorders tested the hypothesis that hypothermia while diving enhances aerobic dive capacity and provided insights into body temperature regulation strategies. By measuring arterial and venous blood temperatures as a proxy for core body temperature, Meir & Ponganis (2010) demonstrated that a high mean core body temperature (36-37°C) is maintained throughout routine diving behavior (10-30 min) of juvenile northern elephant seals (*Mirounga angustirostris*). Additionally, there was no strong relationship between mean blood temperatures and duration of individual dives. These findings suggest that core hypothermia is not a common strategy in routine dives.

Other studies measuring muscle temperature have reported varying degrees of tissue cooling. For example, there was little to no decline in muscle temperatures in adult Weddell seals despite reductions in aortic temperatures during long dives (Ponganis et al., 1993). On the other hand, a decrease of 4°C occurred in the muscle of a diving immature elephant seal (Andrews, 1999). Both authors concluded that the working muscle was either hypometabolic or maintained some level of perfusion to allow dissipation of locally generated heat. They also noted that peripheral cooling extends beyond the insulation into muscle (Andrews, 1999; Hart & Irving, 1959). The degree to which this occurs and where core body temperature measurements are taken influence how the data are interpreted to align with different thermal strategies (McCafferty et al., 2015; Ponganis et al., 2003). As emphasized in these studies, the heterogeneity of body temperature precludes obtaining a representative whole-body temperature from just one location (McCafferty et al., 2015). Multiple measurements at different locations enable a more holistic understanding of heat distribution throughout the body and the mechanisms contributing to heat transfer.

2.5.2 Peripheral perfusion patterns: insights from modeling

Even if multiple simultaneous measurements are possible, numerous factors are impossible to control in the wild, making it difficult to decipher which variables are independent or dependent. To develop a mechanistic understanding of thermal dynamics in a swimming and diving animal, modeling approaches can simulate background variation while testing specific hypotheses regarding variables or parameters of interest. With a time-series of *in situ* measurements to compare model outputs, Boyd (2000) modeled peripheral circulation as 'on-off' states in a heat balance model to gain insight into the processes affecting the temporal dynamics of the temperature gradient between the water and skin of diving Antarctic fur seals (*Arctocephalus gazella*). During dives, the temperature gradient decreased and then increased towards the end of the dive. Transient increases occurred at the bottom of the dive and were attributed to changes in activity. Their model tracked this variability in the temperature gradient reasonably well. Discrepancies between the model output and *in situ* measurements were likely due to an overly simplistic representation of the regulation of perfusion as an abrupt switch between two states rather than a more graded process.

2.5.3 Fine-scale changes in peripheral heat flow while diving

Unlike fur seals which maintain a large temperature gradient between their skin and water (Boyd, 2000), marine mammals relying on blubber will experience more profound variations in their insulation due to changes in peripheral perfusion in response to water temperature and as a result of the dive response. Laboratory experiments have demonstrated the former by measuring physiological variables while exposing marine mammals to temperature-controlled water baths (Hart & Irving, 1959; Heath & Ridgway, 1999; Irving & Hart, 1957; McGinnis et al., 1972). To explore the latter, we recorded heat flux and peripheral temperatures in freely diving juvenile northern elephant seals using custom-made biologgers.

Heat flux showed consistent within-dive patterns: seals generally lost heat throughout most of the dive and gained heat throughout the short post-dive intervals (Figure 2.7A). A departure from this pattern occurred during shallow diving bouts. Instead of gaining heat at the surface, the seals lost heat throughout the ascent and surface interval (Figure 2.7A). This thermal response during shallow diving bouts may occur because their shallow dives are in relatively warm water (>10°C). As a result, they experience smaller changes in water temperature within a dive cycle. Higher arterial temperatures during short, shallow diving bouts observed by Meir & Ponganis (2010) also suggest a greater need to dissipate heat than conserve heat while in relatively warm waters to maintain thermal homeostasis. When they dive deeper into cold waters (~5°C), their skin temperature drops to within a few degrees of water temperature. During the latter portion of their ascent, their skin is colder than the surrounding water, which reverses the temperature gradient resulting in a transition to gaining heat. How these different heat flux patterns ultimately affect their thermal balance—and the relative importance of activity and body size on thermal dynamics—is currently being investigated.

Another variation in pattern is the transition from heat gain to heat loss occurring near the thermocline on the descent, while the opposite transition occurred at deeper and more variable depths on the ascent (Figure 2.7A). Whether dive conditions and an individual's dive capacity contribute to the earlier transition remains to be tested but aligns with temperature profiles on deep dives suggesting increased blood flow and perfusion of the periphery during the ascent (Figure 2.7B). Arterial blood temperature (Meir & Ponganis, 2010) and blubber temperatures on long dives (≥30 mins) declined but always rewarmed before the end of the dive. This is consistent with the anticipatory tachycardia and the resulting redistribution of blood flow that marine mammals experience during the dive ascent (Andrews, 1999; Elmegaard et al., 2019; S. R. Noren et al., 2012; Thompson & Fedak, 1993).

Blubber temperatures showed a distinct gradient, with greater variation across dives than within dives (Figure 2.8B). While the minimum temperature varied among individuals, deep blubber temperatures fell as low as 22.9°C during deep dives (>200 m), resulting in a blubber gradient of 14.2°C. During shallow diving (<100 m) and extended surface intervals, the blubber gradient dropped to <5°C. The transition from a large blubber gradient at low temperatures to a smaller gradient at higher temperatures occurred more abruptly than the opposite transition (Figure 2.8B). Simultaneous changes in diving behavior were not apparent in either case. This suggests that these thermal responses were not simply due to passive warming or cooling from changing water temperatures but were actively regulated through vasomotor changes.

Similarly, Hart & Irving (1959) attributed the rapid changes observed in subcutaneous temperatures of captive harbor seals in response to changing ambient temperatures to active regulation (Figure 2.8A). It is worth comparing blubber temperature data from captive harbor seals (Figure 2.8A) to wild northern elephant seals (Figure 2.8B) to highlight how similar measurements taken 50 years apart yielded valuable insights into peripheral perfusion as a fundamental physiological mechanism in marine mammal thermoregulation. When animals are exposed to constant air or water temperature within their thermal limits, their thermal responses will stabilize after some time. On the other hand, the cyclical nature of diving results in more complex changes mainly in the peripheral body, which will consequently affect heat transfer. While minimum water temperature (at depths >100 m) differed by less than 5°C across dives, shallow blubber temperatures varied as much as 26°C. By measuring similar physiological variables on a freely diving seal, our study replicates past controlled experiments in an uncontrolled setting, incorporating an essential behavioral component (i.e., diving). Our field research builds on previous laboratory findings and extends our understanding of their thermal responses to the natural context.

Our data from freely diving elephant seals further demonstrates the utility of combining multiple continuous measurements at fine resolution to provide insight into the complex physiological responses to the interacting demands of diving and thermoregulation in marine mammals. Together, the heat flux patterns and temperature profiles indicate that allowing peripheral cooling prevents conflict with the dive response, especially during deep-diving bouts. During the short surface intervals (2-3 mins), reperfusion of the periphery associated with a relaxation of the dive response increases blubber temperatures slightly (mean increase of <1°C at all blubber depths, max of 5°C in the shallow blubber). Still, longer periods of shallow diving or extended surface intervals seem to be required to return the deep blubber close to normothermia (35.3±2.1°C). Whether these cyclical changes in perfusion contribute to maintaining whole-body thermal balance or increase thermoregulatory costs is still unknown. Nonetheless, our data supports the idea that regional heterothermy—more specifically, peripheral hypothermia—is preferred over strict homeothermy as a thermal strategy and may offer a compromise between thermal and oxygen demands for continuously diving marine mammals, like elephant seals.

2.6 Considerations for future progress in the field

Understanding how marine mammals survive in such a thermally challenging environment is a complex subject that requires a multi-pronged approach, particularly given the difficulty of studying marine mammals. Here we focused on laboratory or field studies that have provided insight into the role of peripheral perfusion as a physiological mechanism that directly regulates or indirectly influences heat distribution within and across the body. We acknowledge that this is most relevant for marine mammals that primarily rely on blubber for insulation. Integrating *in vivo* and field approaches will deepen our understanding of how thermal responses interact with conflicting physiological demands, such as the dive response. Used together, these approaches will provide ecologically relevant insight into an important but understudied aspect of marine mammal physiology and energetics (Figure 2.2).

2.6.1 Outstanding gaps: The many roles of peripheral perfusion

Future work should address other conflicting physiological demands that require peripheral perfusion and their interactions with thermoregulation. For instance, molting is a necessary phenomenon that requires perfusion of the skin to replace old skin and fur. The form and phenology of molting vary widely, from annual catastrophic molting to continuous gradual molting. It often depends on whether animals can find thermal refugia to minimize the energetic costs of increased heat loss associated with skin perfusion (Durban & Pitman, 2012; Pitman et al., 2019; Thometz et al., 2021; Walcott et al., 2020). Similarly, wound healing requires perfusion of the injured site, potentially leading to a tradeoff in short-term energetic costs and long-term health and survival. Haul-out periods for amphibious species, or seasonal residency at warmer latitudes for long-distance migrators, allow for temporal separation of these physiological demands that would otherwise increase thermoregulatory costs. Finally, unlike fur, blubber is a living tissue that serves as an energy store, and depositing or metabolizing lipid stores also requires perfusion of this layer (Lewden, Enstipp, Bonnet, et al., 2017; Lewden, Enstipp, Picard, et al., 2017; McClelland et al., 2012). Thus, in addition to the dual role associated with thermoregulation and diving that was the primary focus of this review, peripheral perfusion is critical for many other physiological processes. How these conflicting demands interact with each other warrants further investigation.

2.6.2 Challenging but insightful measurements

While temperature measurements are commonly used in biologging studies and have various applications (e.g., stomach temperature telemetry in foraging ecology studies; Kuhn, 2006; Wilson et al., 1995), heat flux has generally been limited to studies directly interested in thermal physiology. Nevertheless, heat flux data have proven to be quite informative. Still, the nature of the measurements is more complex than temperature measurements. The sensor provides thermal resistance at the measurement site, resulting in heat flux values that do not accurately represent heat flux from adjacent skin surfaces (Ducharme et al., 1990). Therefore, it is critical to determine a correction factor for the sensor and the attachment mechanism (Hindle et al., 2015; Kvadsheim et al., 1997; Meagher et al., 2002, 2008; Westgate et al., 2007; Willis & Horning, 2005). Additionally, observations of high variability in heat flux values both among and within individuals are common, which should caution the quantitative interpretation of heat flux values (Erdsack et al., 2018; Meagher et al., 2008).

Some studies have also noted large changes in heat flux associated with small temperature changes between the skin and water. Whether this discrepancy has a physiological underpinning warrants further investigation (Meagher et al., 2002; D. P. Noren et al., 1999; T. M. Williams et al., 1999). Changes in convective heat transfer via blood flow may explain these periodic increases in heat flow at localized skin surface areas (Cuyler et al., 1992; Hampton et al., 1971; Hokkanen, 1990). However, obtaining a direct measure of peripheral blood flow is difficult. Blood flow measurements have only been done on a few captive animals (Bevan & Butler, 1992; Cherepanova et al., 1993; Hochscheid et al., 2002; Jobsis et al., 2001; Ponganis et al., 2006, 2008; West et al., 1992; Zapol et al., 1979). While many direct and indirect methods of measuring blood flow exist and improve human applications (see Chaseling et al., 2020; Low et al., 2020) for methodological reviews), their sensitivity to motion is a significant barrier to their use on free-ranging animals.

As was demonstrated in freely diving juvenile elephant seals, blubber temperature is more readily measured than blood flow and is thus a good proxy for peripheral perfusion. Using indirect measures, such as peripheral temperature and derivatives, to infer peripheral perfusion is not a novel approach (examples primarily from the seabird literature, e.g., Enstipp et al., 2019; Lewden, Enstipp, Bonnet, et al., 2017; Lewden, Enstipp, Picard, et al., 2017; Niizuma et al., 2007; Schmidt et al., 2006) and even has diagnostic potential in biomedical applications (Sagaidachnyi et al., 2019). Unlike the skin surface, blubber is not directly affected by external influences, such as convective heat loss from water flow. Instead, blubber temperatures reflect internal processes that serve to maintain homeostasis.

2.6.3 Integrating behavioral and physiological thermoregulation

While this review focused on the critical role of peripheral perfusion, it is essential to underscore that behavior is generally the first line of defense for maintaining thermal homeostasis. Schlader (2014) noted less than a decade ago that behavioral thermoregulation is often neglected in human studies, even more so than in animal studies. Animals outside their thermoneutral zone employ more energetically costly strategies such as sweating or shivering to restore thermal balance (Figure 2.4). However, conflicting physiological demands may prevent marine mammals from employing these mechanisms. For example, the need to conserve water may explain why California sea lions neither pant nor sweat despite having functional sweat glands, unlike elephant seals. Rather, both species seem to rely on behavior to deal with the warm air temperatures within their home range and prevent heat stress (McGinnis et al., 1972; White & Odell, 1971). Similarly, diving marine mammals cannot employ sweating or shivering while diving (Kvadsheim et al., 2005). Therefore, they must either avoid exceeding their upper and lower critical temperatures or utilize behavioral strategies that increase their sensible heat exchange effectiveness (Figure 2.4).

Natural conditions may allow behavioral interventions to avoid reaching the boundaries of the thermoneutral zone and remain in their thermal comfort zone (Kingma et al., 2014; Schlader, 2014) (Figure 2.4). Within this zone, marine mammals combine physiological mechanisms and behavioral strategies on different timescales to maintain thermal balance. For example, sea otters minimize thermoregulatory costs by spending a significant amount of time floating at the surface and balancing thermal substitution from activity and the heat increment of feeding (Costa & Kooyman, 1982). Marine mammals that haul out can switch between the two media as a form of behavioral thermoregulation (Codde et al., 2016; Norris et al., 2010; Tarasoff & Fisher, 1970; White & Odell, 1971). Deeper diving marine mammals may modify their diving behavior to take advantage of the steep gradients in water temperature to adjust their thermal balance (as observed in ectothermic and/or regional endothermic vertebrates, pelagic tuna and sharks; Adamczak et al., 2020; Bernal et al., 2017; Costa & Sinervo, 2004; Royer, 2020; Thygesen et al., 2016). While regulating peripheral perfusion provides a faster mechanism for adjusting heat transfer, behavioral strategies, such as extended surface intervals, may allow for slower but larger adjustments in overall heat balance that would otherwise conflict with the dive response, especially during non-routine behavior.

To truly integrate our understanding of behavioral and physiological thermoregulation, we need to study wild animals minimally disturbed and behaving naturally (Figure 2.2). Most behavioral thermoregulatory studies of wild marine mammals were carried out on animals on the beach (Beentjes, 2006; Chaise et al., 2019; Gentry, 1973; Liwanag, 2010; Norris et al., 2010; White & Odell, 1971) or at the water's surface near the coastline (Liwanag, 2010) (Figure 2.1). With the rapid integration of inertial measurement units into biologgers, sophisticated interpretations of their non-observable behavior at-sea are now possible (Goldbogen et al., 2017; H. J. Williams et al., 2020). These can be combined with measurements relevant to thermal physiology to determine how activity level and activity-induced thermogenesis influence peripheral dynamics and heat balance.

Studies of how behavior and intense activity modify thermal balance have implications for understanding the thermoregulatory costs of marine mammals exposed to anthropogenic disturbances. Disturbances, such as fisheries interactions, ship traffic, or sonar, can lead to altered diving behavior or haul-out patterns (Figure 2.2). For example, simulated sonar has been shown to cause marine mammals to prolong their dives (Fregosi et al., 2016). If the dive response is modulated by dive conditions, these unanticipated prolongations will reduce heart rate and peripheral perfusion. Such cardiovascular adjustments would result in secondary consequences for heat dissipation or potentially a complete override of thermoregulatory demands.

To investigate these issues related to conservation, we need to study their thermoregulation in an ecophysiologically relevant context (Figure 2.2). By performing controlled exposure experiments on wild animals (Harris et al., 2018; Nowacek et al., 2016; Southall et al., 2016), we can quantify biologically significant and context-dependent responses to disturbances (e.g., Pabst et al., 2002). Minimizing or avoiding activities known to increase the susceptibility of marine mammals to thermal imbalance will help reduce the cumulative impacts of anthropogenic stressors on marine mammals. However, we must first establish a baseline understanding of their thermal physiology during natural behavior before understanding the pathophysiology associated with disturbed behavior.

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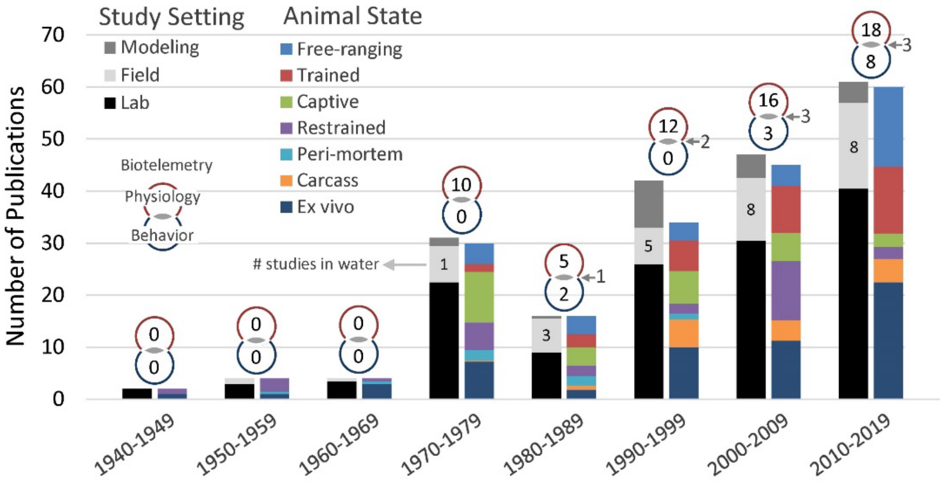
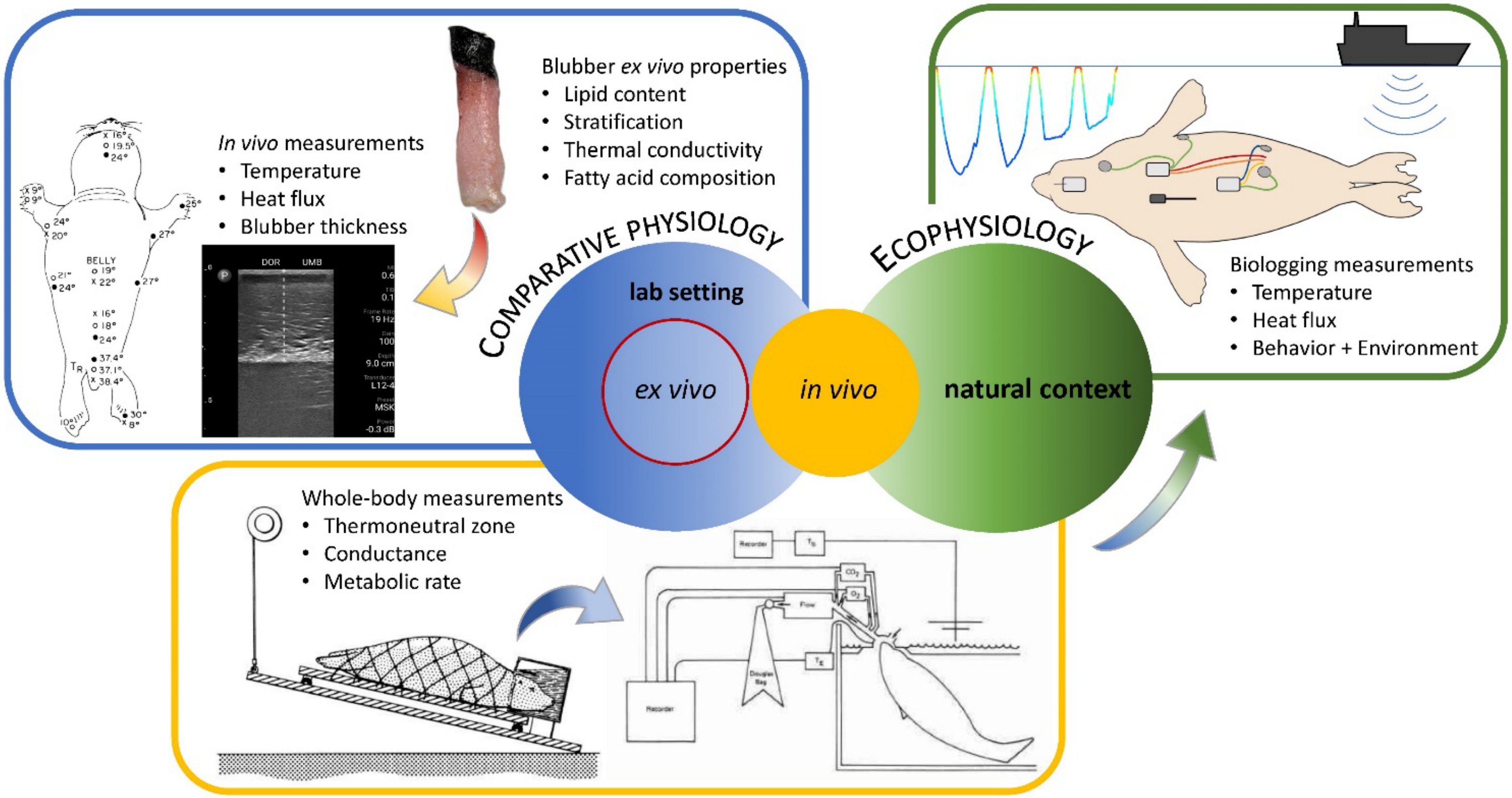


Figure 2.1 Number of publications (total = 207) by decade from 1940 to 2019 relevant to the thermal physiology of marine mammals. Refer to Table A2.1 for the studies included. Studies are classified by setting (i.e., where it was performed) (left bar) and by the state or condition of the animal (right bar; modeling studies that did not make measurements on an animal were not included). Numbers inside the field portion indicate how many of those field studies (if ≥1) involved animals in water (vs. land). Venn-diagrams on top of the bars indicate how many studies during that decade used biotelemetry for remote measurements of physiological variables (e.g., body temperature; top), or behavioral variables (e.g., diving behavior; bottom), or both. Biotelemetry is defined broadly here and includes remote sensing of physiologically relevant data (e.g., infrared thermography) and the use of data loggers (i.e., biologgers) to record continuous measurements on captive animals. Categories for study settings were defined as: lab (i.e., using an experimental approach in a captive and controlled setting), field (i.e., using wild animals in their natural setting), biophysical modeling (e.g., heat transfer models). Categories for animal state were defined as: *ex vivo* (i.e., excised tissue measurements), carcass (i.e., *in situ* measurements on a dead animal), peri-mortem (i.e., measurements taken at or near death), restrained (including sedated), captive (and unrestrained or freely-behaving given surrounding constraints), trained (i.e., accustomed to experimental protocol or performing a task on command), free-ranging (i.e., freely-behaving wild animals). Classification into these categories was inclusive (i.e., one study could be classified into multiple categories) and a study's contribution to multiple categories was weighted evenly. Only research articles were included; book and encyclopedia chapters, theses, reviews, or comments were excluded. Papers that did not include any discussion of thermoregulation even if relevant parameters were measured (e.g., blubber lipid content, body composition, movement patterns in relation to sea surface temperature) were excluded.

Figure 2.2 Graphical depiction of various approaches for understanding the thermal physiology of marine mammals. Both comparative physiology studies performed in the laboratory and ecophysiology studies (i.e., physiology studies conducted in the field where the ecological context is taken into consideration) have contributed to our understanding of marine mammal thermal physiology. However, most have relied heavily on species that are more readily accessible (e.g., seals). The blue box highlights how knowledge gained from *ex vivo* studies on blubber is relevant to understanding its function *in vivo* and its influence on other thermal measurements (e.g., skin temperature and heat flux). *In vivo* studies in the laboratory (yellow box) have provided insights into whole-body thermal dynamics using experimental methods that simulate reality to varying degrees (e.g., forced submersion experiments to trained dives). To understand the ecological relevance of their thermal limits, field studies (green box) using biologgers can record thermal responses during natural behavior and use these baseline measurements to compare those taken under disturbed conditions. Arrows depict efforts to translate findings using different approaches (*ex vivo* to *in vivo*, red to yellow) or in different contexts (lab setting to the natural context, blue to green). Skin and blubber biopsy sample from *Megaptera novaeangliae* and image (courtesy of L. Pallin) collected under scientific research permits NMFS 23095, ACA 2020-016, and UCSC IACUC Friea2004. Ultrasound image from Mirounga angustirostris collected under scientific research permits NMFS 21388 and UCSC IACUC Costad2009-1. Seal outline (© Jessica Kendall-Bar) was modified to depict instrumentation for research conducted under NMFS 19108 and 21388 and UCSC IACUC Costad2009-3. Seal outline depicting body temperature measurements adapted with permission from Miller & Irving (1975). Metabolism and temperature regulation in young harbor seals *Phoca vitulina richardi*. *American Journal of Physiology* 229: 506-511. Schematic of an experimental approach reprinted from Gallivan & Ronald (1979). Temperature regulation in freely diving harp seals (*Phoca groenlandica*). *Canadian Journal of Zoology*, 57: 2256-2263. © Canadian Science Publishing. Figure depicting methods used for forced submersion experiments reprinted with permission from Zapol et al. (1979). Regional blood flow during simulated diving in the conscious Weddell seal. *Journal of Applied Physiology*, 47: 968:973. © American Physiological Society.

Blubber *ex vivo* properties
Lipid content
Stratification
Thermal conductivity
Fatty acid composition
In vivo measurements
Temperature
Heat flux
Blubber thickness
BELLY
DOR
UMB
COMPARATIVE PHYSIOLOGY
lab setting
ex vivo
in vivo
ECOPHYSIOLOGY
natural context
Biologging measurements
Temperature
Heat flux
Behavior + Environment
Whole-body measurements
Thermoneutral zone
Conductance
Metabolic rate
Recorder
Flow
Douglas Bag

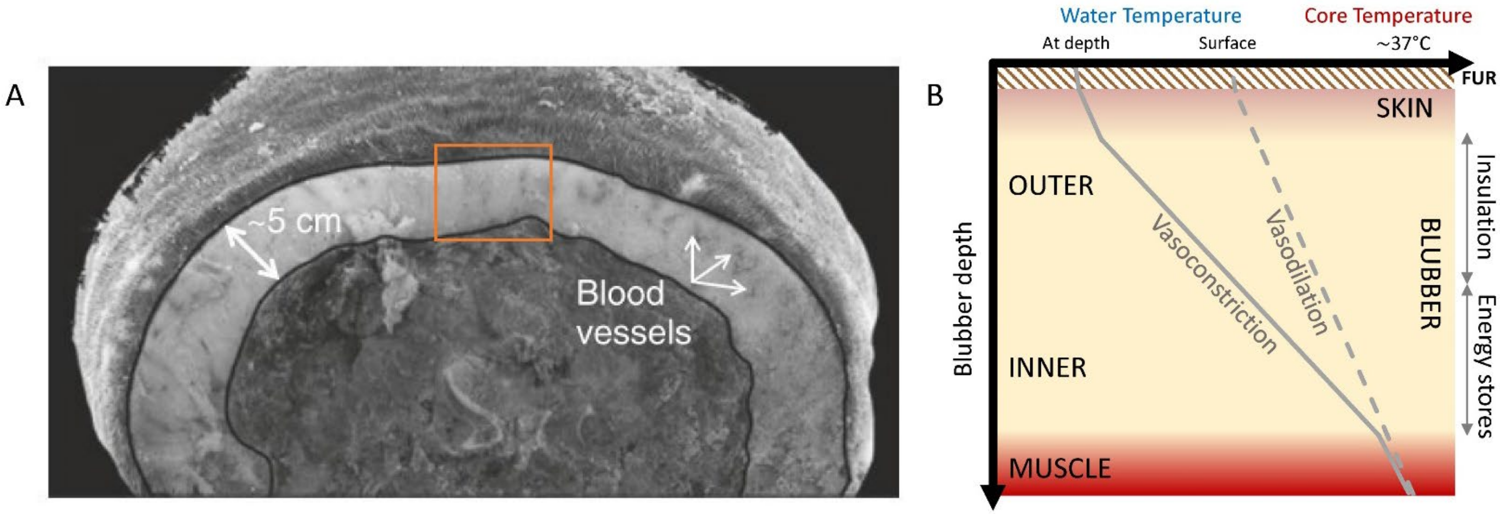


Figure 2.3 A cross-section from an adult Weddell seal (*Leptonychotes weddellii*) with blood vessels visible within the blubber layer. The orange box denotes the area represented in (B). Adapted with permission from Springer Nature: Marine Mammals by Randall W. Davis © 2019 (A). A conceptual figure depicting blubber's various thermal states dependent on peripheral perfusion, and blubber's functional roles due to its stratification. The temperature gradient across the blubber layer will vary based on the degree of peripheral perfusion during a dive. A larger gradient will generally occur at depth where colder water temperatures and peripheral vasoconstriction associated with the dive response lead to cooling of the periphery. The inner and outer blubber layers primarily serve different functions (energy store and insulation, respectively). This stratification is due to the relative proportional composition of fatty acids which confers different physical and biochemical properties (B).

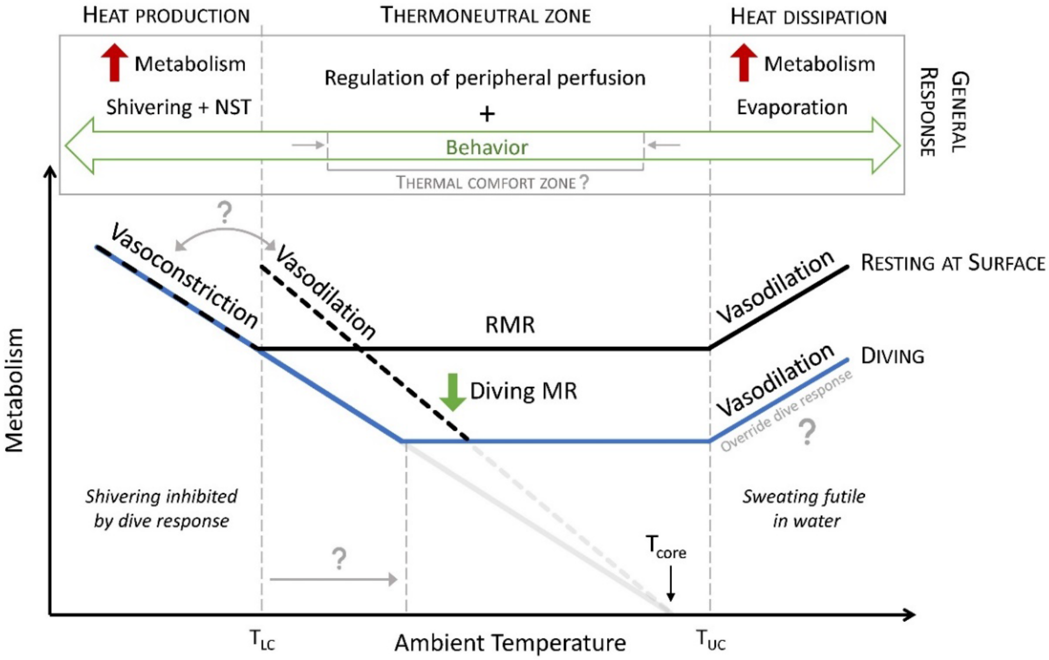


Figure 2.4 Schematic figure depicting the relationship between ambient temperature and metabolism (black line) and the general thermal responses within the thermoneutral zone, above the upper critical temperature (T_{UC}), and below the lower critical temperature (T_{LC}). For marine mammals in water, evaporative heat loss becomes futile, and diving imposes additional constraints on heat production due to the need to conserve oxygen. Therefore, marine mammals must compensate for these limited modes of heat exchange through vasomotor changes and behavior. Several questions remain to address how diving (and the associated metabolic response, blue line) modulates their thermal responses (represented by the question marks).

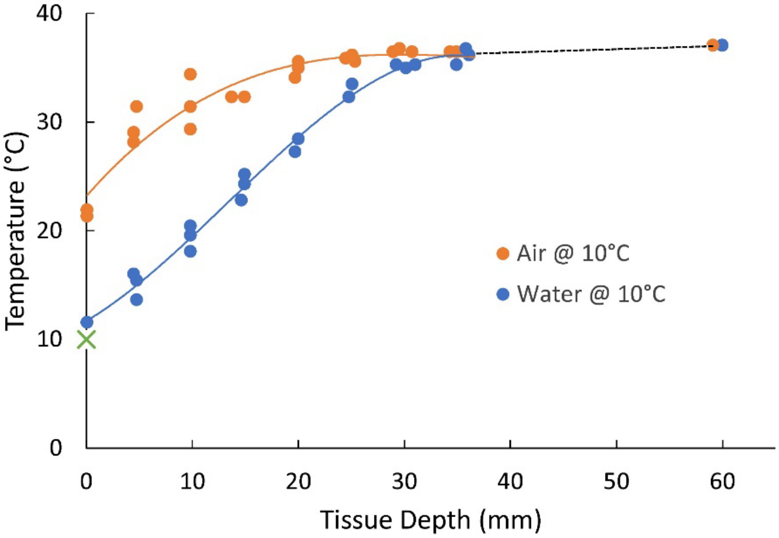


Figure 2.5 Tissue temperature gradients of a harbor seal (*Phoca vitulina*) in air (orange) and water (blue) at 10°C (green 'x' on y-axis). Modified from Irving & Hart (1957). The metabolism and insulation of seals as bare-skinned mammals in cold water. *Canadian Journal of Zoology*, 35: 497-511. © Canadian Science Publishing.

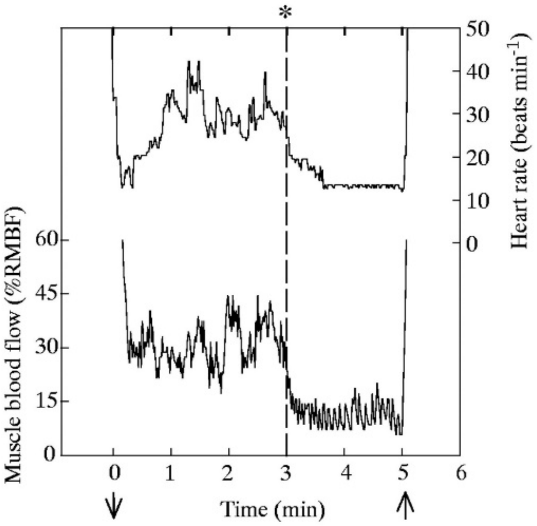


Figure 2.6 Heart rate and muscle blood flow (as a percentage of mean resting muscle blood flow, %RMBF) of a trained harbor seal (*Phoca vitulina*) during a 5-minute submersion. The seal was accustomed to 3-minute submersions after which its heart rate and muscle blood flow declined to levels similar to naïve seals during submersion. The abrupt change at 3 minutes (dashed line) demonstrates the psychological influences on the physiological responses associated with the dive response. Reprinted with permission from Jobsis et al. (2001). Effects of training on forced submersion responses in harbor seals. *The Journal of Experimental Biology*, 204: 3877:3885. © The Company of Biologists Ltd.

Figure 2.7 The dive profile of Toby, a translocated juvenile northern elephant seal (*Mirounga angustirostris*), with the color indicating the direction of heat flux (red = heat gain, blue = heat loss) throughout the dive. The inset shows four deep dives (>200 m) and how the transition from heat gain to heat loss occurs near the thermocline (denoted with an asterisk) on the descent, but the opposite transition occurs at deeper depths during the ascent. Heat flux values [W m^{-2}] in (A) are preliminary values pending post-deployment calibrations. Raw voltage output has been corrected for the added thermal resistance of the sensor and attachment mechanism (determined experimentally) as well as the unique sensor's calibration constant (provided by the manufacturer). A section of the dive profile denoted by the green box containing the seal's deepest dive in (A) is shown in greater detail (B, left) with temperature profiles at three depths within the blubber layer (deep = red, mid = orange, shallow = yellow). The drop in blubber temperature during the deep dive (B, left) is analogous to the drop in arterial temperature (B, right) recorded in Butler, a translocated juvenile northern elephant seal by Meir & Ponganis (2010), although arterial temperature declined more abruptly. Both blubber and arterial temperatures rewarmed before the end of the dive, and arterial temperatures remained comparatively warmer (note the difference in temperature range of the y-axes; the range of arterial temperatures is shown on both figures with the purple dashed lines). The figure showing Butler's data is modified from Meir & Ponganis (2010). Blood Temperature Profiles of Diving Elephant Seals. *Physiological and Biochemical Zoology*, 83(3): 531-540. © The University of Chicago Press.

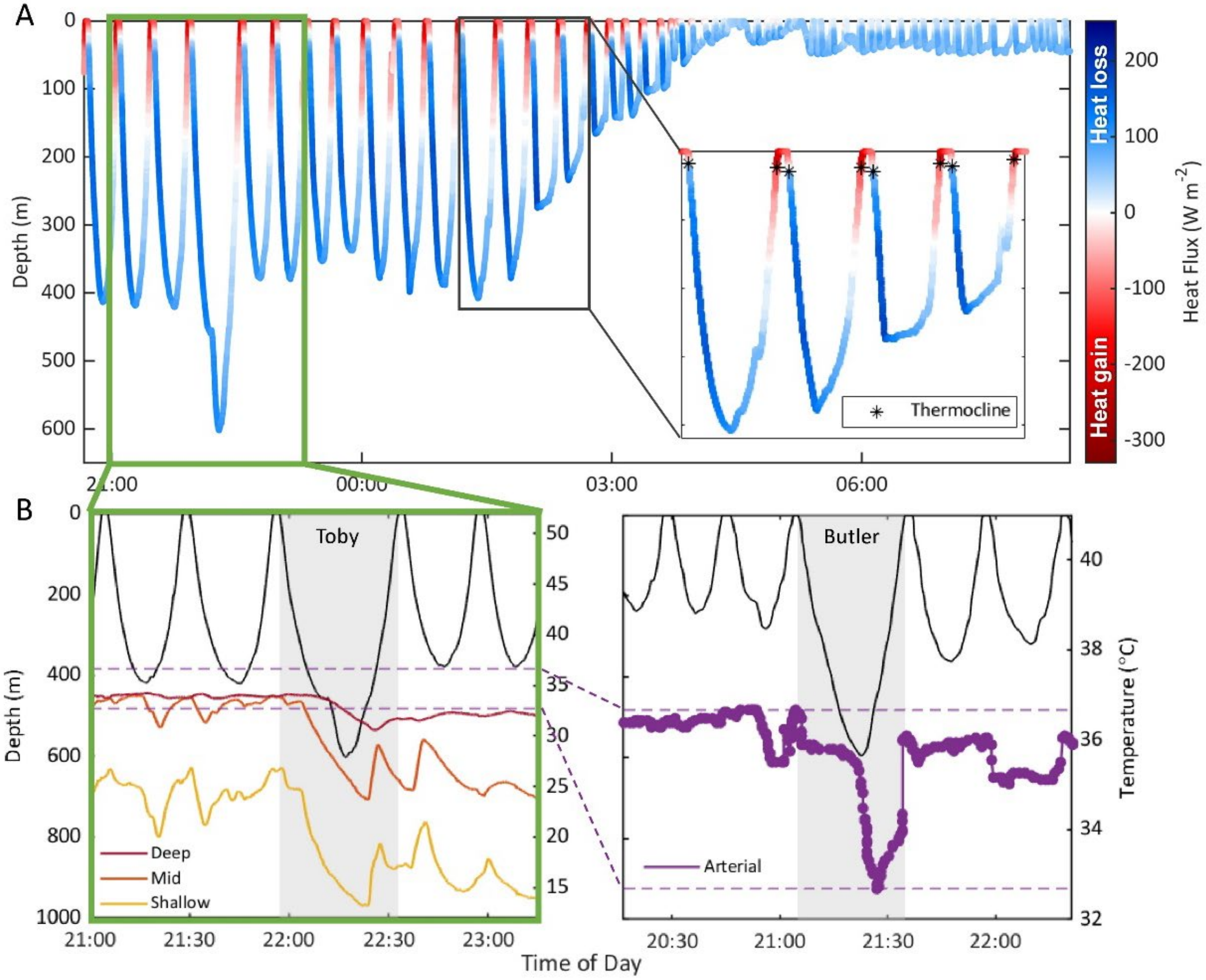
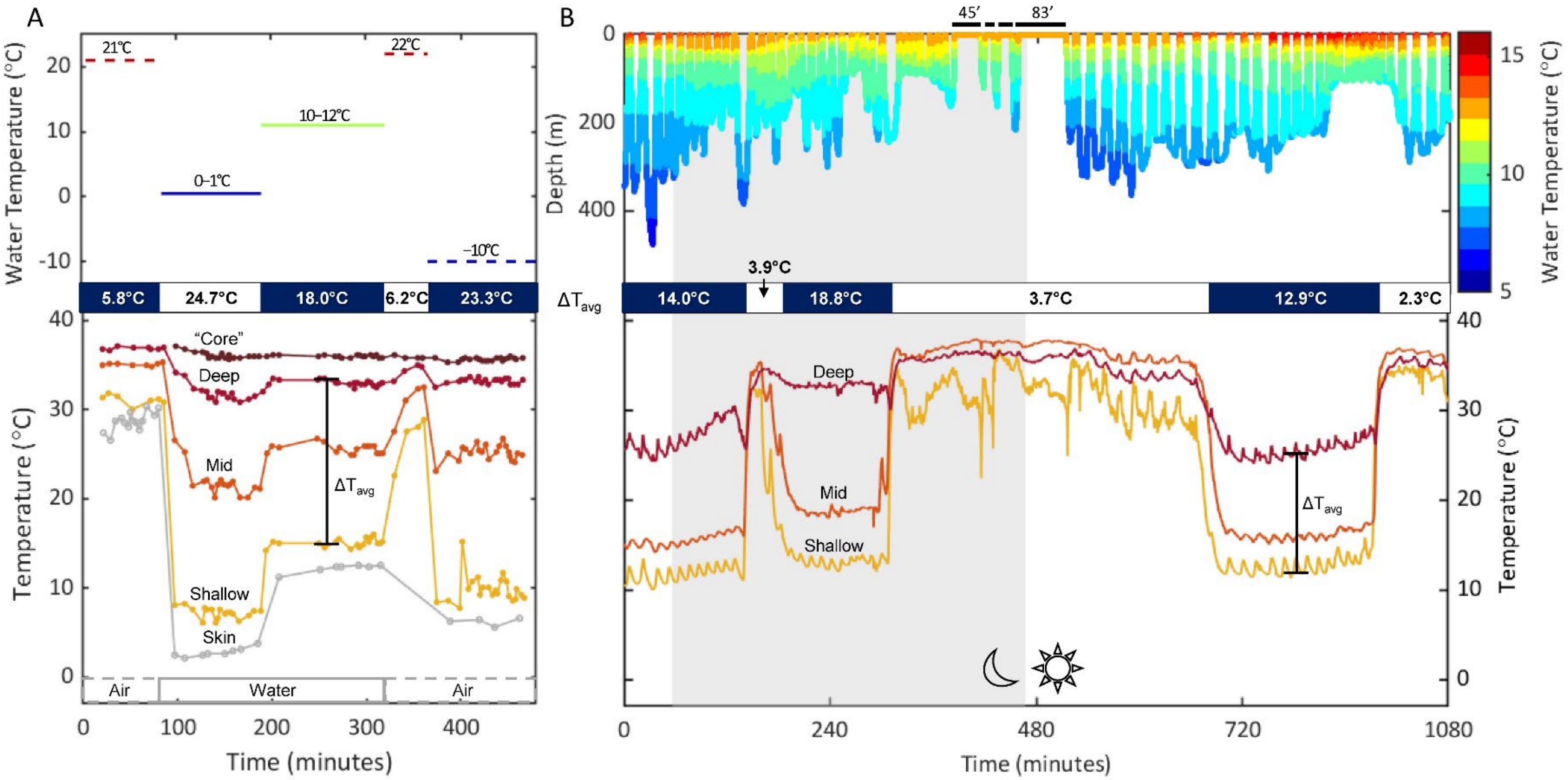

A
0
100
200
300
400
500
600
Depth (m)
21:00
00:00
03:00
06:00
Thermocline
Heat loss
Heat gain
200
100
0
-100
-200
-300
Heat Flux (W m^{-2})
B
Toby
0
200
400
600
800
1000
Depth (m)
50
45
40
35
30
25
20
15
Deep
Mid
Shallow
21:00
21:30
22:00
22:30
23:00
Butler
40
38
36
34
32
Temperature (°C)
Arterial
20:30
21:00
21:30
22:00
Time of Day

Figure 2.8 Skin and tissue temperature measurements of a harbor seal (*Phoca vitulina*) in air and water at temperatures indicated by the dashed and solid line segments, respectively (A). Tissue temperatures were measured at 3 mm (shallow), 13 mm (mid), 23 mm (deep), and 42 mm ("core"), which included the blubber layer (<25 mm thick) and deeper tissue. The seal was allowed to equilibrate for at least one hour at each ambient temperature while recording measurements every 4 minutes. Adapted from Hart & Irving (1959). The energetics of harbor seals in air and water with special considerations of seasonal changes. *Canadian Journal of Zoology*, 37: 447-457. © Canadian Science Publishing. The dive profile of a translocated juvenile northern elephant seal (*Mirounga angustirostris*) that dove continuously for 7 days (18 hours shown in figure) and experienced water temperatures between 5-16°C (B, top). Four consecutive extended surface intervals are marked with thick black bars along with the duration (in minutes) of the first and last extended surface intervals. Temperature profiles at three depths within the blubber layer (deep = red, mid = orange, shallow = yellow) reveal how the temperature gradient within the blubber layer (ΔT_{avg} = average($T_{deep} - T_{shallow}$)) undergoes large variations across dives (B, bottom). The cyclical nature of diving also results in smaller fluctuations within dives that is not observed in the resting harbor seal in (A).


A
Water Temperature (°C)
21°C
22°C
10–12°C
0–1°C
−10°C
5.8°C
24.7°C
18.0°C
6.2°C
23.3°C
"Core"
Deep
Mid
Shallow
Skin
ΔT_avg
Air
Water
Air
Temperature (°C)
Time (minutes)
0
100
200
300
400
B
45′
83′
Depth (m)
0
200
400
Water Temperature (°C)
5
10
15
ΔT_avg
14.0°C
3.9°C
18.8°C
3.7°C
12.9°C
2.3°C
Deep
Mid
Shallow
ΔT_avg
Temperature (°C)
40
30
20
10
0
Time (minutes)
0
240
480
720
1080

Chapter 3

Fine-scale thermal responses of freely diving northern elephant seals

Arina B. Favilla, Markus Horning, Rachel R. Holser, Theresa R. Keates, Milagros G. Rivera, Daphne Shen, Patrick W. Robinson, Daniel P. Costa

3.1 Abstract

Deep-diving marine mammals are well-adapted to their marine environment where they face significant physiological challenges associated with diving and thermoregulation. Both the dive response and thermoregulation require cardiovascular adjustments to meet the physiological challenges of performing deep dives. Little is known about how marine mammals coordinate these physiological demands to maintain thermal balance and homeostasis. Using biologgers with a suite of physiological sensors, we examined fine-scale thermal responses in northern elephant seals (*Mirounga angustirostris*) during normal at-sea diving behavior. Heat flux showed consistent within-dive patterns with passive heat loss occurring throughout most of the dive, but deviations in these patterns occurred during shallow diving. Changes in skin temperature tracked changes in water temperature, resulting in strong correlations between heat flux and water temperature. On deeper dives, peripheral temperatures were lower, indicating a stronger dive response (i.e., peripheral vasoconstriction), and ascending to warmer surface waters led to a transition to heat gain at the end of a dive. At the dive scale, peripheral cooling allows seals to prioritize the dive response and maintain near-normothermic core

temperatures. This is possible given their thick blubber layer, where the temperature gradient could be as high as ~20°C. Blubber temperatures had within-dive fluctuations similar to skin temperature and heat flux, but longer scale patterns revealed occasional large, abrupt changes suggestive of an active physiological switch from a vasoconstricted to a relaxed, vasodilated state. This thermal response often occurred after a change in diving behavior, and sometimes followed slight decreases in core temperature during long, deep diving bouts. These findings support the idea that a shift to nonroutine diving behavior to relax the dive response (e.g., shallow diving and extended surface intervals) may be a form of behavioral thermoregulation modulated by their thermoregulatory debt accrued on deep dives. Additionally, we found body size and trip duration influenced the magnitude of thermal responses, which may suggest a size-dependent thermoregulatory strategy, although further investigation is needed.

3.2 Introduction

Deep-diving marine mammals face significant physiological challenges as they perform long breath-hold dives in an environment that is ~25 times more conductive than air (Boyd, 1997; Dejours, 1987; Pendergast & Lundgren, 2009). In addition to experiencing high pressure and cold temperatures at depth, they must withstand these large pressure and temperature gradients on a repetitive cycle while diving which introduces physiological challenges to maintaining homeostasis (Kooyman & Ponganis, 2018). Marine mammals are air-breathing endotherms that have evolved many morphological and physiological adaptations for maximizing their oxygen stores and conserving body heat to meet the demands of finding food at depth (Favilla & Costa, 2020). The dive response involves a suite of cardiovascular adjustments, including apnea (breath hold), bradycardia (reduced heart rate), and peripheral vasoconstriction (narrowing of blood vessels), that together reduce blood flow and thus oxygen consumption in non-essential tissues to conserve their ‘onboard’ oxygen supply for vital organs, such as the heart and brain (Costa, 2007; Kooyman & Ponganis, 2018). The cardiovascular system is also integral to thermoregulation as the regulation of blood flow allows redistribution of heat within the body (Favilla et al., 2022).

The regulation of peripheral perfusion is particularly important for marine mammals, especially fully aquatic species and deep divers that rely on blubber for insulation. Blubber is a highly vascularized subcutaneous layer of adipose tissue with collagen and elastic fibers (Iverson & Koopman, 2018, 2018). The stratification of blubber in marine mammals makes the outermost layer better suited for thermoregulation while the innermost layer is the metabolically active site of lipid deposition and absorption (Strandberg et al., 2008). While diving, peripheral vasoconstriction at depth serves to conserve oxygen and will reduce heat dissipation. At the surface, vasodilation increases peripheral perfusion which replenishes oxygen to ischemic tissues. Perfusion of the blubber layer will also increase the conductivity of the blubber layer and thus increase heat dissipation (Kanwisher & Sundnes, 1966; Kvadsheim & Folkow, 1997). Essentially, perfusion of the blubber bypasses this insulating layer enabling fine control of heat transfer (Lovegrove, 2017). These physiological responses can either be synergistic or antagonistic depending on the thermal state of the animal (Favilla & Costa, 2020; Whittow, 1987). For example, the dive response may inhibit a marine mammal's ability to dump heat produced during exercise at depth (Meir & Ponganis, 2010; Rosen et al., 2007). For an animal that is well-insulated to conserve heat, a physiological conflict may arise in moments of heat stress—naturally- or disturbance-induced—and a diving marine mammal must prioritize either the dive response or thermoregulation (Gallivan & Ronald, 1979; Hammel et al., 1977; Williams et al., 1999). Little is known about how they coordinate their physiological responses to maintain thermal balance during routine diving behavior.

Studies in diving physiology discuss hypothermia as a strategy to reduce metabolism, conserve oxygen stores, and thus prolong dives. However, conclusions have been equivocal across species and studies partly because the location of the measurement will influence how the temperature data are interpreted. For example, aortic and muscle temperatures measured in a diving Weddell seal led to contradicting conclusions—pre-dive reductions in aortic temperatures suggested seals undergo hypothermia-induced metabolic suppression (Hill et al., 1987; Kooyman et al., 1980) whereas stable muscle temperatures throughout dives suggested that aortic temperatures may not be representative of core body temperatures (Ponganis et al., 1993). Similar measurements have been made on northern elephant seals. In these studies, the lack of reductions in arterial and venous blood temperatures led the authors to refute the hypothermia-induced metabolic suppression hypothesis (Meir & Ponganis, 2010), but a drop of 1°C in the muscle (with much larger decreases in subcutaneous temperatures) suggested seals undergo a shift in thermal strategy once they begin their routine deep diving (Andrews, 1999). These findings demonstrating regional heterothermy mirror those found in diving seabirds (Culik et al., 1996; Enstipp et al., 2017; Green et al., 2003; Ponganis et al., 2003) and emphasize the importance of using several measurements to obtain a more representative view of whole-body thermal dynamics during diving behavior. Despite significant advances in biologging, and more specifically physio-logging, since these early studies on marine mammals (Fahlman et al., 2021; Hawkes et al., 2021), studies that measure variables relevant to thermal physiology in free-ranging marine mammals while at sea are lacking.

As one of the deepest diving pinnipeds that predictably return to their colony twice per year, northern elephant seals (*Mirounga angustirostris*) are an ideal model species for providing insight into the thermoregulatory response of diving marine mammals. They perform continuous dives to depths below the thermocline where temperatures are ~5°C (Hakoyama et al., 1994; Le Boeuf et al., 1988). In addition to having a thick blubber layer, they have a high density of superficial arteriovenous anastomoses over their entire body (Molyneux & Bryden, 1978). Therefore, rather than relying on localized areas for heat dissipation, their entire body can be used as a thermoregulatory surface. Furthermore, the dual role of peripheral perfusion for both thermoregulation and the dive response makes their blubber layer the ideal tissue for investigating the physiological regulation and coordination of these two physiological responses (Favilla et al., 2022). Using custom-made biologgers, we combined multiple continuous measurements of body temperature, including in the blubber layer, and heat flux—the amount of heat transferred between the animal's body and its environment over time—to examine the thermal responses at fine resolution in northern elephant seals during normal at-sea diving behavior.

This is the first study to measure heat flux continuously in a wild, freely diving marine mammal and report on the patterns relative to diving behavior. Most previous heat flux studies were done with hand-held measurements on captive, trained, or temporarily restrained marine mammals in water, including dolphins (Hampton et al., 1971; Heath & Ridgway, 1999; McGinnis et al., 1972; Meagher et al., 2002, 2008; D. P. Noren et al., 1999; Williams et al., 1999), manatees (Erdsack et al., 2018), and harbor seals (McGinnis, 1975), or in air with northern elephant seals (McGinnis, 1975) and Weddell seals (Walcott et al., 2020). These studies investigated the effects of water temperature, molting, activity, and submergence on heat flux, but ecologically relevant findings to diving animals are still lacking. The first studies to design and use an attachment mechanism for continuous heat flux measurements in dolphins (Westgate et al., 2007) and sea lions (Willis et al., 2005; Willis & Horning, 2005) measured heat flux during disturbed or trained behavior, respectively. These studies emphasized the importance of correcting heat flux measurements to account for the increased insulation provided by the attachment mechanism. A few studies on Weddell seals have measured heat flux continuously during undisturbed, voluntary behavior in free-ranging individuals (Hindle et al., 2015; Willis et al., 2005) but have not analyzed the heat flux data relative to diving behavior. We aim to fill this gap by measuring heat flux alongside temperature continuously on wild, freely diving northern elephant seals and examining the thermal variables relative to their diving behavior.

To elucidate how thermoregulation interacts with the dive response, we addressed the following questions: (1) In which conditions are thermal responses actively regulated, and in which conditions are thermal responses a result of passive mechanisms? (2) How can we describe their thermoregulatory strategy, and how does diving behavior affect their thermoregulatory strategy?

Understanding whether thermal responses are actively regulated or passive is an important prerequisite for modeling the costs of thermoregulation (Lovvorn, 2007). Passive thermal responses result from static characteristics (i.e., body size, morphological adaptations) or external factors (i.e., water temperature) whereas active thermal responses require physiological regulation (Hampton & Whittow, 1976; Hart & Irving, 1959; Heath & McGinnis, 1980; Sato, 2014; Schmidt et al., 2006). By measuring a suite of thermal responses across and within the body, we obtained a more holistic representation of the animal's thermal state. We compared patterns in peripheral thermal responses (i.e., heat flux, skin temperature, and blubber temperature) relative to internal temperatures to gain better insight into their thermoregulatory strategy and the timescale at which thermal balance is maintained.

Altogether, this chapter aims to provide a descriptive analysis of thermal responses during routine diving behavior to enhance our understanding of how deep-diving marine mammals maintain thermal balance while encountering steep thermal gradients on a repetitive cycle. By providing a baseline understanding during routine behavior, we can then investigate the plasticity of their thermoregulatory responses. Given that marine mammals are facing increasing disturbance, including sonar and shipping traffic, it is important to understand what conditions may increase their susceptibility to thermal imbalance and incorporate thermoregulation—an important, yet previously overlooked physiological process—into our investigations of the behavioral and physiological consequences of disturbance.

3.3 Methods

3.3.1 Data collection

This research was conducted on juvenile northern elephant seals (<3 years old, mass=197 ± 52 kg, Table 3.1 & Figure 3.1A) from the colony at Año Nuevo State Park (San Mateo County, CA) during the 2018, 2019, and 2022 molting (May-June, n=8) and 2019 pre-breeding (October-November, n=2) seasons using the translocation method (Oliver et al., 1998). Juvenile seals were chosen based on accessibility and body and pelage condition. They were captured on the beach at Año Nuevo State Park following standard protocols (Le Boeuf et al., 2000) and transported by truck to the Long Marine Laboratory (Santa Cruz, CA) for morphometric measurements and instrumentation. After recovering from sedation, the seals were transported by truck to Pacific Grove in Monterey County, CA (36°38’ N

121°56’ W) and released on a beach into the bay. Translocating juveniles from Año Nuevo has proven valuable for at-sea physiological studies (e.g., Meir et al., 2009; Meir & Ponganis, 2010) as the elephant seal colony is ideally situated north of Monterey Bay, where the bathymetry allows for deep dives. After the seals swam back to a haul-out site, the tags were recovered and the high-resolution data stored onboard was downloaded. All animal handling was conducted under National Marine Fisheries Service permit numbers 19108 and 23188 and approved by the University of California, Santa Cruz Institutional Animal Care and Use Committee.

The seals were instrumented with the custom-made biologgers that measure diving depth (resolution = 0.5 m, accuracy = 1% of reading), 3-axis acceleration, water temperature (resolution = 0.05°C, accuracy = ± 0.1°C) and key physiological variables—heat flux (nominal sensitivity = 54 W/m^2/mV) at four locations (neck, axilla, flank, swimming muscle (*longissimus dorsi*)), skin temperature (via the thermistor embedded within the heat flux disc), core body temperature (via a stomach temperature pill, Wildlife Computers, Redmond, WA, USA), and blubber temperature with three subcutaneously-placed NTC thermistors (TE Connectivity 2.2K3D210). All variables were sampled at 1 Hz except for stomach temperature at 1/10 Hz and acceleration at 16 Hz (except in 2018, x- and z-axes were sampled at 8 Hz and y-axis at 32 Hz). These biologgers were custom-built by Wildlife Computers (Redmond, WA, USA) and designed by Willis & Horning (2005) using small (25.4 mm diameter) disc heat flow sensors (built by Concept Engineering, Dummerstorf, Germany). The tags were originally used for a project investigating thermoregulation in Weddell seals in the Antarctic (see Hindle et al., 2015). The tags were refurbished for this project with fresh batteries, new heat flux sensors and free-standing thermistors (to measure blubber temperature). A satellite tag and VHF transmitter were also attached to the head and back, respectively, to facilitate tracking and relocating the seal upon its return.

The configuration of the tags and sensors varied slightly across years and individuals (Table 3.2). Figure 3.2A depicts the general placement of the tags and sensors on the seal for the complete configuration. The tags were attached to high-tension nylon mesh netting with cable ties and fishing line and glued to the fur using 5-minute quick setting epoxy (Loctite). The heat flux sensors were attached to a shaved patch of skin using a tight-fitting custom-made PVC plastic holder with superglue around the edges. Monachine pelts, including that of northern elephant seals, are poor insulators as their fur lacks underhairs (Sharma & Liwanag, 2017); therefore, shaving the skin to attach the sensor will not affect the measurement of interest, that is, heat transfer through their primary insulating layer (i.e., blubber). A thin (~1 mm) coating of thermally conductive silicone paste (OmegaTherm 201) or adhesive epoxy (EpoTek T905BN-4) was also applied to the face of the heat flux sensor in contact with the animal to ensure proper contact. The heat flux sensors were placed on the animal such that positive values indicate heat loss to the environment and negative values indicate heat gain from the environment. Heat flux was measured at up to four locations on the body which were chosen based on Hindle et al.'s (2015) determination of the most representative sites of heat transfer for a phocid. The thermistors were inserted into the blubber layer in the flank region with guidance from an ultrasound. We aimed to place one thermistor near the blubber-muscle interface, one shallow in the blubber layer, and the last one roughly in between the two as depicted in Figure 3.2B. The cables attaching the thermistor to the biologgers were secured at the insertion site with suture. The cables of the heat flux sensors and thermistors were secured by supergluing small sections to the pelage spaced throughout the length of the cables. To insert the stomach temperature pill, we used a ~1 m gastric tube with a plunger to push the pill down into the stomach while the seal was anaesthetized.

3.3.2 Sensor calibrations and quality control

To quantify the insulating effects of this attachment mechanism on heat flux measurements, a correction factor was experimentally determined following Willis & Horning (2005). Briefly, a test rig was built out of PVC fittings insulated with neoprene to create two adjacent compartments that are connected to two temperature-controlled circulating water baths with insulated tubing (Figure 3.S1A). A heat flux sensor placed at the interface of the two compartments inside the rig is in contact with water of different temperatures on either side, which induces heat flow across the surface of the disc. The sensor's output was recorded across a range of temperature gradients for the bare sensor (Figure 3.S1E) as well as when a second dummy heat flux sensor was attached on top of the bare sensor (Figure 3.S1D) using the same attachment mechanism used to secure the sensor onto the seal's skin (i.e., the thermally conductive paste or epoxy and the PVC ring with superglue). By regressing the outputs from the bare sensor against those when covered by the entire attachment mechanism for the same temperature gradients, the correction factor for the attachment mechanism was calculated from the regression slope (Figure 3.S1E). Two correction factors were determined—one for the silicone paste and one for the adhesive epoxy.

Additional calibrations were run on the heat flux sensors to confirm the zero offset by placing the heat flux sensor in a temperature-controlled water bath and checking that the heat flux reading is within the expected error of zero after the sensor has equilibrated. The response time of the heat flux sensor and embedded thermistor were quantified by immersing the entire sensor into the temperature-controlled water bath, letting it stabilize (~1 min), and then quickly switching it to a second temperature-controlled water bath set to a different temperature and determining the time required to reach 63.2% of the final value (which is defined as the time constant) and 99.3% of the final value, which is the response time (or 5 times the time constant). This process was repeated for 8 different temperature gradients that were tested in both directions (i.e., from the warmer to colder water, and then from the colder to warmer water).

The last batch of heat flux sensors purchased for the final season of fieldwork in 2022 had a different type of NTC thermistor embedded in the heat flux sensors, which led to a slight offset in temperature values since the biologger's circuit board was programmed to incorporate the previous thermistor's NTC curve for converting the resistance values into temperature readings. To correct the temperature values for these heat flux sensors, we compared the temperature readings from the new batch of heat flux sensors to the readings from the same type of NTC thermistors that were previously used and the known temperature of the water at several increments across a temperature range of 40°C. The difference in offsets between the two thermistors was subtracted from the embedded thermistor's temperature reading and then divided by the ratio of the slopes of the thermistors when regressed against the true water temperature.

Pre- and post-deployment calibrations were performed to initially assess the reusability of the heat flux sensors. We set up a temperature gradient across the heat flux sensors using two temperature-controlled water baths and recorded the heat flux value at incremental temperature gradients spanning -5 to 35°C to cover the range that a seal could experience (assuming a mammalian core temperature). The slope of the regression line provided the sensitivity of the sensor in mV per °C. A comparison of the pre-deployment versus post-deployment calibration slopes showed a marked decrease in the heat flux sensors' sensitivity after deployment. Subsequent post-deployment calibrations done weeks or months later showed inconsistent changes across sensors—some improved after drying for several days while others stayed the same or worsened. Additional experiments testing the effects of pressure and immersion on the heat flux sensors suggested that the heat flux sensors are hygroscopic as they absorb water and gain mass asymptotically up to about 200 hours after immersion (Figure 3.S2). We found that the absorption of water significantly reduced the sensitivity of the sensor. These tests were performed using freshwater, so the added effects of salinity are yet to be determined. For these reasons, we only analyzed the direction of heat flux (i.e., heat gain versus heat loss) since the zero offset was shown to be reliable. Further quantitative analyses of the magnitude of heat flux will require a better understanding of how the heat flux sensor's sensitivity changes over time due to the combined effects of pressure and immersion in saltwater.

3.3.3 Data processing

Data processing and statistical analyses were conducted in R (version 4.2.2; R Core Team, 2022) and MATLAB R2022b. Argos and GPS locations were filtered and processed using the aniMotum R package (version 1.1-06), which uses a continuous time state-space model that incorporates location error estimates when available to predict locations at evenly spaced time steps (Jonsen et al., 2023), in this instance, on an hourly basis. Geographic locations for each dive were interpolated from these hourly locations based on the start time of the dive. Solar elevation was calculated for each dive using the SolarAzEl MATLAB function (Koblick, 2023) and the start time and location of the dive to designate daytime (solar elevation ≥ 0°) and nighttime (solar elevation < 0°) dives.

Depth data were zero-offset corrected and processed using a custom-written toolbox in MATLAB (Costa et al., in prep). Individual dives that were deeper than 15 m and longer than 32 s and occurred between surface intervals were detected. The bottom phase was defined by a change in the descent and ascent slope that occurs deeper than 50% of the maximum dive depth where the vertical speed (calculated as distance over time) becomes less than 20% of the vertical speed calculated from the descent and ascent portion, respectively, up to 50% of the maximum depth. The following dive summary metrics were calculated for each dive: dive start time, dive duration, maximum dive depth, time at maximum dive depth, descent phase duration, descent rate, bottom phase duration, ascent phase duration, ascent rate, post-dive interval duration.

For each seal, dives were categorized based on maximum dive depth and dive duration using k-means clustering (k=3) with the two extreme clusters classified as short-shallow and long-deep dives (Figure 3.S3). The percentage of dives classified into each group for each seal and the cluster centroids for dive depth and duration are given in Table 3.3. Dives were also categorized based on activity level by setting thresholds based on the number of strokes per dive. Active dives were defined by a stroke rate greater than the 80th percentile of stroke rates on all dives while nonactive dives had a stroke rate less than the 20th percentile (Table 3.3). Dive bouts were defined as 3 or more consecutive dives of each category.

Water temperature measured by the Mk10 thermistor on the satellite tag was processed according to the suggestions of Simmons et al. (2009)—0.05°C was subtracted and a 1-s time lag was applied to the entire record. Due to the tag's location on the seal's head, the thermistor likely measured both air and water temperature during the seal's surface intervals, resulting in rapid temperature fluctuations since air temperature is generally colder than surface water temperature near the Monterey Bay. To obtain representative temperatures of the surface water, a linear interpolation was performed between the maximum temperature during the last half of the ascent and first half of the surface interval and the maximum temperature during the last half of the surface interval and first half of the descent of the subsequent dive. This approach was validated by comparing the corrected surface interval water temperature to the water temperature measured by a detached heat flux sensor with embedded thermistor near the flank of the seal, which likely remained submerged throughout the surface interval.

To determine the depth of the thermocline on the descent and ascent of each dive, the water temperature data were first interpolated to 1-m intervals using a piecewise cubic Hermite interpolating polynomial from the Gibb's Sea Water Oceanographic ToolBox in MATLAB after converting depth to pressure (McDougall & Barker, 2011). Using the resulting down- and up-casts of water temperature, thermocline depth was determined using two approaches. The first approach determined the thermocline depth to be the depth at which the gradient of the temperature cast reaches a maximum. The second approach adapts the methods described in Holte & Talley (2009) to find the center depth of the thermocline. The casts for which both methods successfully identified a thermocline depth >1 m and the two thermocline depths were within 5 m of each other were retained. Additionally, thermocline depths were discarded if the thermocline depth determined on the ascent of a dive was not within 100 m of the thermocline depth on the descent of the following dive since those should occur relatively close in space and time.

Overall dynamic body acceleration (ODBA) was calculated from the 3-axis accelerometry data. First, the static component of each axis was removed by subtracting the smoothed data from the raw data. The data was smoothed using a moving mean over a 3-s window as recommended by Shepard et al. (2008). The absolute values of the resulting dynamic acceleration for each axis were summed to obtain ODBA.

Flipper stroke rate was derived from the y-axis dynamic acceleration since seals swim by moving their rear flippers laterally. Peaks in the dynamic y-axis acceleration were detected using the MATLAB function findpeaks. The threshold criteria specified in the function included a minimum peak separation of 0.5 s since the mean stroke cycle frequency of elephant seals is known to be 0.66 Hz (Sato et al., 2007), and a minimum amplitude of 0.75 after inspecting the peaks to determine what should be considered a full stroke.

Records of the physiological variables were visually inspected to determine the end of usable data if the tag did not properly record or if the sensor became detached during the seal's time at sea. Unrealistic spikes in the signals of heat flux and temperature data were removed with a 3-point median filter. If some spikes remained, additional filtering was applied on a case-by-case basis. To analyze long-term fluctuations in the skin and blubber temperature data, the signals were gaussian smoothed using a window equivalent to four times the individual's mean dive duration. To analyze short-term fluctuations in the blubber temperature data relative to diving and stroking behavior, the long-term signal was subtracted from the original data to obtain values centered around zero.

Seals with a stomach temperature pill (n=4) were used to investigate the effects of peripheral thermal responses on their thermal balance. Stomach temperature data included several precipitous drops in temperature followed by an exponential rise which is characteristic of ingestion events (Kuhn & Costa, 2006; Wilson et al., 1992). To obtain a proxy for the seal's internal temperature around the viscera, the stomach temperature data was processed to exclude the temperature dips associated with ingestion. After identifying the ingestion intervals, local maxima that occurred outside of the ingestion intervals were used to perform a cubic spline interpolation, resulting in an approximation of the stomach temperature without ingestion events. We will hereafter refer to the processed stomach temperature as core temperature for ease, although we recognize that a true core temperature is hard to define and even harder to measure (McCafferty et al., 2015; Polymeropoulos et al., 2018). For our purposes, the temperature around the viscera measured by the stomach temperature pill is considered a good proxy for internal temperatures deep within the body.

3.3.4 Data analysis

To examine when thermal responses are actively versus passively regulated, we identified the depth and timing of heat flux values transitioning from positive to negative (heat loss to heat gain) or the reverse (heat gain to heat loss) and compared these occurrences to environmental and behavioral variables. We compared the number and direction of transitions occurring during each dive phase. To determine if heat flux transitions are a result of the changing water temperature as the seal dives, we examined relationships between heat flux transitions and various metrics of water temperature including: the minimum water temperature experienced on the dive, the surface water temperature during the previous surface interval, and the depth of the thermocline on the descent and ascent of each dive. Heat flux transitions were also examined relative to stroking effort and ODBA to determine if activity modulates heat transfer. We report the relationships with the strongest correlations across all seals. Heat flux sensors placed at different body locations (axilla, neck, flank, *longissimus dorsi*) were compared within seals. The relative amount of time spent gaining heat versus losing heat at each sensor location was quantified and compared within seals and the same sensor locations were compared across seals.

To compare blubber temperatures in the deep, mid, and shallow blubber layer within seals, the average blubber temperature during the dive was linearly regressed against dive duration and the y-intercept (extrapolated to where dive duration=0) was considered the representative blubber temperature following the methods used in Meir & Ponganis (2010). Given the variable and uncertain depth of the thermistors within the blubber layer (see section 3.5.5), the average of the three representative blubber temperatures per seal was used to compare blubber temperatures across seals. Core temperature was also linearly regressed against dive duration to remove the effects of diving and obtain a representative core temperature.

To understand how internal temperatures (i.e., core and blubber) change with diving behavior, average temperature and the range of temperatures were compared for short-shallow dives versus long-deep dives as well as active versus nonactive dives. In addition to within-dive comparisons, longer-term trends were compared by calculating the average temperature and the range of temperatures for dive bouts of similar dives. Active vasomotor regulation affects blubber temperatures and could be associated with either the dive response or thermal responses. Therefore, we predicted that the magnitude and temporal scale of changes in blubber temperature should indicate whether peripheral circulatory adjustments are associated with either the dive response or thermal responses. For example, we expected cyclical changes would most likely be associated with the dive response and its magnitude (or range) should be greater for long-deep dives.

A lag analysis was performed following Sato et al. (1994) to assess temporal correlations between physiological temperatures and water temperature and stroking activity. The physiological temperature data (i.e., skin, blubber at deep, mid, shallow, and core) was shifted backwards and forwards in time in step increments relative to either water temperature or stroke rate. At each step increment, the Spearman's rank correlation coefficient was calculated between the two variables using the corr function in MATLAB to determine the degree to which the variables are correlated at that time lag. The time lag with the highest absolute coefficient was the time lag for which the two variables were most correlated. This analysis was performed on the fine-scale data to assess correlations in short-term fluctuations relative to water temperature and stroke rate with a time step of 10 s as well as on a moving average of the temperature data (across a window equivalent to the average duration of 4 dives) to assess correlations in long-term fluctuations with water temperature using a time step of 10 min.

3.4 Results

3.4.1 Diving behavior

The seals in this study exhibited continuous diving behavior throughout their time at sea. Trip and dive statistics are provided in Table 3.4. The seals swam back to a haul-out site (Año Nuevo, n=7; Piedras Blancas, n=2) within a median of 2.4 days (range=1.3 – 7.9 days). The seals performed on average 82 ± 9 dives per day. The overall grand mean dive depth was 201.6 ± 172.9 m and grand mean dive duration was 15.1 ± 8.1 min. The deepest dive was 847.5 m performed by seal Frank, and the longest dive was 54.0 min performed by seal Anisa. Grand mean surface intervals were 1.9 ± 3.7 min, and extended surface intervals (>5 mins) were rare (<3% of dives), except for Snora who had 18 extended surface intervals that accounted for 10.6% of dives. Seal Snora's dives were also generally shallower and shorter compared to the other seals' dives.

Dives classified as short-shallow dives had higher stroke rates than long-deep dives (Table 3.5). Similarly, dives classified as active were generally shallower than nonactive dives, but depths were more variable and stroke rates were higher than the short-shallow dives. Stroke rates were higher on ascent than descent, especially for long-deep dives, for all seals except Snora (Table 3.6 & Figure 3.S4). When stroking frequency was compared between ascents and descents of similar vertical transit rates, stroking was generally higher on ascents suggesting that the seals must work harder to overcome their negative buoyancy while ascending from a dive. These differences between ascent and descent stroking effort were not as evident for three of the larger seals (Anisa, Snora, and Penny), suggesting they may be closer to neutral buoyancy.

3.4.2 Heat flux

Seals generally lost heat for most of the dive but transitioned to gaining heat during the end of the ascent and surface interval (Figure 3.3). For all seal-sensor combinations, heat loss occurred at least 78% of the time spent at sea (Figure 3.4A & Table 3.S1). The flank lost heat for the greatest percentage of time (grand mean = 93.0%, n=10 seals) while the neck lost heat for the lowest percentage of time (grand mean = 87.6%, n=5 seals). Smaller seals (mass range = 122-172 kg, n=5 seals, 8 sensors) lost heat between 79.6-90.4% of the time (average across all sensors for each seal) while larger seals (mass range = 234 – 259 kg, n=5, 18 sensors) lost heat between 90.0-97.0% of the time. However, none of the smaller seals had heat flux data at the swimming muscle, which was the location with the second highest percentage of heat loss time.

All seals had dives in which they lost heat the entire time; however, the number of dives varied by seal and sensor location (Table 3.7). These dives had overall grand mean depths of 43.3 ± 30.8 m (neck, n=376 dives), 52.5 ± 54.2 m (axilla, n=463 dives), 65.3 ± 74.7 m (*long. dorsi*, n=584), and 95.5 ± 114.2 m (flank, n=1066 dives), which are shallower than the grand mean depth of all dives (201.6 m, n=3104 dives, Table 3.4). The minimum temperatures on these dives were higher (9.6°C, 9.5°C, 9.1°C, and 9.1°C for the neck, axilla, *long. dorsi*, and flank, respectively) than the average minimum temperature of all dives (8.4°C). Stroke rate was generally higher compared to all other dives (Figure 3.5). When comparing the frequency of these dives across sensor locations with complete records, the flank had the highest percentage of dives during which only heat loss occurred for 6 of 7 seals who had a flank sensor plus at least one other sensor for comparison. Of those 6 seals, seal Penny was the only seal that lost heat throughout all the dives at the flank sensor. At Penny's other sensor locations, 21% or fewer of the dives were entirely heat loss dives.

When comparing short-shallow dives versus long-deep dives, heat loss generally occurred for a greater percentage of time on short-shallow dives across all sensor locations (Figure 3.4B & Table 3.S1). The only exceptions were OJ's flank and Xena's *long. dorsi*, where slightly more time was spent losing heat on long-deep dives. There were no clear patterns when comparing the percentage of heat loss or gain between active versus nonactive dives (Figure 3.4C).

When comparing the patterns in the timing of heat flux transitions across sensor locations within a seal, the smaller seals (OJ, CJ, Luna, and Cheia) were most consistent across heat flux sensor locations; however, none of these seals had neck or *long. dorsi* heat flux data (Figure 3.6). The bottom phase is when the fewest heat flux transitions occurred for all seals and sensor locations. Transitions during the bottom phase generally resulted in brief moments of heat gain and often coincided with a dive reversal and either increased stroking, change in water temperature, or both (Figure 3.7).

Most transitions from losing to gaining heat occurred during the ascent phase of the dive (>71% for each seal), regardless of the heat flux sensor location (Figure 3.8 & Table 3.S2). For three seals (Luna, Anisa, and Snora), the ascent phase accounted for all the heat loss to gain transitions at one or more sensor locations. Transitions from gaining to losing heat occurred mostly during the descent phase or during the surface interval but varied depending on seal and sensor location (Figure 3.8 & Table 3.S2). All seals 150 kg or smaller (OJ, CJ, Luna, and Cheia) had >64% of heat gain to loss transitions occurring during the descent phase for all their sensor locations and >73% for their flank. For seals larger than 170 kg, the flank had the most heat gain to loss transitions during the surface interval (>54%, and >80% if Frank is excluded) whereas the other sensor locations were more variable across seals.

To compare the depths at which the heat flux transitions occur, we focused on transitions from heat gain to loss during the descent and transitions from heat loss to gain during the ascent at similar transit speeds. Most transitions during the ascent (heat loss to gain) occurred deeper than transitions during the descent (heat gain to loss). If the transitions occur as a result of passing through the thermocline, a lag proportional to the transit rate is expected due to the response time of the heat flux sensor (Figure 3.9 & Figure 3.S5). After accounting for this lag, the transition from heat gain to loss on the descent occurred closer to the thermocline (averages per sensor ranging from 31-35 m above the thermocline at a transit speed of 1.0 m/s) compared to the opposite transition on the ascent (averages per sensor ranging from 58-108 m below the thermocline at a transit speed of 1.0 m/s). The difference between the transition depth and the thermocline depth was not correlated with dive depth for the descent transition for most seal-sensor combinations but was positively correlated with dive depth for the ascent transition for 23 of 26 seal-sensor combinations (Table 3.8 & Figure 3.S6C). That is, the difference between the transition depth and the thermocline depth on the ascent increased for deeper dives. The strength of this relationship was generally weakest for the flank (except for OJ) and strongest for the neck or axilla depending on the seal.

These relationships were examined with dive duration or stroking activity and found to be weaker than the relationship with dive depth across seal-sensor combinations (Figure 3.S6D-E). Even stronger relationships that were more consistent across all seals and sensor locations were found between the ascent transition depth and the minimum water temperature during the dive (Table 3.9 & Figure 3.S6B). This was no surprise given that water temperature is negatively correlated with dive depth.

3.4.3 Physiological temperatures

Skin temperatures had consistent within-dive patterns that tracked changes in water temperature. For the three seals (OJ, CJ, and Cheia) with skin temperature measurements at two locations (flank and axilla), the difference between those two locations was generally less than 0.35°C with no consistent patterns between dive phases. The difference between skin temperature and water temperature was examined both with and without incorporating the individual time lags determined in the lag analysis (see section 3.4.4). The patterns across seals were more consistent when analyzed with the time lags so these results are presented. The largest absolute difference between skin and water temperatures was on average 1.47 ± 1.13°C and occurred during the bottom phase (Table 3.10). Skin temperature was on average colder than the surrounding water during the surface interval for only two seals (OJ and Cheia). Both seals also had skin temperatures lower than water temperatures for over 10% of the time (regardless of dive phase) compared to 4% or less for all other seals (Figure 3.10). The skin-water temperature difference was ~3°C or lower for at least 80% of the time for all seals, and all but three seals (Luna, Snora, and Penny) had a majority (>50%) under 2°C.

The average blubber temperature on a dive was strongly correlated with dive duration for all seals with blubber thermistors (Table 3.11). Average core temperature had a weaker but significant relationship with dive duration for 3 out of 4 seals. Seal Snora was the only seal whose relationship between average core temperature and dive duration was not significant ($F_{1,169} = 1.10$, $p > 0.1$). The y-intercept of these linear regressions was taken as the representative core and blubber temperatures at the different thermistor depths for each seal (Figure 3.S7). These temperatures ranged from 37.11 to 37.34°C for core temperatures and from 36.91 to 37.43°C for blubber temperatures. Most seals had overlapping 95% confidence intervals for the three thermistor depths, except for Frank's mid thermistor and Toby's shallow thermistor (Table 3.11). There was no significant relationship between the average representative blubber temperature value for each seal and seal mass ($F_{1,6} = 0.409$, $p = 0.55$; Figure 3.S8).

The distribution of blubber temperature across the entire trip varied greatly between seals; however, all seals had peak densities between 32.8-37.3°C for the shallow blubber, 35.0-36.7°C for the mid blubber, 34.6-36.9°C for the deep blubber, and 36.7-37.5°C for the core (Table 3.12). Seals Toby and Frank had highly bimodal distributions in both their mid and deep blubber temperatures as well as Toby's shallow blubber temperature (Figure 3.S9). The two peak densities were separated by >10°C for the deep blubber, >18°C for the mid blubber, and 21°C for Toby's shallow blubber. Both seals were at sea longer compared to the other 6 seals with blubber temperature records that did not have bimodal temperature distributions (~7 days vs. <3 days). These bimodal temperature distributions were also evident in their time series data (Figure 3.11)—blubber temperatures fluctuated between near-core body temperatures to much lower temperatures on the scale of several hours with often relatively abrupt transitions between the two states.

Across all seals, cyclical fluctuations in blubber temperature occurred systematically with dive cycles. Within dives, blubber temperatures generally increased first before decreasing during the latter half of the dive. These fluctuations were generally more evident in the shallow blubber than in the deep blubber (Figure 3.12A). The resulting temperature gradient in the blubber increased first then decreased during the latter half of the dive, although a lot of variability is present (Figure 3.12B). Temperature gradients as large as ~20°C was measured in seal Toby, who was one of the smallest seals with blubber temperature data (seal Luna was smaller but only had data from one thermistor). The blubber temperature gradients in the other seals were generally <10°C.

To assess how diving behavior affects within-dive fluctuations, blubber and core temperatures were compared between short-shallow dives and long-deep dives. Long-deep dives had lower average blubber and core temperatures as well as larger temperature ranges (Table 3.13 & Figure 3.S10). The range of blubber temperatures varied drastically across seals with average minimum blubber temperatures being as high as 35.7°C or as low as 16.1°C during long-deep dives. Core temperatures on long-deep dives were on average between 0.5-1.0°C lower than on short-shallow dives. Similar patterns were observed when comparing active versus nonactive dives, where nonactive dives had lower blubber temperatures and larger temperature ranges (Table 3.14 & Figure 3.S10). No consistent patterns in core temperature were observed between active versus nonactive dives as well as dives with and without ingestion events.

When comparing internal temperatures across dive bouts of at least 3 consecutive dives, long-deep dives generally had decreasing trends in core and blubber temperatures while short-shallow dives had increasing trends (Table 3.15). Seal Snora had the most extreme core temperature values (lowest minimum, highest maximum, and largest range), but upon further inspection, the lowest values and largest ranges coincided with multiple consecutive ingestion events (Figure 3.S11). Excluding Snora's data, the lowest core temperature was 34.8°C during a 29-dive bout of long-deep dives during the latter half of Frank's trip. Frank's core temperatures dropped as much as 2.2°C during a long-deep diving bout and rose as much as 2.4°C during a short-shallow diving bout. Typical values for changes in Anisa's and Snora's core temperature were 0.2-0.4°C increases and 0.3-0.7°C decreases for short-shallow and long-deep diving bouts, respectively.

3.4.4 Time lags in physiological temperatures

Short-term, fine-scale fluctuations in physiological temperatures were examined using a lag analysis to identify temporal correlations with water temperature and stroking activity. Skin temperature was highly correlated with water temperature for all but one seal (Anisa) with a median time lag of 25 s, but time lags ranged from 10 to 50 s (Table 3.16A). Stroking activity (defined as strokes per min) had >50% correlation with skin temperature for only 3 seals and the time lag varied from 110 to 600 s. A few other correlations between 50-70% were present but not consistent across seals (Table 3.16A).

More correlations existed when using the long-term moving average of these physiological temperature data. Skin temperature was highly correlated with water temperature with a maximum rho coefficient at a time step of 0 min ±1 time step of 10 min, except for seal Anisa who had a much higher time lag (Table 3.16B). Shallow, mid and deep blubber temperature had correlations >63% except for Frank's mid blubber (ρ=0.467). Time lags varied greatly between seals, but overall median time lags were between 50-100 min for blubber temperatures and around 200 min for core temperature (Table 3.16).

3.5 Discussion

3.5.1 Within-dive patterns in thermal responses

Skin temperature and heat flux had the most consistent within-dive patterns among all thermal responses we examined. Changes in skin temperature tracked changes in water temperature, keeping skin temperature within a few degrees of water temperature, as shown in other marine mammals (Hansen & Lavigne, 1997; Meagher et al., 2008; D. P. Noren et al., 1999). Skin temperatures got as cold as ~5°C at the bottom of deeper dives. Heat flux patterns showed that seals lose heat throughout the dive, as expected when a warm-bodied mammal dives into colder waters (Figure 3.13). Interestingly, heat gain generally occurred during the end of the ascent phase and continued throughout the surface interval for at least some proportion of dives for all seals and sensor locations except for the flank of seal Penny.

Most heat flux transitions occurred during the ascent or descent phase of the dive when seals experienced the greatest changes in water temperature. Seals descend/ascend with vertical rates ~1.5-2.0 m s^{-1} (Sato et al., 2007); therefore, a short time lag for the skin to approach water temperature is to be expected. On the descent, this lag indicates that skin temperature was slightly higher than the water temperature, resulting in heat loss. The reverse occurred on the ascent into warmer waters—their skin was initially colder than the surrounding water, which reverses the temperature gradient resulting in a transition to heat gain. Of all the variables we examined, including stroke rate, the minimum water temperature strongly correlated with the depth at which this transition occurred on the ascent. During the descent, the transition to heat loss generally occurred near and above the thermocline depth with little variability compared to the opposite transition on ascent, and no correlations examined were consistent across seals. Overall, the predictable heat flux patterns and correlation with water temperature suggests that heat flux primarily results from passive mechanisms.

Heat loss during a dive aligns with a cooling of the periphery via passive heat loss due to peripheral vasoconstriction associated with the dive response (Ponganis et al., 2003). We would expect a relaxation of the dive response during the ascent resulting from anticipatory tachycardia (Hill et al., 1987). Increased blood flow would reoxygenate ischemic tissues throughout the surface interval and result in convective heat transfer to rewarm the periphery (Favilla & Costa, 2020). The latter portion of the ascent and surface interval would allow the seal to dump excess heat without overriding the dive response; however, heat gain generally occurred instead of heat loss, suggesting that seals rewarm from the outside-in (due to increasing water temperature) faster than they do from the inside-out (due to the redistribution of internal heat). We did not observe the delayed thermal responses (i.e., increased heat dissipation) reported in trained dolphins after surfacing from stationed dives to a certain depth and post-exercise (D. P. Noren et al., 1999; Williams et al., 1999). Given that we could not accurately quantify the magnitude of heat flux across seals and sensor locations, we compared the relative magnitude for each sensor across dive phases. We found that the highest heat dissipation occurred during the descent and bottom phases of the dive. In contrast, in the dolphin studies, heat loss was attenuated at depth except when intense exercise was performed prior to the dive. The authors concluded that the dolphins prioritize oxygen conservation during the dive and delay thermoregulation. However, they retained some flexibility in this coordination.

These differences are likely due to differences in the species' thermal windows and their relative field metabolic rates. The closest equivalent to a dolphin's dorsal fin would be a seal's hind flippers, which have been described as thermal windows, but primarily in warmer conditions (Gallivan & Ronald, 1979; Irving & Hart, 1957; Khamas et al., 2012; Kvadsheim et al., 1997; Mauck et al., 2003). However, securing sensors to the highly maneuverable flippers would be logistically challenging and likely result in shorter duration records (Hindle et al., 2015). Additionally, water temperature and activity level differences are likely key factors driving the different heat flux patterns. The dolphins were in warm waters and exercising (Bahamas and Hawaii). They, thus, were not experiencing the thermal gradient that the seals in our study experienced while diving, and they were likely also generating more internal heat from exercising.

A departure from these heat flux patterns was observed and depended on diving behavior and sensor location. All seals had dives in which heat loss occurred over the entire dive. These dives were generally much shallower and warmer than the average dive and had slightly higher stroke rates (Figure 3.13 & Figure 3.5). Therefore, the thermal gradients experienced on these dives were much smaller, and thus more comparable to what the dolphins experienced in the two aforementioned studies. That our seals continued to lose heat throughout the entire dive when performing shallower dives in warmer waters aligns with the results from the dolphin studies (D. P. Noren et al., 1999; Williams et al., 1999). This could be explained in part by increased heat production due to higher stroking activity on these shallow dives, similar to the exercising dolphins. Possible explanations for the role of these shallower dives in warmer waters are discussed in section 3.5.3.

The proportion of dives during which only heat loss occurred varied drastically between sensor locations. The flank sensor had the greatest proportion across most seals, and these dives were slightly deeper and colder on average compared to the other sensor locations. Across all dives, the heat flux sensors placed more caudally on the body (flank and *long. dorsi*) had greater heat loss time overall. Similarly, Willis & Horning (2005) found that areas close to locomotory muscles on swimming Steller sea lions had the highest heat flux. The sensors' proximity to the swimming muscle (i.e., *long. dorsi* in elephant seals) and muscular thermogenesis caused by stroking could explain this localized heat dissipation. Yet, on deeper dives, there was a transition to gaining heat on ascent even though more stroking occurred. This further supports the idea that water temperature has a greater influence on heat flux, while activity level may help explain some differences observed across heat flux sensors.

Activity level also influenced peripheral temperatures, with nonactive dives having lower blubber temperatures. However, we did not observe variations in core temperature during active versus nonactive dives. This is in contrast to what has been observed in small cetaceans and sea otters, which maintained thermal balance by storing heat from increases in activity, resulting in variation in core temperature (Costa & Kooyman, 1984; Hampton et al., 1971; Hampton & Whittow, 1976; McGinnis et al., 1972). This should not be surprising as elephant seals are larger and better insulated than sea otters and small cetaceans. The added advantage of this extra insulation is that they can exist on a lower mass-specific metabolic rate.

3.5.2 Interactions between dive response and thermoregulation

As we lacked heart rate data to examine the intensity of the dive response, we used blubber temperatures as a proxy of peripheral circulation (see Enstipp et al., 2017; Lewden et al., 2017 for examples in seabird literature) to examine the magnitude and timescale of circulatory adjustments relative to diving behavior. Although only the outermost layer of the blubber is metabolically inactive (Rea & Costa, 1992), we assumed little metabolic activity in this tissue (i.e., no lipolysis) given the short duration of the trip at sea. As such, we attributed temperature increases to perfusion of warm blood and decreases in temperature to reduced peripheral perfusion (Culik et al., 1996). The regressions showed that blubber temperatures decreased with increasing dive duration, as is expected if longer dives have a greater dive response (i.e., lower heart rate, less blood flow; Fedak et al., 1988; Zapol et al., 1979). Cyclical fluctuations in blubber temperature loosely matched the dive cycle and were generally most evident in the shallow blubber layer (Figure 3.12 & Figure 3.14A). Given the variability between dives, even if the longer-term fluctuations were removed from the signal, there were no convincing patterns across seals in correlations between blubber temperature and water temperature or stroking.

The magnitude of these within-dive fluctuations was small relative to the changes in blubber temperature observed across the trip, particularly for seals on longer trips (see section 3.5.4). These larger magnitude changes that occurred irregularly across the trip rather than on a dive-by-dive basis were characterized by slow cooling of the blubber layer that resulted in a larger blubber gradient and abrupt increases in blubber temperature that reduced the blubber gradient quickly (Figure 3.14). If increases in temperature result from peripheral perfusion, while decreases in temperature are due to reduced perfusion, these patterns are consistent with switching between vasodilation and vasoconstriction. The dive-by-dive fluctuations are superimposed on these larger fluctuations suggesting that the smaller scale fluctuations are due to the circulatory adjustments associated with the dive response. In contrast, the larger variation across dives may be more related to the overall thermal balance of the seal.

3.5.3 Thermoregulatory strategy

Representative core temperatures (determined from the linear regressions of dive duration and average core temperature, which essentially removed the effects of diving) were within the expected mammalian range (Clarke & Rothery, 2008). We found negative relationships between core temperature and dive duration for 3 of 4 seals but with much shallower slopes compared to blubber temperatures. The lowest core temperatures observed (after removing ingestion events) were between 35.8-36.7°C on long-deep dives. A 1-3°C decrease in body temperature has been estimated to reduce oxygen consumption by 10-20% (Hill et al., 1987; Odden et al., 1999). Core temperatures below 36°C occurred for seals Snora, Anisa, and Frank for average durations of 116.9, 136.5, and 522.4 mins (n=2, 4, 7 occurrences), which accounted for 9.5, 29.8, and 33.6% of their time at sea, respectively. The initiation of these lower core temperatures occurred on dives >400 m during bouts with dives >30 min, except for seal Snora, whose low core temperatures may be a byproduct of several consecutive ingestion events (Figure 3.S10). These findings align with previous results based on arterial and venous blood temperatures from Meir & Ponganis (2010) that northern elephant seals do not rely on hypothermia-induced metabolism depression to perform their routine dives (10-30 min).

Occasionally on longer dives, Meir & Ponganis (2010) found temperature drops in the extradural vein and aorta as low as 30°C and 32.7°C, respectively, and rewarming occurred before the end of the dive. The lowest core temperatures in our study remained much higher but generally occurred for several dives and coincided with even lower blubber temperatures. All long-term temperature trends (skin, blubber, and core) were correlated with water temperature but with different time lags. As expected, time lags generally increased for body temperatures from outside to inside the body (skin < blubber < core). The time lags for core temperature were on the order of magnitude of a few hours (equivalent to a minimum of 5 average dives), suggesting they are sufficiently well-insulated to buffer the repetitive thermal gradient experienced on a series of dives. Thus, they primarily undergo peripheral cooling—a form of regional heterothermy—to prioritize the dive response and maintain near-normothermic core temperatures, particularly during long-deep diving bouts. Our results are consistent with earlier studies that suggest marine mammals' ability to maintain homeothermy relies on the heterothermy of their peripheral tissues (Gallivan et al., 1983; Gallivan & Ronald, 1979; Irving & Hart, 1957).

In contrast to long-deep dives, internal temperatures (blubber and core) were higher during short-shallow diving bouts in warmer waters despite often being dives during which heat loss occurred the entire time (as discussed above in section 3.5.1). Compared to all other dives that had both periods of heat loss and heat gain, these dives had slightly higher stroke rates. Higher activity levels and a less severe dive response would suggest higher metabolic activity and, thus, internal heat production, contributing to the higher internal temperatures. In this scenario, the motivation for performing these shallow diving bouts might be to relax their dive response and recover from deep-diving bouts (e.g., nitrogen washout and greater oxygen uptake). This strategy has been suggested in deep-diving beaked whales to recover while minimizing time at the surface where they are most vulnerable to predators (Aguilar de Soto et al., 2020; Tyack et al., 2006). Beaked whale dives during the inter-deep-dive interval are ~10% of their typical dive depth. In comparison, the shallow diving behavior of the seals in our study was closer to ~25%. Heart rates on these short-shallow dives that are higher than average dive-level heart rates (as seen in Andrews et al., 1997) would support this recovery hypothesis.

If deep-diving marine mammals are so well-insulated, being active in warmer waters may be more thermally challenging than their routine deep diving, and they may risk overheating. This strategy may therefore have a thermoregulatory cost depending on the species thermal comfort zone and activity level. A few studies investigating the upper thermal limits of marine mammals have found that the blubber layer can be used as a buffer zone to store heat and delay the onset of hyperthermia (Heath & Ridgway, 1999; see Bagge et al., 2012; Dunkin et al., 2005 for mechanisms). Marine mammals can fully or partially override the dive response when heat stressed (Hammel et al., 1977; D. P. Noren et al., 1999). However, physiological imbalances may occur when additional stressors disrupt their behavior and physiological coordination (Fregosi et al., 2016; Williams et al., 2017). It has been hypothesized that military exercises using sonar disrupted the diving behavior of beaked whales resulting in mass strandings in warm water likely due to a combination of heat stress and decompression sickness (Bernaldo de Quirós et al., 2019; DeRuiter et al., 2013; Filadelfo et al., 2009; Hooker et al., 2009; *ONR Marine Mammal Diving Physiology Workshop*, 2017). This, along with the paucity of studies on the thermal physiology of freely diving marine mammals, motivated this study. Our findings suggest that deep-diving marine mammals, particularly those large and well-insulated, are likely to be more susceptible to thermal imbalance in shallow, warmer waters and at the end of a dive when, despite a relaxation of the dive response, heat gain occurs as their cooled periphery meets warmer waters. Therefore, the timing of a disturbance during the dive cycle as well as an animal's current thermal state will factor into its capacity to adjust physiological responses and thus determine the severity of the consequences of the disturbance.

An alternative explanation for shifting to shallow diving from their routine diving behavior could be a behavioral thermoregulation strategy to rewarm after a bout of long-deep dives. Shallow-diving bouts often occur after or between deep-diving bouts (except for those at the beginning or end of the trip that are likely due to bathymetric constraints). In several instances, an increase in blubber and core temperatures was observed shortly after this change in diving behavior, which was often accompanied by extended surface intervals (Figure 3.14 & Figure 3.15). Lower heat dissipation (facilitated by the lower temperature gradient between the core and water), increased activity levels (and thus increased muscular thermogenesis), and a less severe dive response during these shallow diving bouts would increase internal temperatures. The fact that core temperatures declined slowly during deep-diving bouts for all seals and even dropped below 36°C a few times (more often for seal Frank, who had the longer trip) suggests that seals may accrue a thermoregulatory debt during routine diving behavior. Thus, the shift to nonroutine diving behavior may be modulated by their thermoregulatory needs to pay off that debt and regain thermal balance. Quantifying the magnitude of heat loss versus heat gain would provide additional evidence for this thermoregulatory debt hypothesis or alternatively suggest that internal heat production and time spent gaining heat on deeper dives is sufficient to compensate for heat loss and maintain thermal balance.

3.5.4 Influence of size and trip duration

Clear differences in some thermal responses were observed between smaller (mass range = 122-172 kg, n=5 seals) and larger seals (mass range = 234 – 259 kg, n=5), suggesting a size-dependent thermoregulatory strategy. A larger body has a smaller surface-area-to-volume ratio, which would aid in heat conservation (i.e., minimize heat loss; Innes et al., 1990). Previous studies have noted that differences in size among closely related species (Adamczak et al., 2020; McGinnis et al., 1972; Niizuma et al., 2007) or different age classes within a species (Hansen & Lavigne, 1997; Liwanag et al., 2009; S. R. Noren et al., 2008) partially explain differences in their thermoregulatory strategies. Larger seals in our study spent more time losing heat and had a greater proportion of dives in which they lost heat during the entire dive. Of the four sites where heat flux was measured, the flank seems to be the primary location of heat loss for these larger seals. The larger seals had an average blubber depth of 47.6 ± 2.9 mm, while the smaller seals had an average blubber depth of 35.1 ± 6.6 mm, resulting in a positive relationship between mass and average blubber thickness ($F_{1,9} = 21.76$, $p < 0.01$; Figure 3.1B). The larger seals' thicker blubber layer may over-insulate them, and their smaller surface area-to-volume ratio would make dumping heat less efficient. These differences in heat flux patterns between the two size groups of seals in our study suggest that their thermoregulatory ability is size-dependent. Sampling seals in the 170-230 kg size range would provide more insight into whether capabilities fall on a continuum related to body size or whether there is a size threshold.

We lacked sufficient core temperature measurements on seals of different sizes (234-258 kg, n=4) to directly assess the influence of size on variability in core temperatures. However, we did have sufficient blubber temperature data from seals over a sufficiently large range (122-259 kg, n=7) to assess size influencing internal temperatures. Individual differences observed in the overall range of blubber temperatures across the trip seem to depend on an interaction between seal size and trip duration. Smaller seals and seals on trips longer than 2 days generally had larger temperature ranges. Longer-term, larger fluctuations were observed in the only two seals that spent ~7 days at sea, which resulted in bimodal temperature distributions (Figure 3.11). The smaller of the two (Toby, 172 kg) had some of the lowest blubber temperatures observed across all seals—sustained temperatures of around 11.8°C in the shallow blubber and a blubber gradient of >14°C for as long as 13 hours. The larger seal (Frank, 258 kg) maintained higher blubber temperatures with sustained temperatures as low as 16.7°C and a gradient of 8.5°C.

Seal Luna had a more extended trip than seals Toby and Frank, but she hauled out after the first 1.3 days at sea for ~8 hours before returning to sea for over a month. We, therefore, included only the first 1.3 days in the analyses as the sensors can be damaged when they are on land. However, it is worth noting that larger temperature fluctuations similar to Toby's and Frank's were observed during Luna's second trip at sea after roughly 7 days and continued until the instrument stopped recording after ~28 days (Figure 3.16). We only have data from one of the three thermistors (the deepest placed thermistor) due to instrument failure, but this thermistor measured sustained blubber temperatures as low as ~17°C, which is colder than the lowest sustained temperatures observed in Toby's and Frank's deep blubber layer. Luna's low deep blubber temperatures are not surprising given that Luna was the smallest seal (122 kg) with the thinnest blubber layer (23.6 mm; Table 3.1). While low temperatures could also be attributed to the thermistor slightly pulling out and becoming shallower than originally placed, maximum blubber temperatures during the latter portion of the trip were just as high as those at the beginning, suggesting that thermistor displacement is not likely to be the case.

Seal Frank was the only one of the three seals with stomach temperature data and a longer trip to assess whether these large fluctuations in blubber temperature are reflected in changes to the core temperature. A time lag between 80-120 min was found with long-term averaged water temperature and core and blubber temperatures (Table 3.16). This delay is evident in the time series data (Figure 3.17). After shifting from short-shallow diving to long-deep diving or vice versa, there are generally a few to several dives before a large change in blubber or core temperature is observed. Further, core temperatures reflect the changes in blubber temperatures, but the magnitude of changes in core temperature is smaller. Even though Frank was of similar size and blubber thickness to the other three seals with core temperature data, Frank had the largest range in core temperature (34.8-37.8°C) and the largest drop in core temperature of 2.2°C during a long-deep diving bout. Therefore, even larger seals may no longer be over-insulated on longer trips and must modulate their diving behavior to regain thermal balance after deep-diving bouts.

3.5.5 Benefits and challenges of multiple sensors

By combining several physiological sensors into a biologger, we could examine the fine-scale thermal responses of free-ranging northern elephant seals while diving. Given the amount of individual variability reported in thermal responses, particularly heat flux measurements (Erdsack et al., 2018; Meagher et al., 2008), we recommend measuring as many variables as possible in the same individual to achieve a holistic understanding of their thermal physiology. We acknowledge an ethical limit to how many sensors are attached to or implanted in an animal (Forin-Wiart et al., 2019; Horning et al., 2017, 2019). This was one reason we did not add a biologger and sensors required to measure heart rate. However, heart rate data would have allowed us to measure the dive response. Still, we found that variables relevant to thermal physiology measured externally are primarily influenced by water temperature. In contrast, those measured internally are the combined signals of the dive response and thermal responses. The challenges we encountered with some of the sensors limited the scope of our analyses and are discussed below.

We demonstrated that blubber temperatures and a gradient within the blubber can be measured throughout a short-term deployment without major effects on the insertion area (personal observation). However, obtaining clear ultrasound images to measure the thermistors' depth proved challenging, particularly when using an ultrasound device without a mode for needle guidance or enhancement. For the thermistors with poor ultrasound images, we confirmed their relative depths by comparing the post-procedure and pre-release blubber temperatures while seals recovered from anesthesia in the transportation cage. We compared these temperatures to those post-trip (immediately after the seal hauled out) to determine if any of the thermistors may have pulled out during the time at sea. We also marked the cable at 0.5 cm intervals to compare the thermistor's position at recovery with that at deployment. Seals Xena and Penny were the only two seals whose three thermistors were in the same position at recovery. In the other four seals, there were six instances where the thermistors stayed in place and two cases where the thermistors completely pulled out after the seal hauled out (evidenced by a sharp temperature drop after diving behavior ended). The rest were still inserted at recovery but had pulled out slightly, likely after the seal hauled out.

Interestingly, the temperature data showed periods of inverse gradients in the blubber layer for all seals, including Penny, for whom we were confident in the thermistor placements at deployment (via good ultrasound images) and recovery (via the marked cable). Seal Frank had the largest inverse gradients—the shallow thermistor often measured higher temperatures than the deep and mid thermistors but only during periods that we hypothesize represent vasoconstriction (Figure 3.11B). While thermistors were generally inserted ~1-3 cm apart along the flank, Frank's thermistors were spaced slightly further apart (3.5 cm). Meagher et al. (2002) found that the vasculature of an area significantly affects the measurements of a thermal variable (in that instance, heat flux). We suggest the inverted gradients could be due to variable blubber thickness and/or vasculature and perfusion across this area. However, we cannot confirm whether these inversions are real or due to uncertain placement or thermistors pulling out. Ideally, thermistors would be placed vertically stacked throughout the depth of the blubber. With exact placement depths of the thermistors, the blubber gradient could be analyzed more thoroughly. For example, gradients could be calculated over the distance between the thermistors (i.e., °C/mm), and gradients between the deep-mid and mid-shallow blubber layers could be compared to determine differential perfusion or cooling across the blubber layer.

Stomach temperature pills are generally used as a tool to study foraging ecology (Austin et al., 2006; Kuhn et al., 2009; Kuhn & Costa, 2006), but they can also be used to obtain a proxy of continuous core body temperature in a relatively noninvasive way which has been done in several early studies on thermoregulation in marine mammals, although mostly in lab settings (e.g., Gallivan et al., 1983; Hampton et al., 1971; Hampton & Whittow, 1976; Whittow et al., 1974). We developed a custom-written script to filter out temperature spikes from ingestion events, which could be applied to other species. The algorithm worked best if intervals between ingestions were long enough that the asymptote associated with rewarming the cold prey was apparent. There were instances where ingestion events occurred so frequently that post-prandial rewarming for each ingestion signal was not observed. To determine if this effect produced a detectable difference in the processed core temperature signal, we examined the average core temperature and range of core temperatures between feeding and nonfeeding dives. Still, we did not find any consistent differences, even when comparing similar dives (i.e., short-shallow and long-deep dives). Although we did not detect the immediate thermal effects of ingestion (either of cold prey or water) on their core temperature, it is important to consider how feeding might affect their thermal physiology given the other physiological changes that occur with feeding (e.g., increased perfusion of the viscera for digestion, increased metabolism associated with the heat increment of feeding;

Rosen et al., 2007). Previous studies on pinnipeds suggest that the heat increment of feeding does not significantly affect thermoregulation (Rosen & Trites, 2003; Willis et al., 2005) and that digestion may be delayed until after active foraging bouts to minimize conflict with the dive response (Crocker et al., 1997; Sparling et al., 2007). Distinguishing between ingestion of prey and water would be the first step to determine whether feeding occurred (and how much) during these relatively short translocation trips and whether feeding had noticeable effects on behavior or thermal physiology (Hedd et al., 1996; Wilson et al., 1995).

As mentioned in the methods, heat flux was only analyzed in a binary way (which only required reliable zero offsets) because several calibration experiments revealed inconsistent sensitivity of the sensors. More calibration experiments are necessary to fully understand the combined effects of pressure and immersion on the sensitivity of the sensors. Analyzing the direction and magnitude of heat flux using the data collected for this study would require determining if the sensitivity changes predictably and then applying an appropriate correction to the data. Ideally, to use these sensors to study the thermal physiology of diving animals, the sensor must be designed more robustly to avoid changes in sensitivity during immersion and pressure cycles associated with diving.

Heat flux data are often incorporated into whole-body heat transfer models (e.g., Erdsack et al., 2018; Hindle et al., 2015; Kvadsheim et al., 1997). Due to the high variability in heat flux values among and within individuals, we caution against the quantitative interpretation and comparison of heat flux values (Erdsack et al., 2018; Meagher et al., 2008). Additionally, if point measurements are extrapolated to whole-body thermal dynamics, it is critical to determine the most representative sites of the entire body (Hindle et al., 2015). Nonetheless, heat flux measurements have vastly improved our understanding of the spatial and temporal variability in heat transfer across the body in relation to anatomy, water temperature, and exercise.

A significant challenge with analyzing time series data from multiple sensors is the different response times of sensors. For example, the thermistor embedded in the heat flux sensor used to measure skin temperature has a slower response time than the exposed thermistor on the Mk10 satellite tag used to measure water temperature. The response time of our heat flux sensor thermistor (see methods) was determined to be ~35 s (or 8 s time constant), slightly faster than the 10 s time constant quoted on the product datasheet. When correlations were examined using the fine-scale data, the only consistent correlation across all seals was between water temperature and skin temperature with a time lag of ~25 s, roughly the difference in response times between the two thermistors. Another consequence of these response time differences was the inconsistencies between the skin-water temperature gradient and heat flux direction. According to thermodynamics, the direction and magnitude of heat flux is determined by the temperature difference between the skin and water. However, there were often examples in the time series data where the direction of heat flux was opposite to the direction predicted by the skin-water temperature difference. Incorporating a seal-specific time lag improved the consistency of patterns across seals when analyzing the skin-water temperature differences. This approach could be used in other studies analyzing fine-scale data from two or more sensors that differ slightly in response time.

3.5.6 Conclusions and future work

By measuring multiple physiological variables in freely diving seals, we found that thermal responses are influenced by water temperature at the dive level, by diving behavior at the bout level, and by body size and time at-sea at the trip level. Blubber temperatures revealed the complex interaction between the dive response and thermoregulation. Elephant seals maintained relatively stable core temperatures during routine diving behavior by undergoing peripheral cooling during the dive and adjusting their blubber temperature gradient across dives. Evidence of behavioral thermoregulation (i.e., a shift to nonroutine diving behavior) was observed, often occurring after long, deep diving bouts that resulted in a slight thermoregulatory debt. Given their large size, thick blubber, and deep-diving behavior, elephant seals can provide valuable insight into the physiology of large cetaceans that cannot be readily studied. This work provides a baseline for incorporating thermal physiology into our understanding of the cumulative impacts of stressors on marine mammals. Additional studies are needed to better understand the plasticity of their thermoregulatory responses and what conditions may increase their susceptibility to thermal imbalance.

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Table 3.1 Seal morphometrics measured during deployment procedure.

Seal	Sex	Mass (kg)	Standard Length (cm)	Curve Length (cm)	Girth (cm)	Blubber Depth (mm)
OJ	F	145	169	183	137	$41.9^{D,L}$
CJ	F	150	174	193	133	$37.7^{D,L}$
Xena	F	259	206	228	167	44.9
Toby	M	172	191	204	142	40.1*
Luna	F	122	168	182	125	23.6
Cheia	F	144	175	189	134	32.3
Anisa	F	234	201	219	157	43.7
Snora	F	247	203	220	165	51.4
Penny	F	240	203	222	164	48.5
Frank	M	258	206	222	167	49.3**

Standard length is the straight line length from the nose to the tip of the tail.
Curve length is the curvilinear distance from the nose to the tip of the tail.
Girth reported is the average between measurements at the axillary, sternum, and midsection.
Blubber depth is the average between measurements at the axillary, sternum, and midsection measured dorsally^{D}, laterally^{L}, and ventrally^{V}.
*Missing axillary dorsal and midsection lateral measurement.
**Missing midsection ventral measurement.

Table 3.2 Sensor configuration on each seal and the completeness of data records available from each sensor.

Year	Season	Seal	Sensor Configuration	Heat Flux				Skin Temp		Blubber Temp			Stomach Temp Pill	Accelerometry Sampling Frequency (Hz)		
				Ax	Neck	Flank	LD	Ax	Flank	Shallow	Middle	Deep		X	Y	Z
2018	Spring	OJ	HFS	X		X		X	X					8	32	8
2018	Spring	CJ	HFS	X		/		X	/					8	32	8
2019	Spring	Xena	HFS + BlubberT	O	O	X	X			X*	X*	X*		16	16	16
2019	Spring	Toby	HFS + BlubberT	O	X	/X			/	X	X*	X*		16	16	16
2019	Fall	Luna	HFS + BlubberT	O	O	//			/	O	O	/		16	16	16
2019	Fall	Cheia	HFS	X		X		X	X					16	16	16
2022	Spring	Anisa	HFS + BlubberT + STP	X	X	X	X		X	X*	X	X	X	16	16	16
2022	Spring	Snora	HFS + BlubberT + STP	X	X	X	X		X	X*	X	X	X	16	16	16
2022	Spring	Penny	HFS + BlubberT + STP	X	X	X	X		X	X*	X*	X*	X	16	16	16
2022	Spring	Frank	HFS + BlubberT + STP	X	X	X	X		X	X	X	X*	X	16	16	16

HFS – heat flux sensor (with or without embedded thermistor to measure skin temperature), BlubberT – blubber thermistors, STP – stomach temperature pill

Ax – axilla, LD – *longissimus dorsi*

Complete record (X), Partial record (/), Failed record (O), Thermistor remained at same blubber depth (*)

Table 3.3 Dive categorization based on k-means clustering (k=3). The centroids for dive depth and duration as well as the percentage of dives in each cluster are shown for the two extreme clusters referred to as short-shallow dives and long-deep dives. The top 20th and bottom 20th percentiles of stroke rate used as thresholds to identify active vs. nonactive dives are shown.

Seal	No. Dives	Short-Shallow dives			Long-Deep dives			Nonactive dives	Active dives
		%	Depth (m)	Duration (min)	%	Depth (m)	Duration (min)	Strokes per min	Strokes per min
OJ	150	32.0	35.5	7.4	34.0	304.3	23.6	13.7	36.5
CJ	613	25.6	44.1	6.9	51.1	385.6	20.2	16.5	30.5
Xena	200	38.5	76.3	10.1	24.5	387.8	27.6	12.6	28.0
Toby	600	30.7	46.3	5.3	41.2	377.8	21.1	23.4	38.9
Luna	112	33.0	52.9	7.7	37.5	362.4	19.4	28.8	38.6
Cheia	396	21.2	49.0	6.8	46.7	419.2	24.0	18.8	32.0
Anisa	116	46.6	40.2	7.2	11.2	379.4	31.0	11.3	21.3
Snora	170	54.7	39.6	4.3	12.9	397.0	24.3	17.7	38.6
Penny	129	25.6	48.6	6.6	24.8	347.6	22.5	16.2	31.3
Frank	618	53.1	40.1	6.8	21.7	518.8	33.1	15.9	43.6

Table 3.4 Summary statistics for the trip and diving behavior of each seal. Overall averages and standard deviations are weighted by the number of dives per seal. ESI = extended surface intervals greater than 5 min.

Seal	Days at Sea	Recovery Location	No. Dives	No. Dives per Day	Dive Depth (m)		Dive Duration (min)		Surface Interval Duration (min)		No. ESI
					mean ± SD	median (min – max)	mean ± SD	median (min – max)	mean ± SD	median (min – max)	
OJ	1.9	ANNU	150	81	140.1 ± 153.3	72.5 (15.0 – 591.0)	15.6 ± 7.1	15.6 (1.0 – 31.6)	1.6 ± 0.7	1.5 (0.02 – 4.0)	0
CJ	7.9	PIBL	613	77	252.5 ± 160.4	309.5 (15.0 – 538.0)	15.6 ± 6.0	17.6 (1.5 – 34.2)	1.9 ± 6.1	1.6 (0.02 – 151.7)	4
Xena	2.8	ANNU	200	71	202.2 ± 145.7	153.0 (16.5 – 656.5)	17.6 ± 7.5	17.3 (1.4 – 43.5)	2.4 ± 4.0	2.0 (0.07 – 51.4)	3
Toby	7.0	PIBL	600	85	213.0 ± 157.5	194.3 (16.0 – 602.5)	13.9 ± 7.1	14.2 (0.6 – 35.9)	2.1 ± 4.0	1.8 (0.08 – 83.0)	6
Luna§	1.3	SRIS	112	88	207.4 ± 154.9	146.5 (21.5 – 695.5)	14.1 ± 5.6	14.8 (0.7 – 35.3)	1.6 ± 0.4	1.6 (0.37 – 2.5)	0
Cheia	5.8	ANNU	396	68	274.6 ± 169.2	322.5 (15.5 – 703.5)	17.8 ± 7.2	19.2 (0.8 – 36.7)	2.2 ± 1.1	2.0 (0.02 – 9.2)	5
Anisa	1.3	ANIS	116	91	109.8 ± 119.1	66.3 (15.0 – 461.5)	13.3 ± 8.2	12.4 (2.6 – 54.0)	1.9 ± 2.0	1.5 (0.03 – 20.7)	3
Snora	1.7	ANNU	170	100	89.7 ± 124.6	42.0 (15.0 – 517.0)	10.0 ± 7.4	7.7 (0.9 – 36.0)	2.8 ± 4.8	1.4 (0.03 – 43.8)	18
Penny	1.6	ANNU	129	79	144.4 ± 129.3	90.5 (15.5 – 499.0)	14.2 ± 6.1	14.0 (0.9 – 29.5)	1.7 ± 1.0	1.5 (0.03 – 8.6)	1
Frank‡	7.6	ANNU	618	82	167.0 ± 202.9	68.8 (15.0 – 847.5)	15.1 ± 11.0	11.4 (0.7 – 47.4)	1.4 ± 0.8	1.2 (0.02 – 9.6)	1
Overall	3.9		∑ =3104	82 ± 9	201.6 ± 172.9		15.1 ± 8.1		1.9 ± 3.7		

Recovery Location: ANNU-Año Nuevo mainland, ANIS-Año Nuevo Island, PIBL-Piedras Blancas mainland, SRIS-Santa Rosa Island

§ Hauled out at ANNU after 1.3 days at sea. Returned to sea after ~8 hr. Tag recovered at SRIS after 41.1 days. Data before first haul-out is analyzed.

‡ Returned with a shark bite wound.

Table 3.5 Summary statistics for dives classified as short-shallow versus long-deep and nonactive versus active. Averages ± SD are reported.

Seal	Total No. Dives	No. Dives	Depth (m)	Duration (min)	Strokes per min
		Short-Shallow Dives			
OJ	150	48	35.5 ±24.6	7.4 ±2.5	35.7 ±12.2
CJ	613	157	44.1 ±29.8	6.9 ±2.6	31.5 ±13.1
Xena	200	77	76.3 ±47.7	10.1 ±3.3	31.4 ±14.3
Toby	600	184	46.3 ±26.7	5.3 ±2.4	37.6 ±8.8
Luna	112	37	52.9 ±19.3	7.7 ±2.5	39.3 ±6.4
Cheia	396	84	49.0 ±33.7	6.8 ±2.8	38.4 ±12.3
Anisa	116	54	40.2 ±21.2	7.2 ±2.0	17.2 ±8.3
Snora	170	93	39.6 ±29.4	4.3 ±2.2	33.6 ±9.8
Penny	129	33	48.6 ±29.9	6.6 ±2.5	39.2 ±13.4
Frank	618	328	40.1 ±23.7	6.8 ±2.8	39.3 ±10.7
		Long-Deep Dives			
OJ	150	51	304.3 ±158.3	23.6 ±2.9	15.0 ±7.3
CJ	613	313	385.6 ±60.7	20.2 ±2.4	21.7 ±5.2
Xena	200	49	387.8 ±88.1	27.6 ±3.5	13.2 ±3.5
Toby	600	247	377.8 ±68.4	21.1 ±3.1	26.7 ±6.8
Luna	112	42	362.4 ±99.4	19.4 ±3.1	29.7 ±5.7
Cheia	396	185	419.2 ±75.2	24.0 ±2.9	22.9 ±5.7
Anisa	116	13	379.4 ±65.3	31.0 ±8.7	10.9 ±2.3
Snora	170	22	397.0 ±63.0	24.3 ±3.4	18.0 ±2.9
Penny	129	32	347.6 ±81.6	22.5 ±2.9	16.9 ±4.1
Frank	618	134	518.8 ±125.6	33.1 ±4.6	14.4 ±3.5

Table 3.5 (continued) Summary statistics for dives classified as short-shallow versus long-deep and nonactive versus active. Averages ± SD are reported.

Seal	Total No. Dives	No. Dives	Depth (m)	Duration (min)	Strokes per min	Descent Rate (m/s)	Ascent Rate (m/s)
		Nonactive Dives					
OJ	150	29	109.6 ±90.1	21.3 ±5.4	7.6 ±3.5	0.72 ±0.12	0.74 ±0.19
CJ	613	122	214.7 ±136.5	16.8 ±4.8	12.0 ±3.5	0.76 ±0.11	0.87 ±0.19
Xena	200	39	280.3 ±128.5	24.7 ±7.1	10.2 ±1.5	0.88 ±0.18	0.87 ±0.17
Toby	600	119	316.9 ±143.2	20.9 ±6.1	20.0 ±2.3	0.83 ±0.15	0.95 ±0.21
Luna	112	21	268.4 ±174.0	19.0 ±5.6	23.5 ±4.5	0.99 ±0.14	0.98 ±0.22
Cheia	396	78	266.8 ±145.6	20.5 ±5.7	14.1 ±3.6	0.78 ±0.15	0.82 ±0.20
Anisa	116	22	138.7 ±155.4	18.3 ±13.1	7.1 ±3.0	0.53 ±0.19	0.58 ±0.23
Snora	170	33	120.5 ±153.8	16.7 ±6.8	13.8 ±3.2	0.74 ±0.16	0.69 ±0.19
Penny	129	25	217.6 ±144.3	19.3 ±5.8	13.4 ±2.2	0.97 ±0.17	0.98 ±0.13
Frank	618	123	411.7 ±224.1	29.0 ±9.8	11.6 ±3.0	0.89 ±0.18	0.91 ±0.20
		Active Dives					
OJ	150	30	42.0 ±28.6	7.5 ±2.9	44.0 ±5.5	0.94 ±0.24	0.99 ±0.26
CJ	613	123	122.2 ±112.5	9.5 ±5.0	39.5 ±7.8	0.86 ±0.22	0.87 ±0.24
Xena	200	40	93.8 ±61.6	9.6 ±3.9	42.5 ±11.1	0.98 ±0.28	0.88 ±0.30
Toby	600	120	109.0 ±95.0	8.3 ±4.2	45.0 ±5.0	0.80 ±0.22	0.77 ±0.25
Luna	112	22	87.1 ±87.4	8.8 ±3.3	43.0 ±5.4	0.87 ±0.13	0.68 ±0.23
Cheia	396	79	124.3 ±139.8	9.4 ±5.3	42.0 ±9.1	1.02 ±0.32	1.00 ±0.29
Anisa	116	23	80.2 ±60.6	10.7 ±4.7	27.0 ±6.3	0.57 ±0.19	0.79 ±0.33
Snora	170	34	25.6 ±13.0	3.3 ±1.9	44.8 ±3.4	0.74 ±0.25	0.54 ±0.27
Penny	129	26	55.2 ±37.9	6.9 ±3.0	44.0 ±10.9	0.93 ±0.37	0.89 ±0.29
Frank	618	124	32.4 ±18.6	5.0 ±2.0	50.0 ±4.5	0.85 ±0.35	0.82 ±0.27

Table 3.6 Results from Wilcoxon signed rank test testing the one-sided hypothesis that ascent stroke rates are higher than descent stroke rates. Bolded *p*-values are significant.

Seal	All Dives		Short-Shallow Dives		Long-Deep Dives	
	z-statistic	*p*-value	*z*-statistic	*p*-value	*z*-statistic	*p*-value
OJ	5.715	**5.48E-09**	-2.231	9.87E-01	6.191	**2.99E-10**
CJ	20.851	**7.54E-97**	7.711	**6.24E-15**	15.333	**2.29E-53**
Xena	6.642	**1.55E-11**	0.888	1.87E-01	5.730	**5.03E-09**
Toby	19.127	**7.49E-82**	6.296	**1.53E-10**	13.624	**1.44E-42**
Luna	9.178	**2.19E-20**	5.265	**7.01E-08**	5.639	**8.54E-09**
Cheia	16.580	**4.86E-62**	4.734	**1.10E-06**	11.794	**2.09E-32**
Anisa	-1.530	9.37E-01	-4.340	1.00E+00	1.887	**2.96E-02**
Snora	-8.449	1.00E+00	-6.045	1.00E+00	1.136	1.28E-01
Penny	-1.946	9.74E-01	-2.260	9.88E-01	2.889	**1.93E-03**
Frank	6.615	**1.86E-11**	-3.596	1.00E+00	9.876	**2.65E-23**

Table 3.7 The number and percentage of dives during which only heat loss occurred for each heat flux sensor location. Average ± SD dive depth and minimum water temperature are provided for those dives.

Seal	Sensor Location	No. Dives	% Dives	Average Dive Depth (m)	Average Min. Temp (°C)
OJ	Ax	18	12%	26.4 ±7.9	11.0 ±0.3
CJ	Ax	27	4%	41.5 ±78.0	9.7 ±1.1
	Flank	41	11%	25.8 ±10.9	9.9 ±0.6
Xena	Flank	113	57%	146.0 ±135.7	8.6 ±1.7
	LD	2	1%	21.3 ±3.9	11.8 ±0.5
Toby	Flank	9	24%	27.8 ±17.7	12.9 ±1.1
	Neck	48	8%	33.3 ±13.6	11.6 ±0.9
Luna	Flank	48	43%	65.6 ±36.4	10.3 ±0.7
Cheia	Ax	21	5%	24.8 ±11.5	13.9 ±1.4
	Flank	29	7%	52.4 ±88.1	13.4 ±2.2
Anisa	Ax	66	57%	59.2 ±56.6	9.4 ±0.6
	Flank	105	91%	104.4 ±115.4	9.0 ±1.0
	LD	65	56%	83.3 ±100.8	9.2 ±0.8
	Neck	58	50%	52.7 ±37.0	9.4 ±0.4
Snora	Ax	85	50%	33.5 ±16.2	10.2 ±0.5
	Flank	163	96%	74.8 ±103.3	9.7 ±1.0
	LD	139	82%	40.8 ±27.7	10.0 ±0.5
	Neck	109	64%	37.3 ±16.2	10.0 ±0.5
Penny	Ax	25	19%	47.9 ±22.9	9.5 ±0.2
	Flank	129	100%	144.4 ±129.3	8.7 ±0.9
	LD	27	21%	51.8 ±35.0	9.4 ±0.3
	Neck	9	7%	61.9 ±118.7	9.3 ±0.9
Frank	Ax	221	36%	64.4 ±62.4	8.8 ±0.5
	Flank	429	69%	87.5 ±110.8	8.7 ±0.8
	LD	351	57%	73.0 ±81.6	8.8 ±0.6
	Neck	152	25%	46.1 ±27.1	8.9 ±0.4
Overall	Ax	∑ = 463		52.5 ±54.2	9.5 ±1.3
	Neck	∑ = 376		43.3 ±30.8	9.6 ±1.0
	Flank	∑ = 1066		95.5 ±114.2	9.1 ±1.4
	LD	∑ = 584		65.3 ±74.7	9.1 ±0.8

Table 3.8 Regression statistics for the difference between heat flux transition depths on descent or ascent and thermocline depth against max dive depth. Regressions significantly different from the constant model are bolded.

Seal	Sensor Location	Descent				Ascent			
		F-statistic	*p*-value	Adj. R^2	RMSE	*F*-statistic	*p*-value	Adj. R^2	RMSE
OJ	Ax	3.386	6.89E-02	0.024	18.95	103.835	**1.43E-17**	0.481	27.95
	Flank	0.558	4.57E-01	-0.004	17.02	497.617	**1.29E-46**	0.789	27.75
CJ	Ax	0.124	7.25E-01	-0.002	45.53	384.257	**1.45E-66**	0.388	55.55
	Flank	1.431	2.33E-01	0.002	48.99	177.800	**1.04E-32**	0.350	51.72
Xena	Flank					9.487	**3.03E-03**	0.114	18.46
Toby	Neck	39.259	**8.22E-10**	0.073	12.31	2600.972	**1.27E-209**	0.826	27.40
	Flank					8.702	**7.18E-03**	0.243	8.82
Luna	Flank	3.422	7.00E-02	0.044	17.25	11.489	**1.16E-03**	0.130	58.20
Cheia	Ax	15.399	**1.07E-04**	0.045	22.65	1688.202	**2.51E-144**	0.811	40.99
	Flank	16.878	**5.16E-05**	0.050	21.71	1313.720	**3.18E-125**	0.776	41.99
Anisa	Ax	5.569	**4.00E-02**	0.293	14.51	41.261	**5.63E-08**	0.451	22.79
	Neck	13.329	**2.37E-03**	0.435	20.01	63.652	**1.38E-10**	0.542	22.26
	Flank					1.992	1.96E-01	0.099	23.96
	LD	15.555	**2.30E-03**	0.548	14.15	36.071	**2.64E-07**	0.422	20.78
Snora	Ax	0.480	4.94E-01	-0.019	50.35	119.314	**3.64E-17**	0.609	45.76
	Neck	0.011	9.16E-01	-0.052	58.74	61.107	**2.81E-10**	0.536	51.47
	Flank					0.299	6.13E-01	-0.163	19.79
	LD	0.108	7.47E-01	-0.063	58.42	19.487	**1.37E-04**	0.389	49.86
Penny	Ax	2.353	1.34E-01	0.034	11.30	170.463	**4.35E-23**	0.634	24.11
	Neck	3.633	5.99E-02	0.028	26.60	289.109	**3.62E-33**	0.713	30.31
	LD	0.223	6.42E-01	-0.038	12.61	142.149	**1.20E-20**	0.593	16.88
Frank	Ax	10.174	**1.59E-03**	0.033	72.94	114.862	**3.61E-23**	0.258	116.64
	Neck	4.105	**4.35E-02**	0.008	71.74	651.008	**4.70E-84**	0.633	84.63
	Flank	0.259	6.13E-01	-0.010	73.40	15.028	**1.49E-04**	0.073	109.83
	LD	4.802	**3.00E-02**	0.024	74.14	27.184	**4.05E-07**	0.100	114.67

Table 3.9 Regression statistics for the ascent transition depth against minimum water temperature or the difference between thermocline temperature and minimum water temperature. Regressions significantly different from the constant model are bolded. The regression with the highest adjusted R^2 bolded for each seal-sensor combination is bolded.

Seal	Sensor Location	Min. Water Temp				Thermocline Temp – Min. Water Temp			
		F-statistic	*p*-value	Adj. R^2	RMSE	*F*-statistic	*p*-value	Adj. R^2	RMSE
OJ	Ax	333.98	**1.80E-36**	**0.733**	18.44	83.34	**1.42E-14**	0.467	24.98
	Flank	661.90	**1.63E-55**	**0.821**	26.25	138.00	**1.81E-21**	0.539	41.00
CJ	Ax	990.94	**9.01E-130**	**0.619**	38.70	721.34	**1.31E-97**	0.600	39.71
	Flank	920.67	**9.45E-98**	**0.734**	26.02	484.70	**1.59E-61**	0.648	29.88
Xena	Flank	29.39	**9.30E-07**	0.301	12.25	31.08	**6.22E-07**	**0.330**	11.86
Toby	Neck	3236.47	**2.10E-231**	**0.856**	25.22	1494.38	**2.78E-153**	0.746	33.46
	Flank	4.14	5.36E-02	0.116	7.86	4.14	5.40E-02	**0.120**	8.01
Luna	Flank	87.65	**6.56E-14**	**0.553**	30.61	45.81	**6.21E-09**	0.423	32.38
Cheia	Ax	1384.26	**5.27E-131**	**0.778**	44.32	749.89	**4.25E-91**	0.668	54.22
	Flank	1071.67	**6.60E-113**	**0.737**	45.25	569.30	**3.94E-76**	0.612	54.64
Anisa	Ax	146.15	**3.57E-16**	**0.748**	21.52	44.27	**3.68E-08**	0.490	31.34
	Neck	129.85	**7.19E-16**	**0.705**	24.81	33.79	**4.83E-07**	0.401	34.60
	Flank	8.81	**1.79E-02**	**0.465**	13.13	5.19	5.69E-02	0.343	15.20
	LD	79.05	**8.57E-12**	**0.610**	23.63	22.17	**2.51E-05**	0.320	31.88
Snora	Ax	333.39	**2.54E-29**	**0.814**	32.18	175.34	**9.66E-21**	0.711	40.29
	Neck	186.87	**1.10E-18**	**0.781**	34.51	108.55	**1.09E-13**	0.696	41.94
	Flank	1.35	3.10E-01	**0.065**	19.31	1.06	3.62E-01	0.012	19.85
	LD	52.36	**7.08E-08**	**0.639**	34.18	41.94	**7.29E-07**	0.603	37.04
Penny	Ax	232.64	**1.64E-27**	**0.703**	19.87	190.99	**2.86E-24**	0.669	21.29
	Neck	365.94	**1.58E-37**	**0.759**	26.60	243.45	**9.41E-30**	0.684	30.54
	LD	192.57	**1.13E-24**	**0.664**	13.76	121.99	**1.30E-18**	0.563	15.82
Frank	Ax	1207.25	**3.99E-112**	**0.785**	48.63	841.98	**1.76E-87**	0.744	54.59
	Neck	2625.64	**3.25E-172**	**0.874**	50.39	970.01	**3.27E-101**	0.741	72.70
	Flank	203.64	**2.70E-31**	**0.531**	43.03	177.61	**1.38E-27**	0.528	43.96
	LD	453.55	**5.85E-57**	**0.655**	43.22	350.49	**3.55E-46**	0.630	45.99

Table 3.10 Average differences (± SD) in temperature (°C) between the skin (at the flank) and water per dive phase and for the entire dive (descent + bottom + ascent). The time lag (in seconds) with the highest Spearman correlation coefficient determined from lag analysis for skin temperature was incorporated (see Table 3.16). Negative values (in red) indicate that on average skin temperature was colder than the water. The dive phase that had the greatest absolute difference is bolded for each seal.

Seal	Lag	No. Dives	Descent	Bottom	Ascent	Surface	Dive
OJ	10	141	0.29 ±0.34	**0.59 ±0.11**	0.37 ±0.24	-0.35 ±0.28	0.52 ±0.07
CJ	50	564	1.44 ±0.18	**1.52 ±0.18**	1.12 ±0.16	0.39 ±0.37	1.40 ±0.14
Xena	10	191	1.47 ±0.21	**1.59 ±0.28**	1.39 ±0.09	1.43 ±0.47	1.53 ±0.21
Toby	10	36	0.57 ±0.19	**0.72 ±0.14**	0.47 ±0.15	0.37 ±0.22	0.59 ±0.11
Luna	40	73	2.03 ±0.27	**2.51 ±0.45**	2.22 ±0.42	1.23 ±0.68	2.35 ±0.42
Cheia	20	377	0.38 ±0.36	**0.59 ±0.37**	0.28 ±0.31	-0.47 ±0.47	0.48 ±0.30
Anisa	20	97	2.11 ±1.74	**2.64 ±2.56**	2.17 ±2.12	1.52 ±1.60	2.46 ±2.28
Snora	30	141	2.55 ±1.91	**2.90 ±2.19**	2.66 ±2.26	2.23 ±2.14	2.77 ±2.01
Penny	30	100	2.17 ±0.74	**2.46 ±0.93**	2.15 ±0.81	1.49 ±0.73	2.34 ±0.79
Frank	30	589	1.12 ±0.79	**1.35 ±0.86**	1.22 ±0.94	0.70 ±0.97	1.29 ±0.84
Overall		2309	1.25 ±0.98	**1.47 ±1.13**	1.19 ±1.10	0.60 ±1.15	1.36 ±1.06

Table 3.11 Representative core and blubber temperature determined as the y-intercept from the regression of mean blubber and core temperature against dive duration (see Figure 3.S7). The 95% confidence intervals (low and high C.I.) are provided for the y-intercept. Test statistics comparing the regression to the constant model are provided. Regressions significantly different from the constant model are bolded.

Seal	Thermistor Location	Regression of Mean Temperature vs. Dive Duration						
		y-intercept			Slope	Adj. R^2	*F*-statistic	*p*-value
		Estimate	Low C.I.	High C.I.				
Xena	Deep	36.20	35.93	36.47	-0.054	0.22	57.33	**1.37E-12**
	Mid	35.68	35.22	36.13	-0.071	0.14	34.58	**1.71E-08**
	Shallow	35.56	35.12	36.00	-0.071	0.15	36.27	**8.23E-09**
Toby	Deep	36.82	36.19	37.45	-0.314	0.28	234.86	**5.88E-45**
	Mid	36.52	35.10	37.95	-0.589	0.21	162.10	**5.01E-33**
	Shallow	33.15	31.69	34.60	-0.685	0.26	209.78	**5.72E-41**
Luna	Deep	36.91	36.06	37.76	-0.391	0.63	190.05	**1.02E-25**
Anisa	Core	37.11	36.92	37.30	-0.030	0.16	23.47	**4.02E-06**
	Deep	36.94	36.30	37.57	-0.116	0.21	31.55	**1.39E-07**
	Mid	35.81	34.72	36.91	-0.172	0.16	23.46	**4.04E-06**
	Shallow	35.21	34.68	35.73	-0.102	0.23	35.28	**3.16E-08**
Snora	Core	37.27	37.09	37.46	-0.008	6.11E-4	1.10	2.95E01
	Deep	37.42	37.30	37.54	-0.048	0.37	100.61	**7.53E-19**
	Mid	37.29	37.16	37.42	-0.054	0.38	104.89	**1.98E-19**
	Shallow	37.43	37.00	37.85	-0.100	0.16	33.10	**4.05E-08**
Penny	Core	37.34	37.20	37.47	-0.023	0.17	28.03	**5.09E-07**
	Deep	36.69	36.56	36.83	-0.035	0.33	64.77	**5.17E-13**
	Mid	36.54	36.34	36.75	-0.044	0.26	45.04	**5.77E-10**
	Shallow	36.59	36.36	36.81	-0.049	0.25	44.44	**7.22E-10**
Frank	Core	37.18	37.09	37.26	-0.036	0.30	265.77	**6.13E-50**
	Deep	34.92	34.07	35.77	-0.281	0.19	146.57	**2.05E-30**
	Mid	31.91	30.93	32.89	-0.261	0.13	94.50	**7.07E-21**
	Shallow	35.77	35.47	36.07	-0.148	0.34	324.77	**1.24E-58**

Table 3.12 Peak values of core and blubber temperature distributions. Seals Toby and Frank had bimodal distributions and the temperature at the two highest peaks are provided (see Figure 3.S9).

Seal	Core Temp (°C)	Blubber Temp (°C)			Blubber Temp Gradient (°C)		
		Deep	Mid	Shallow	Deep-Shallow	Deep-Mid	Mid-Shallow
Xena		34.6	35.2	34.4	0.46	0.20	0.27
Toby		36.3	36.6	32.8	14.02	9.68	4.14
		25.5	15.9	11.8	3.80	-0.29	0.93
Luna		34.7					
Anisa	37.2	36.4	35.0	34.3	1.57	0.87	0.67
Snora	37.5	36.9	36.7	37.3	0.13	0.20	-0.01
Penny	36.7	36.3	36.0	36.0	0.19	0.20	0.02
Frank	37.3	36.2	35.6	35.3	1.14	4.91	0.40
		20.8	16.7		-12.42	0.99	-6.36

Table 3.13 Summary statistics of water temperature and body temperature (skin, blubber, and core) for short-shallow (SS) and long-deep (LD) dives. Temperature values are averages of the dive's median, minimum, and maximum values.

Seal	Cluster	No. Dives	Water Temp (°C)			Skin Temp (°C)			Blubber Temp (°C)									Core Temp (°C)		
									Shallow			Mid			Deep					
			Med	Min	Max	Med	Min	Max	Med	Min	Max	Med	Min	Max	Med	Min	Max	Med	Min	Max
OJ	SS	48	11.1	10.9	13.6	11.6	11.4	13.4												
	LD	51	8.2	7.5	13.0	8.8	8.1	12.8												
CJ	SS	157	9.6	9.4	11.5	11.0	10.8	12.3												
	LD	313	6.8	6.0	11.7	8.3	7.6	12.2												
Xena	SS	77	9.8	9.5	12.9	11.3	10.9	14.6	34.9	34.6	35.1	35.1	34.9	35.3	35.7	35.5	35.8			
	LD	49	6.7	5.9	12.9	8.4	7.4	14.3	33.5	32.7	34.0	33.8	33.2	34.2	34.5	34.2	34.8			
Toby	SS	184	11.4	11.0	13.1	12.9	12.3	14.3	29.8	29.3	30.3	33.7	33.5	33.9	35.1	35.0	35.2			
	LD	247	7.8	7.1	13.9				17.5	16.1	20.0	23.3	22.1	24.1	29.6	28.9	30.4			
Luna	SS	37	10.6	10.5	11.5	13.8	13.6	14.5							34.4	34.3	34.5			
	LD	42	7.2	6.3	12.6	9.6	8.7	13.7							28.9	28.0	29.3			
Cheia	SS	84	13.3	13.1	15.0	13.8	13.6	14.9												
	LD	185	7.7	6.8	14.7	8.3	7.5	14.2												
Anisa	SS	54	9.7	9.6	10.9	11.3	11.2	12.0	34.5	34.4	34.6	34.5	34.2	34.8	36.1	36.0	36.2	37.0	36.9	37.0
	LD	13	7.5	7.0	10.8	11.9	10.6	14.6	32.3	31.4	32.9	31.2	28.7	32.4	33.9	32.6	34.5	36.3	36.2	36.4
Snora	SS	93	10.2	10.0	10.9	12.6	12.3	13.1	36.8	36.7	36.9	37.0	36.9	37.0	37.1	37.1	37.2	37.1	37.1	37.2
	LD	22	7.8	7.0	11.4	11.0	9.6	14.1	33.8	31.8	34.5	35.4	35.2	35.6	35.7	35.5	35.9	36.5	36.4	36.6
Penny	SS	33	9.6	9.4	10.9	12.1	11.9	12.9	36.2	36.1	36.3	36.2	36.1	36.3	36.5	36.4	36.5	37.2	37.1	37.2
	LD	32	7.8	7.3	11.0	10.5	9.9	13.0	35.5	34.9	35.7	35.5	35.1	35.7	35.9	35.7	36.0	36.7	36.7	36.8
Frank	SS	328	9.2	9.0	10.2	10.6	10.5	11.3	34.8	34.5	34.9	30.1	29.9	30.4	33.1	32.8	33.3	36.9	36.9	36.9
	LD	134	6.6	6.0	10.3	7.6	7.0	10.5	30.7	29.8	31.5	23.6	22.4	24.4	25.9	24.7	26.7	35.9	35.8	35.9

Table 3.14 Summary statistics of water temperature and body temperature (skin, blubber, and core) for active (A) and nonactive (N) dives. Temperature values are averages of the dive's median, minimum, and maximum values.

Seal	Cluster	No. Dives	Water Temp (°C)			Skin Temp (°C)			Blubber Temp (°C)									Core Temp (°C)		
									Shallow			Mid			Deep					
			Med	Min	Max	Med	Min	Max	Med	Min	Max	Med	Min	Max	Med	Min	Max	Med	Min	Max
OJ	A	30	10.7	10.6	13.2	11.2	11.1	13.0												
	N	29	9.4	9.3	13.4	10.1	9.8	13.2												
CJ	A	123	8.8	8.4	11.8	10.3	9.9	12.4												
	N	122	8.0	7.5	11.7	9.5	9.0	12.3												
Xena	A	40	9.5	9.2	12.8	11.0	10.6	14.7	34.8	34.3	35.0	35.2	35.0	35.3	35.5	35.4	35.7			
	N	39	7.5	7.0	13.1	9.3	8.4	14.5	33.8	32.8	34.2	33.9	33.4	34.4	34.9	34.6	35.2			
Toby	A	120	10.4	10.0	13.5	12.5	11.9	14.2	25.2	24.3	25.9	29.2	28.8	29.6	33.4	33.2	33.7			
	N	119	8.3	7.8	13.5	13.7	13.5	14.4	22.9	21.0	25.3	28.4	27.3	29.3	31.9	31.1	32.5			
Luna	A	22	10.1	9.9	11.6	11.7	11.2	13.9							33.9	33.7	34.0			
	N	21	8.1	7.5	12.4	10.4	9.5	13.8							29.9	29.2	30.2			
Cheia	A	79	11.9	11.5	15.1	12.4	12.1	14.9												
	N	78	9.4	8.7	14.5	10.1	9.4	14.4												
Anisa	A	23	9.5	9.3	11.3	11.3	10.9	12.3	32.6	32.1	32.8	30.9	29.9	31.3	34.0	33.4	34.3	36.2	36.2	36.3
	N	22	9.0	8.8	10.6	11.2	10.6	12.5	33.7	33.3	34.1	33.5	32.4	34.2	35.3	34.7	35.7	36.9	36.8	36.9
Snora	A	34	10.6	10.3	11.0	12.4	12.3	12.7	36.9	36.8	36.9	37.1	37.1	37.1	37.2	37.2	37.3	37.0	36.9	37.1
	N	33	9.4	9.2	10.9	12.6	11.8	14.4	36.2	35.6	36.4	36.6	36.5	36.7	36.8	36.7	36.9	37.3	37.3	37.4
Penny	A	26	9.5	9.3	10.9	12.0	11.8	12.9	36.2	36.0	36.3	36.3	36.1	36.3	36.6	36.5	36.6	37.0	37.0	37.0
	N	25	8.6	8.3	11.0	10.7	10.4	12.5	35.5	34.7	35.8	35.5	35.0	35.7	35.8	35.7	36.0	37.0	37.0	37.1
Frank	A	124	9.2	9.0	10.0	10.8	10.6	11.3	34.6	34.4	34.7	31.6	31.3	31.9	34.1	33.9	34.2	36.9	36.8	36.9
	N	123	7.2	6.7	10.2	8.5	8.0	10.9	32.1	31.3	32.8	27.7	26.4	28.4	30.2	29.2	30.8	36.4	36.3	36.5

Table 3.15 Minimum, maximum, and range of core and blubber temperature (°C) during short-shallow and long-deep dive bouts (>3 consecutive dives). For both short-shallow and long-deep dive bouts, the dive bout with the most dives, the lowest minimum, the highest maximum, and the largest range are bolded for each seal. Trends indicate whether the median temperatures from the first to the last dive are increasing (+), decreasing (-), or constant (empty).

Seal		No. Dives	Depth (m)	Duration (mins)	Core				Deep Blubber				Mid Blubber				Shallow Blubber			
					Min	Max	Range	Trend	Min	Max	Range	Trend	Min	Max	Range	Trend	Min	Max	Range	Trend
Anisa	SS	7	30.1 ±6.3	5.0 ±1.3	36.8	37.0	0.2	+	35.8	**36.8**	**0.9**	+	33.1	**35.8**	2.7	+	**34.1**	**35.1**	**1.0**	+
		18	46.4 ±20.8	7.8 ±1.5	37.2	**37.3**	0.1	+	36.3	36.6	0.3		34.8	**35.8**	0.9	+	34.7	**35.1**	0.4	+
		4	37.4 ±4.5	7.6 ±1.9	37.0	**37.3**	0.3	-	36.2	36.4	0.2	-	35.3	35.7	0.4	-	34.4	34.8	0.4	-
		15	29.3 ±7.8	6.8 ±2.0	**36.7**	37.1	**0.4**	+	**35.6**	36.5	**0.9**	+	**32.8**	**35.8**	**3.0**	-	34.2	34.8	0.6	-
	LD	4	410.3 ±53.3	28.2 ±5.2	35.8	36.4	0.6	-	32.6	35.0	2.4	-	27.6	33.6	6.0	-	31.3	33.3	1.9	-
Snora	SS	6	42.2 ±27.1	2.4 ±1.4	**33.3**	36.3	**3.0**	-	**36.3**	37.1	**0.8**	+	**36.1**	36.9	**0.8**	+	35.8	37.1	1.3	+
		11	24.1 ±5.5	4.0 ±1.6	36.7	37.4	0.7	+	37.1	37.5	0.4	+	36.9	37.3	0.4	+	36.5	37.3	0.8	+
		7	50.1 ±28.3	6.4 ±1.8	37.6	**37.8**	0.2	+	37.2	**37.6**	0.4	+	37.1	**37.6**	0.5	+	37.1	**37.6**	0.5	+
		5	19.4 ±1.6	4.6 ±2.7	37.8	**37.8**	0.0		37.3	37.5	0.2		37.2	37.4	0.2		37.2	37.4	0.2	
		16	55.2 ±11.3	5.2 ±1.9	37.2	37.6	0.4	-	37.0	37.3	0.4	-	36.8	37.2	0.3	-	**35.4**	37.2	**1.8**	-
		27	34.1 ±16.6	3.3 ±1.7	37.3	37.6	0.3	+	36.9	37.5	0.6	+	36.7	37.3	0.7	+	35.5	37.3	**1.8**	+
	LD	**12**	371.5 ±64.0	23.7 ±2.1	36.4	**37.6**	**1.2**	-	35.5	**37.0**	**1.5**	-	35.2	**36.7**	**1.5**	-	32.2	**36.9**	4.8	-
		4	408.4 ±24.9	23.4 ±1.7	**35.7**	36.3	0.7	-	**34.7**	35.5	0.8	+	**34.4**	35.0	0.5		**21.5**	34.7	**13.2**	+
Penny	SS	7	31.9 ±9.7	4.1 ±2.8	**36.9**	**37.3**	**0.4**	+	**36.5**	**37.1**	**0.6**	+	**36.1**	**36.9**	**0.8**	+	36.0	**37.0**	**1.0**	+
		8	26.1 ±11.5	7.2 ±1.7	37.0	37.2	0.2	+	**36.5**	37.0	0.5	+	36.3	36.7	0.5	+	**35.8**	36.6	0.7	+
	LD	9	310.6 ±59.3	23.7 ±3.6	36.6	**37.3**	**0.7**	-	**35.2**	36.5	**1.3**	-	**32.7**	36.3	**3.6**	-	**31.0**	36.5	**5.5**	-
		12	400.1 ±41.4	22.9 ±2.1	**36.5**	36.8	0.3	-	35.5	36.1	0.6	+	34.7	36.0	1.3	+	34.8	35.8	1.0	+
		8	321.8 ±83.5	21.6 ±3.0	36.7	37.1	0.4	-	35.8	**37.0**	1.2	-	34.7	**36.8**	2.0	-	33.7	**36.8**	3.0	-

Table 3.15 (continued) Minimum, maximum, and range of core and blubber temperature (°C) during short-shallow and long-deep dive bouts (>3 consecutive dives). For both short-shallow and long-deep dive bouts, the dive bout with the most dives, the lowest minimum, the highest maximum, and the largest range are bolded for each seal. Trends indicate whether the median temperatures from the first to the last dive are increasing (+), decreasing (-), or constant (empty).

Seal		No. Dives	Depth (m)	Duration (mins)	Core				Deep Blubber				Mid Blubber				Shallow Blubber			
					Min	Max	Range	Trend	Min	Max	Range	Trend	Min	Max	Range	Trend	Min	Max	Range	Trend
Frank	SS	5	21.5 ±4.9	5.8 ±2.2	37.2	37.6	0.4	+	35.2	35.8	0.7	+	35.3	35.7	0.5		33.7	34.6	0.9	+
		4	41.1 ±13.6	6.4 ±3.4	36.1	36.2	0.0	+	33.1	34.0	0.9	+	24.5	25.8	1.4	+	29.2	30.8	1.6	+
		9	45.1 ±20.3	5.7 ±2.1	36.4	36.9	0.5	+	33.7	35.8	2.1	+	26.9	35.4	8.5	+	31.0	34.5	3.5	+
		9	39.9 ±20.4	5.7 ±2.5	**35.3**	**37.7**	**2.4**	+	32.6	36.7	4.1	+	22.9	36.2	13.3	+	30.2	35.8	5.5	+
		4	44.9 ±9.3	9.0 ±1.9	37.3	**37.7**	0.4	+	35.6	36.8	1.2	+	30.7	36.0	5.3	+	34.3	35.5	1.2	+
		56	39.4 ±27.8	6.0 ±2.2	35.9	37.6	1.7	+	32.2	37.0	4.8	+	25.8	36.3	10.6	+	32.3	**36.3**	4.0	+
		9	40.2 ±19.8	7.1 ±3.5	37.3	37.4	0.1	+	36.2	36.7	0.5	+	35.3	36.2	0.9	+	35.1	35.8	0.7	+
		5	42.2 ±12.0	7.0 ±2.4	37.0	37.0	0.0		35.5	36.1	0.6	+	32.5	35.3	2.8	-	34.4	35.3	0.9	-
		23	34.7 ±15.7	6.3 ±2.5	35.6	37.1	1.5	+	23.6	36.5	**12.9**	+	23.6	36.0	12.4	+	32.8	**36.3**	3.5	+
		15	41.1 ±18.4	7.2 ±2.6	36.0	37.3	1.3	+	30.8	37.8	7.0	+	30.4	36.6	6.2	+	35.2	**36.3**	1.2	+
		11	23.2 ±12.0	3.7 ±2.3	**35.3**	36.3	1.1	+	18.5	23.3	4.8	+	16.7	23.3	6.5	+	**26.6**	34.7	**8.2**	+
		35	35.7 ±17.0	5.6 ±2.1	37.0	37.3	0.3	+	36.7	**37.8**	1.1	+	34.1	**36.7**	2.6	+	35.6	36.2	0.6	-
		49	34.2 ±19.8	5.7 ±2.3	36.6	37.3	0.7	+	25.6	37.4	11.8	-	17.4	36.3	**19.0**	-	30.6	35.6	5.0	-
		19	32.4 ±6.5	8.8 ±1.9	36.3	36.8	0.5	+	**20.3**	22.7	2.4	+	**15.3**	17.4	2.1	+	32.9	35.2	2.3	+
		6	42.3 ±3.4	9.5 ±1.4	36.2	36.7	0.5	-	20.8	22.2	1.4	-	16.5	17.1	0.6	-	33.5	35.1	1.6	+
		4	39.3 ±1.6	10.7 ±0.8	37.0	37.1	0.1	+	21.6	23.9	2.4	+	16.8	17.2	0.5	+	35.1	35.6	0.5	+
		20	26.5 ±7.3	7.5 ±2.5	37.0	37.2	0.2	+	27.3	34.3	7.1	+	17.3	21.9	4.6	+	34.8	36.0	1.2	+

Table 3.15 (continued) Minimum, maximum, and range of core and blubber temperature (°C) during short-shallow and long-deep dive bouts (>3 consecutive dives). For both short-shallow and long-deep dive bouts, the dive bout with the most dives, the lowest minimum, the highest maximum, and the largest range are bolded for each seal. Trends indicate whether the median temperatures from the first to the last dive are increasing (+), decreasing (-), or constant (empty).

Seal		No. Dives	Depth (m)	Duration (mins)	Core				Deep Blubber				Mid Blubber				Shallow Blubber			
					Min	Max	Range	Trend	Min	Max	Range	Trend	Min	Max	Range	Trend	Min	Max	Range	Trend
Frank	LD	13	492.6 ±75.8	34.5 ±2.9	35.0	37.0	2.0	-	26.8	35.3	8.5	-	19.7	33.8	14.2	-	26.4	33.0	6.6	-
		5	466.6 ±44.9	29.2 ±2.4	36.5	**37.4**	0.9	-	32.1	35.2	3.1	-	24.7	28.0	3.3	-	31.3	33.8	2.6	-
		4	440.6 ±24.3	32.3 ±6.0	36.2	36.6	0.4	-	32.5	35.4	2.9	-	25.8	35.2	9.4	-	31.9	34.7	2.8	-
		14	535.8 ±86.3	34.3 ±3.8	35.6	37.2	1.6	-	19.3	36.3	17.0	-	20.4	34.3	13.9	-	31.2	35.8	4.6	-
		4	590.1 ±86.3	30.1 ±1.6	35.6	35.7	0.1	-	19.3	22.6	3.4	+	20.2	24.1	3.9	+	32.1	33.4	1.3	+
		17	577.2 ±139.4	34.2 ±5.4	35.1	37.3	**2.2**	-	17.3	**37.3**	**20.1**	-	16.8	**36.3**	19.6	-	27.1	**36.0**	8.9	-
		9	345.1 ±67.1	31.4 ±4.0	35.5	35.8	0.3	+	18.6	21.4	2.9	-	17.8	21.1	3.3	-	30.4	32.9	2.6	+
		15	554.0 ±127.9	35.3 ±4.8	34.9	36.4	1.5	-	17.1	35.8	18.7	-	15.4	33.7	18.4	-	**18.8**	34.7	**16.0**	-
		29	601.7 ±103.8	34.0 ±5.3	**34.8**	36.8	2.0	-	**16.9**	36.4	19.6	-	**14.3**	35.6	**21.3**	-	20.6	35.5	14.9	-
		6	443.1 ±115.7	31.1 ±2.9	36.2	37.3	1.1	-	27.0	37.2	10.3	-	24.4	35.2	10.8	-	32.1	35.0	2.9	-

Table 3.16 Time lags in seconds (A) and minutes (B) between water temperature or stroke rate and physiological temperatures for short-term (A) and long-term (B) fluctuations determined by the maximum Spearman's rank correlation coefficient (ρ). Long-term fluctuations are filtered out of the dynamic blubber temperatures. Correlations >50% are bolded.

A	Skin		Shallow Blubber		Dynamic		Mid Blubber		Dynamic		Deep Blubber		Dynamic	
Seal	ρ	Lag	ρ	Lag	ρ	Lag	ρ	Lag	ρ	Lag	ρ	Lag	ρ	Lag
Water Temperature														
OJ	**0.991**	**10**												
CJ	**0.987**	**50**												
Xena	**0.979**	**10**	0.473	500	0.306	-300	0.478	600	0.234	-300	0.487	600	0.228	-300
Toby	**0.908**	**10**	**0.507**	**140**	**0.516**	**140**	0.411	510	0.299	460	0.386	220	0.281	240
Luna	**0.948**	**40**									**0.600**	**430**	**0.556**	**-100**
Cheia	**0.987**	**20**												
Anisa	0.320	20	0.488	600	0.309	40	0.440	520	0.300	-300	**0.506**	**580**	0.300	-300
Snora	**0.602**	**30**	0.427	600	0.328	-130	0.399	600	0.172	600	0.402	600	0.256	-300
Penny	**0.657**	**30**	0.487	580	0.370	30	0.458	600	0.393	60	0.449	560	0.333	-300
Frank	**0.853**	**30**	0.447	600	0.173	590	0.278	600	0.242	-300	0.406	600	0.241	-300
Median	0.928	25	0.480	590	0.318	35	0.425	600	0.271	-120	0.449	580	0.281	-300
Stroke Rate														
OJ	0.374	200												
CJ	0.443	300												
Xena	0.477	190	0.172	600	0.303	-300	0.191	600	0.254	-300	0.151	600	0.203	110
Toby	0.255	-50	0.114	420	0.391	390	0.034	20	0.287	30	0.085	600	0.272	0
Luna	**0.961**	**600**									0.214	600	**0.528**	**140**
Cheia	0.480	300												
Anisa	0.195	30	0.107	600	0.299	600	0.104	600	0.275	550	0.099	600	0.309	600
Snora	0.306	10	0.233	600	0.237	-120	0.291	600	0.162	600	0.296	600	0.215	-300
Penny	**0.504**	**110**	**0.551**	**600**	0.246	-300	**0.602**	**600**	0.261	140	**0.632**	**600**	0.182	-300
Frank	**0.616**	**140**	0.464	600	0.136	600	0.279	600	0.248	10	0.328	600	0.263	20
Median	0.460	165	0.202	600	0.273	135	0.235	600	0.258	85	0.214	600	0.263	20

Table 3.16 (continued) Time lags in seconds (A) and minutes (B) between water temperature or stroke rate and physiological temperatures for short-term (A) and long-term (B) fluctuations determined by the maximum Spearman's rank correlation coefficient (ρ). Long-term fluctuations are filtered out of the dynamic blubber temperatures. Correlations >50% are bolded.

B	Water									
	Skin		Shallow Blubber		Mid Blubber		Deep Blubber		Core	
Seal	ρ	Lag	ρ	Lag	ρ	Lag	ρ	Lag	ρ	Lag
OJ	**0.999**	**0**								
CJ	**0.989**	**0**								
Xena	**0.976**	**0**	**0.693**	**70**	**0.751**	**90**	**0.736**	**50**		
Toby	**0.907**	**-10**	**0.695**	**120**	**0.659**	**130**	**0.673**	**160**		
Luna	**0.927**	**10**					**0.885**	**20**		
Cheia	**0.991**	**0**								
Anisa	**0.650**	**370**	**0.725**	**50**	**0.699**	**360**	**0.783**	**50**	**0.796**	**340**
Snora	**0.644**	**10**	**0.685**	**40**	**0.631**	**30**	**0.641**	**30**	**0.579**	**280**
Penny	**0.561**	**0**	**0.726**	**20**	**0.652**	**20**	**0.659**	**20**	**0.790**	**100**
Frank	**0.890**	**10**	**0.662**	**80**	0.459	110	**0.647**	**120**	**0.843**	**110**
Median	0.898	5	0.694	60	0.656	100	0.673	50	0.793	195

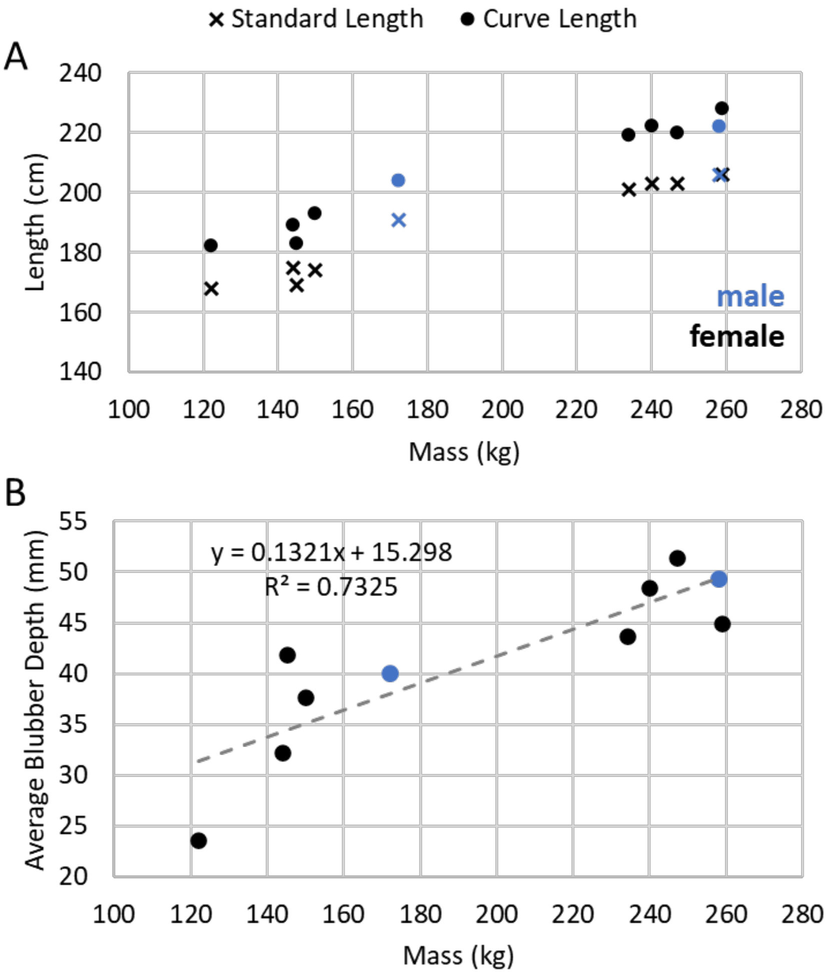


Figure 3.1 (A) Mass-length relationship shows two distinct size groups. (B) Positive correlation between mass and average blubber depth.

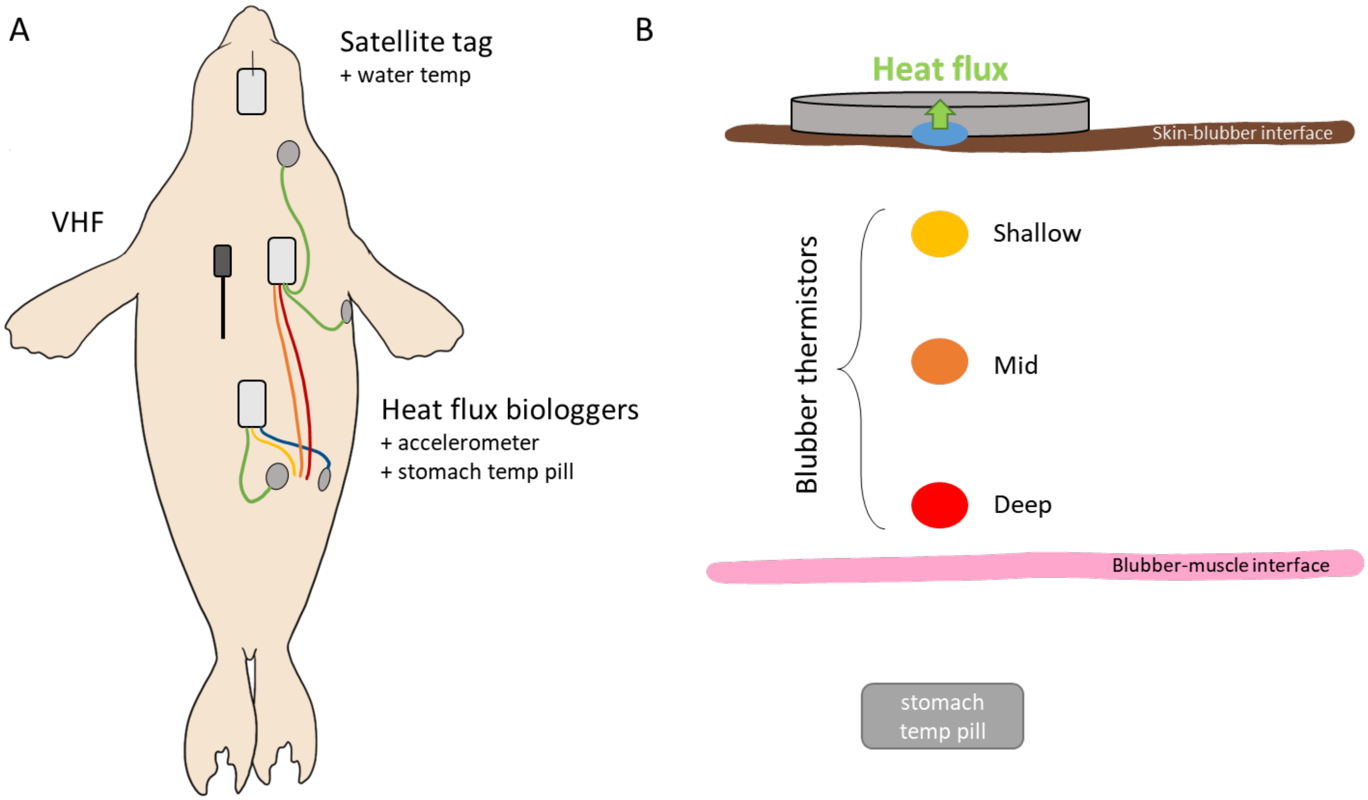


Figure 3.2 (A) Diagram shows the placement of the tags and sensors on the seals. Blue and green cables lead to heat flux sensors with and without an embedded thermistor, respectively, to measure skin temperature. Red, orange, and yellow cables lead to free-standing thermistors inserted into the blubber layer at different depths as depicted in (B). Seal outline ©Jessica Kendall-Bar

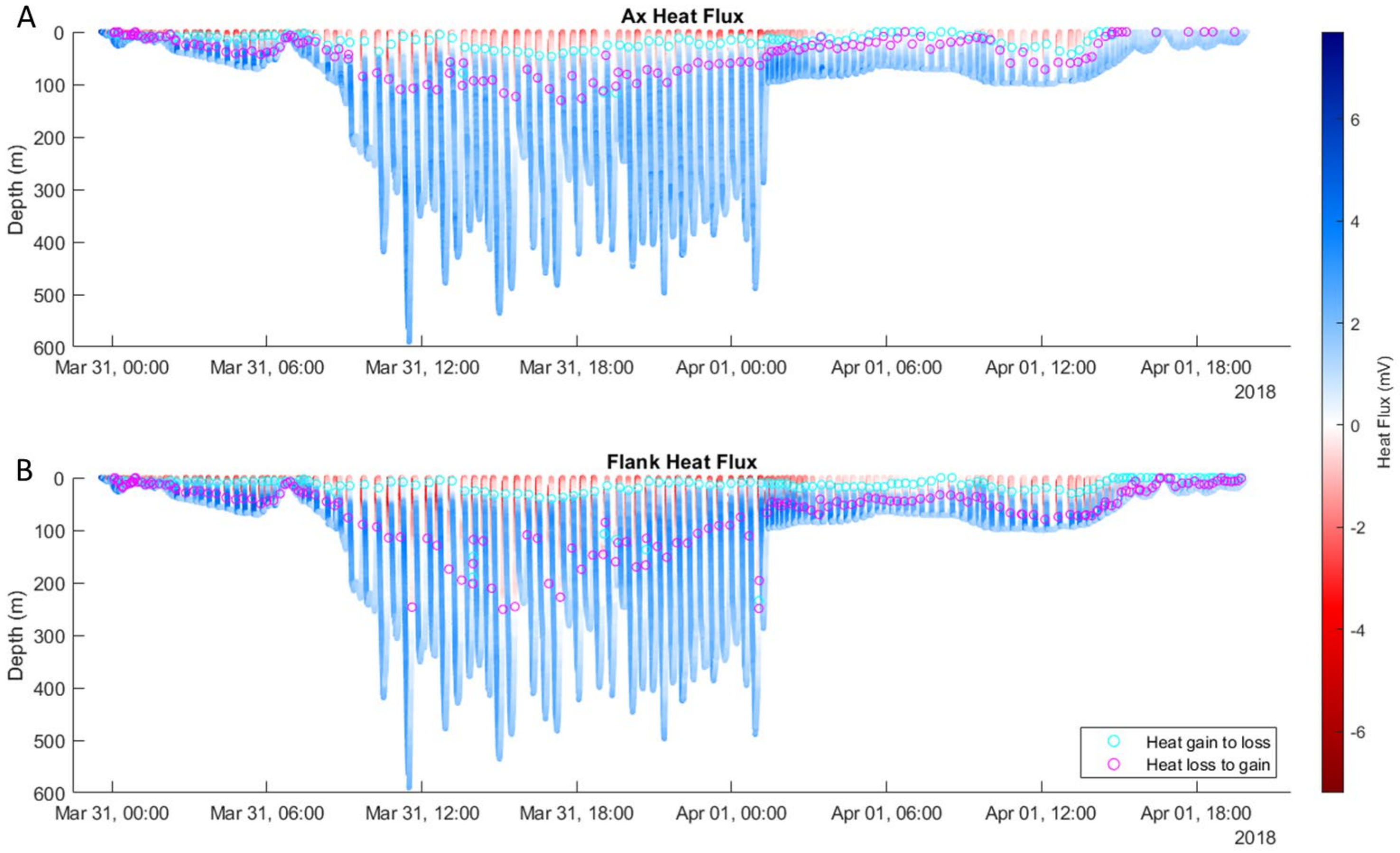


Figure 3.3 Example of heat flux patterns along the dive profile from sensors at the ax (A) and flank (B). Blue indicates heat loss and red indicates heat gain. The dots show where the transitions between heat gain and loss and vice versa occur.

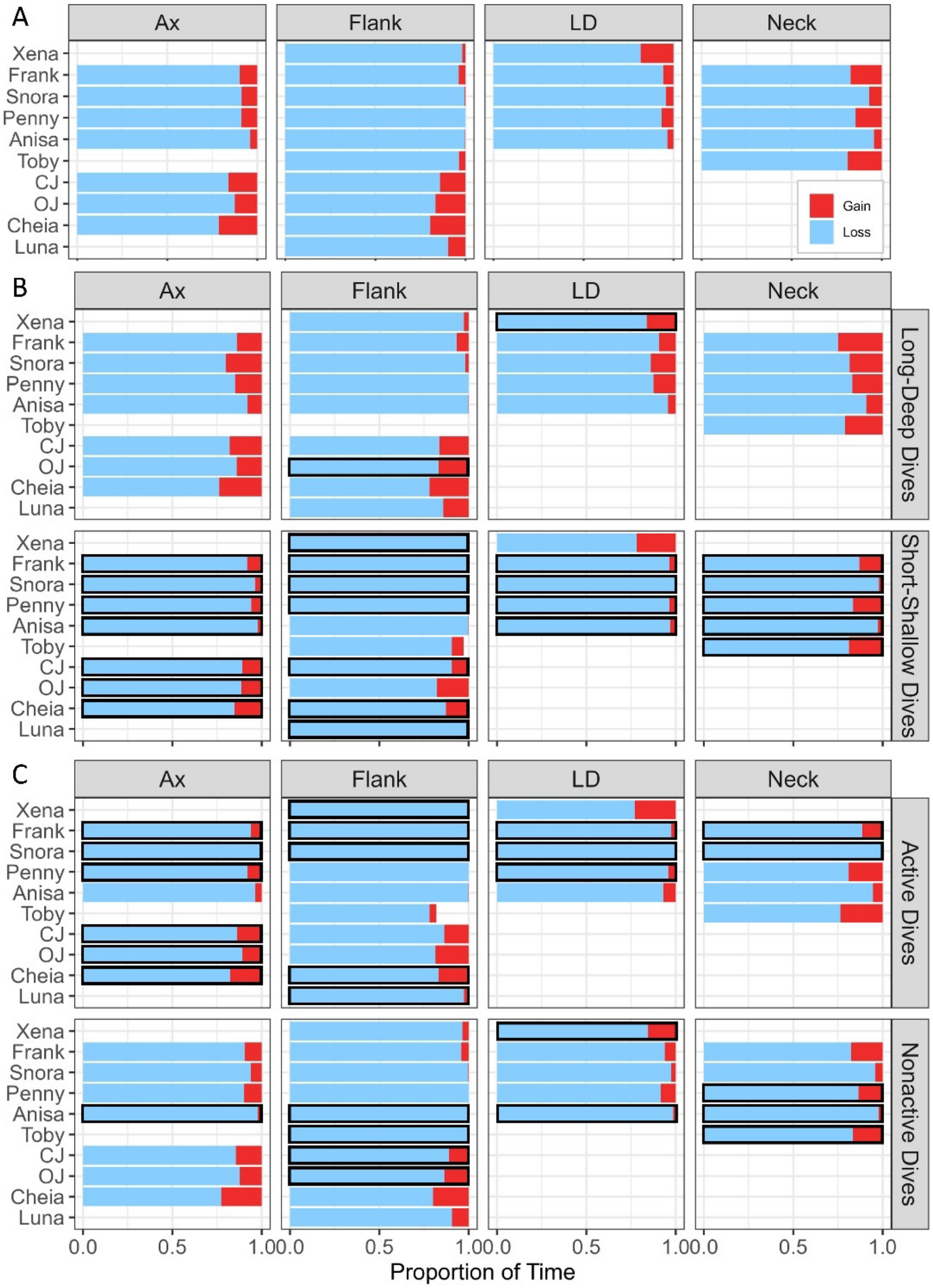


Figure 3.4 The proportion of time that heat gain (red) vs. heat loss (blue) occurred on all dives (A), long-deep dives vs. short-shallow dives (B), and active vs. nonactive dives (C) for each seal-sensor combination. The largest proportion of heat loss when comparing dive types in (B) and (C) for each seal-sensor combination is outlined in black. Seals are ordered from smallest to largest (bottom to top) based on mass.

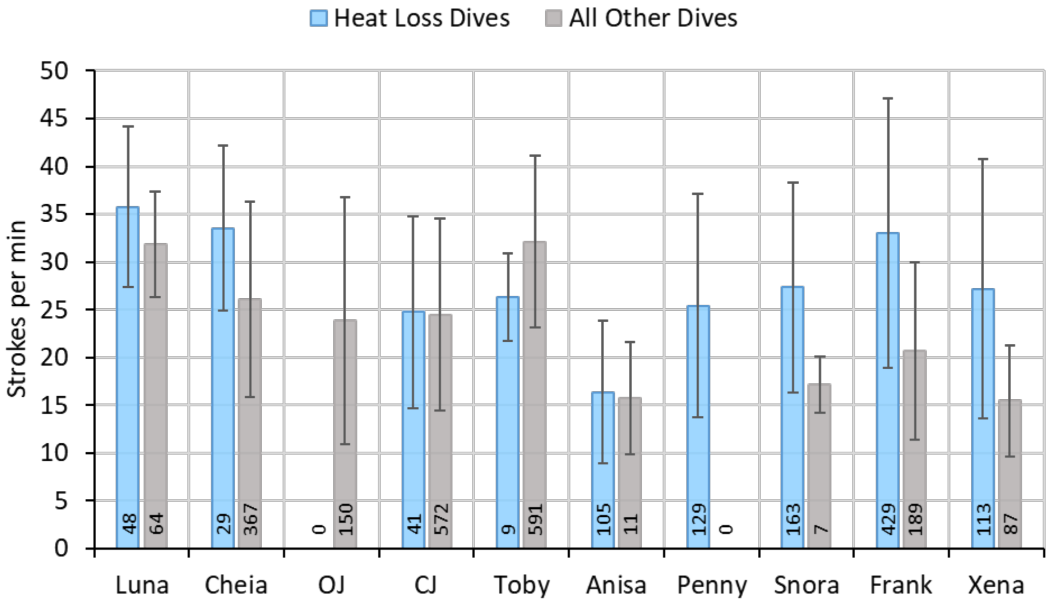


Figure 3.5 Average stroke rate for dives during which heat loss at the flank occurred the entire time compared to all other dives. The number of dives are provided at the base of each bar. Error bars are standard deviations. Seals are ordered from smallest to largest (left to right) based on mass.

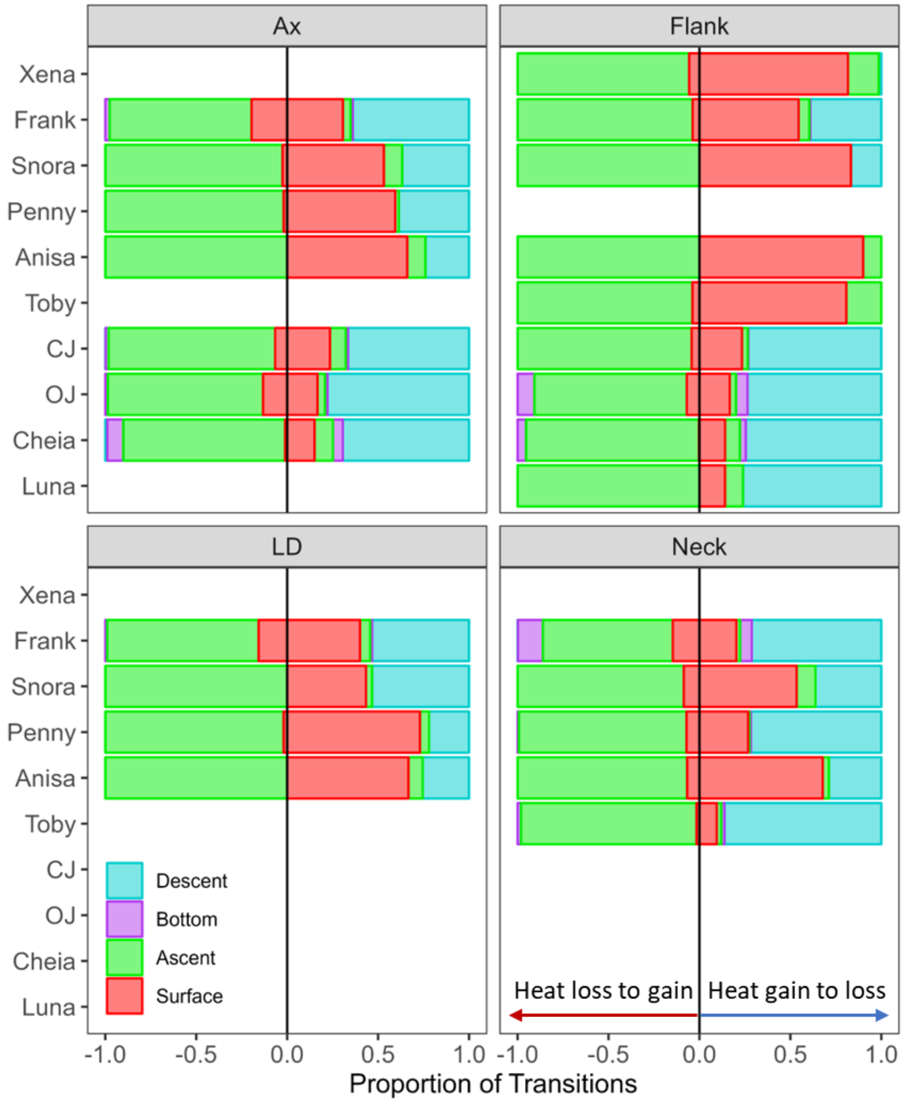
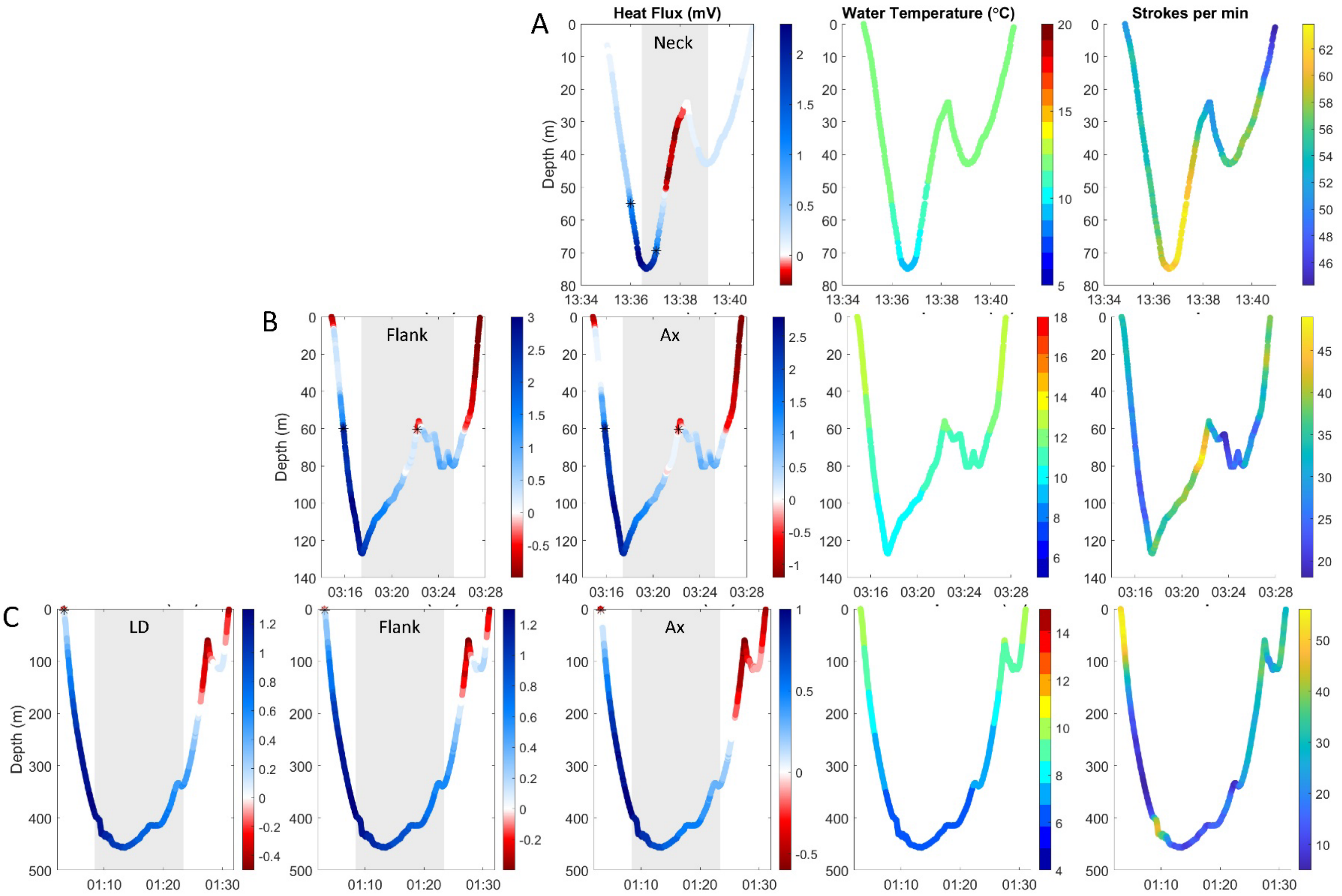


Figure 3.6 The proportion of heat flux transitions that occurred during each dive phase for each seal-sensor combination. Seals are ordered from smallest to largest (bottom to top) based on mass.

Figure 3.7 Examples of dive reversals and associated heat flux patterns, water temperature, and stroke rate for (A) Toby, (B) Cheia, and (C) Frank. The dive reversal for Toby and Cheia occurred during the bottom phase (shaded gray) on relatively shallow dives whereas the dive reversal for Frank occurred during the ascent phase on a deeper dive. Heat flux from multiple sensor locations are shown for comparison for Cheia and Frank.


A
Heat Flux (mV)
Water Temperature (°C)
Strokes per min
Neck
Depth (m)
0
10
20
30
40
50
60
70
80
13:34
13:36
13:38
13:40
2
1.5
1
0.5
0
20
15
10
5
62
60
58
56
54
52
50
48
46
B
Flank
Ax
Depth (m)
0
20
40
60
80
100
120
140
03:16
03:20
03:24
03:28
3
2.5
2
1.5
1
0.5
0
-0.5
-1
18
16
14
12
10
8
6
45
40
35
30
25
20
C
LD
Flank
Ax
Depth (m)
0
100
200
300
400
500
01:10
01:20
01:30
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
0.5
-0.5
14
12
10
8
6
4
50
40
30
20
10

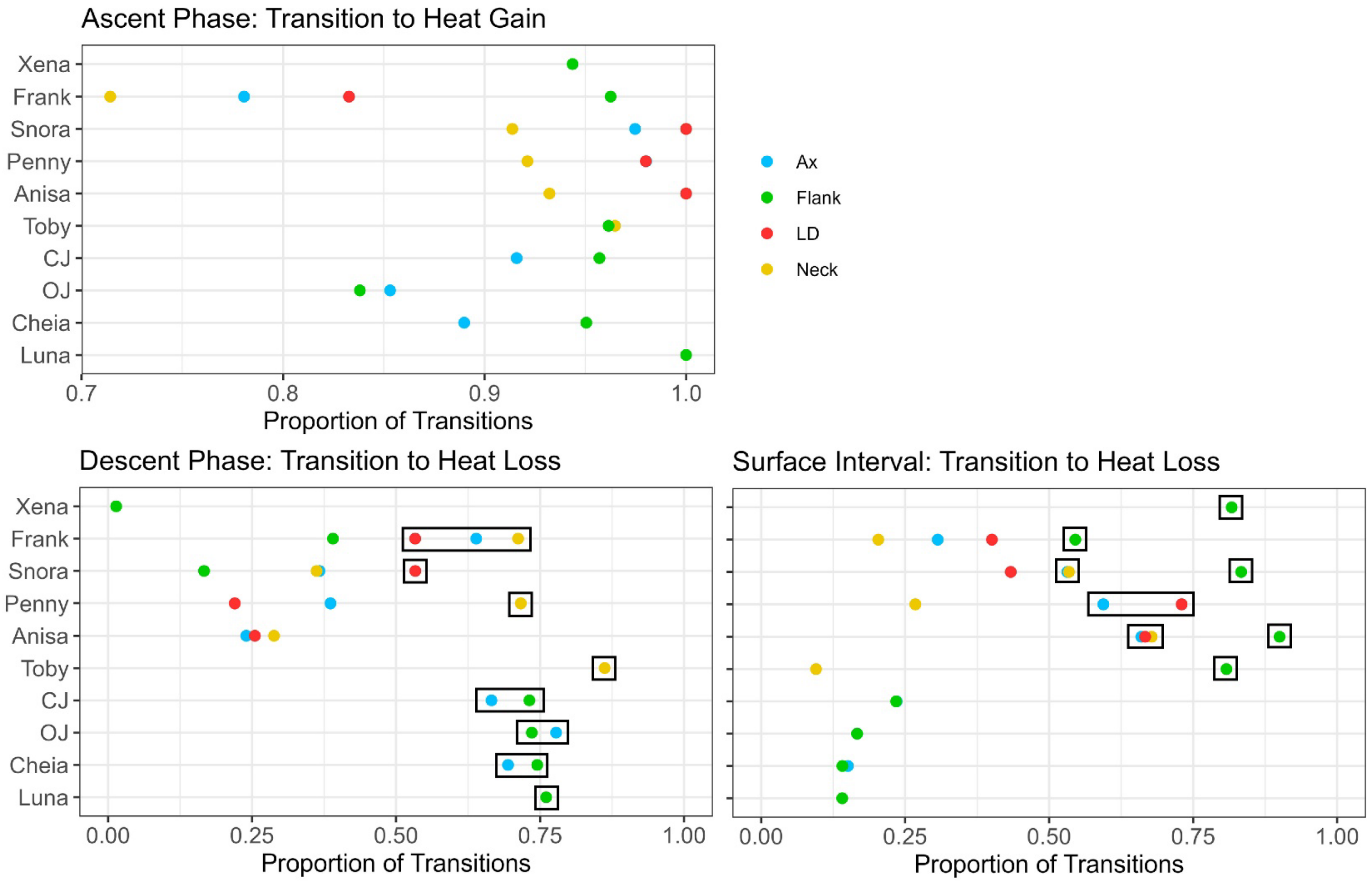


Figure 3.8 The proportion of heat flux transitions occurring for the most common combinations of dive phase and transition direction. For transitions from heat gain to loss (bottom panels), the dive phase (descent or surface interval) with the larger proportion for each sensor location is denoted with a box.

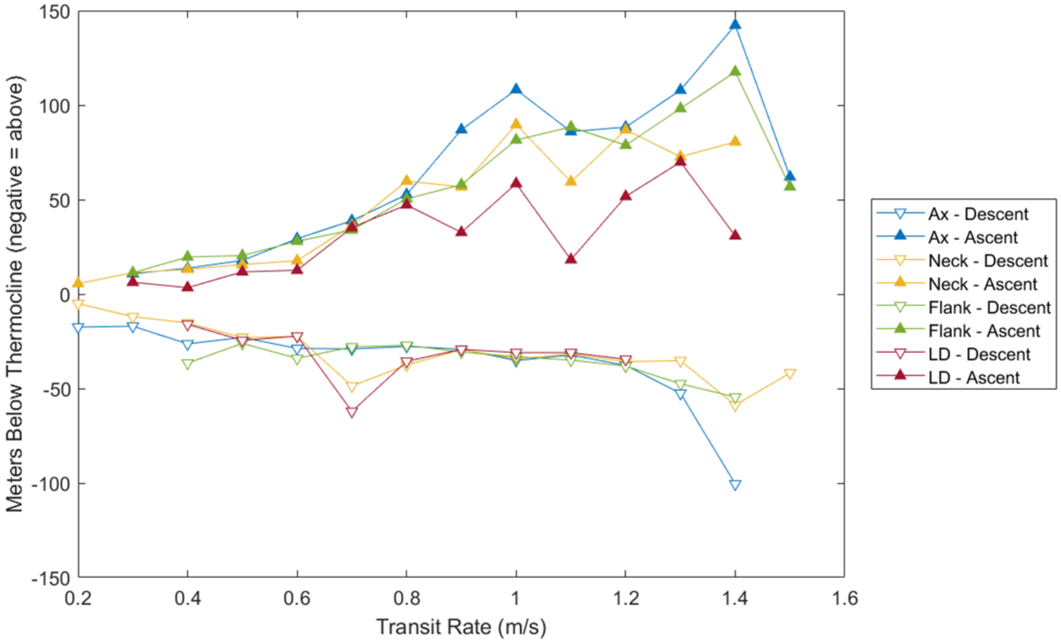
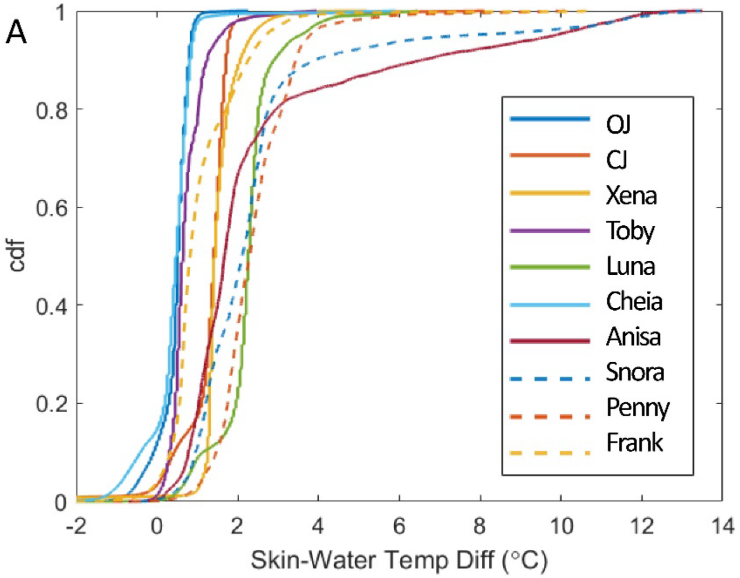


Figure 3.9 Heat flux transition depths on descent (open triangle) and ascent (filled triangle) relative to the thermocline depth averaged across seals at binned transit rates for each sensor location. Values were adjusted accordingly at each transit rate to account for the 30-second response time of the heat flux sensor.



B

Seal	Temperature at Percentile			Percentile below Temperature			
	20th	50th	80th	0°C	1°C	2°C	3°C
OJ	0.30°	0.50°	0.70°	11.6%	98.7%	100.0%	
CJ	1.10°	1.40°	1.60°	3.3%	17.3%	98.0%	99.3%
Xena	1.30°	1.45°	1.75°	1.0%	2.4%	88.6%	98.9%
Toby	0.45°	0.65°	1.00°	1.5%	78.2%	98.0%	99.4%
Luna	1.95°	2.25°	2.50°	0.2%	8.9%	22.5%	91.2%
Cheia	0.20°	0.50°	0.70°	14.7%	97.6%	99.4%	99.6%
Anisa	1.03°	1.67°	2.95°	0.4%	18.4%	66.5%	80.3%
Snora	1.21°	2.10°	2.76°	0.4%	11.1%	45.9%	84.1%
Penny	1.75°	2.29°	3.09°	0.1%	3.0%	35.5%	77.9%
Frank	0.56°	0.82°	1.71°	4.0%	62.6%	85.8%	96.9%

Figure 3.10 (A) Cumulative distribution function of the skin-water temperature difference for each seal at the flank sensor with temperatures at the 20th, 50th, and 80th percentiles extracted as well as the percentile of temperatures below 0°C, 1°C, 2°C, and 3°C (B).

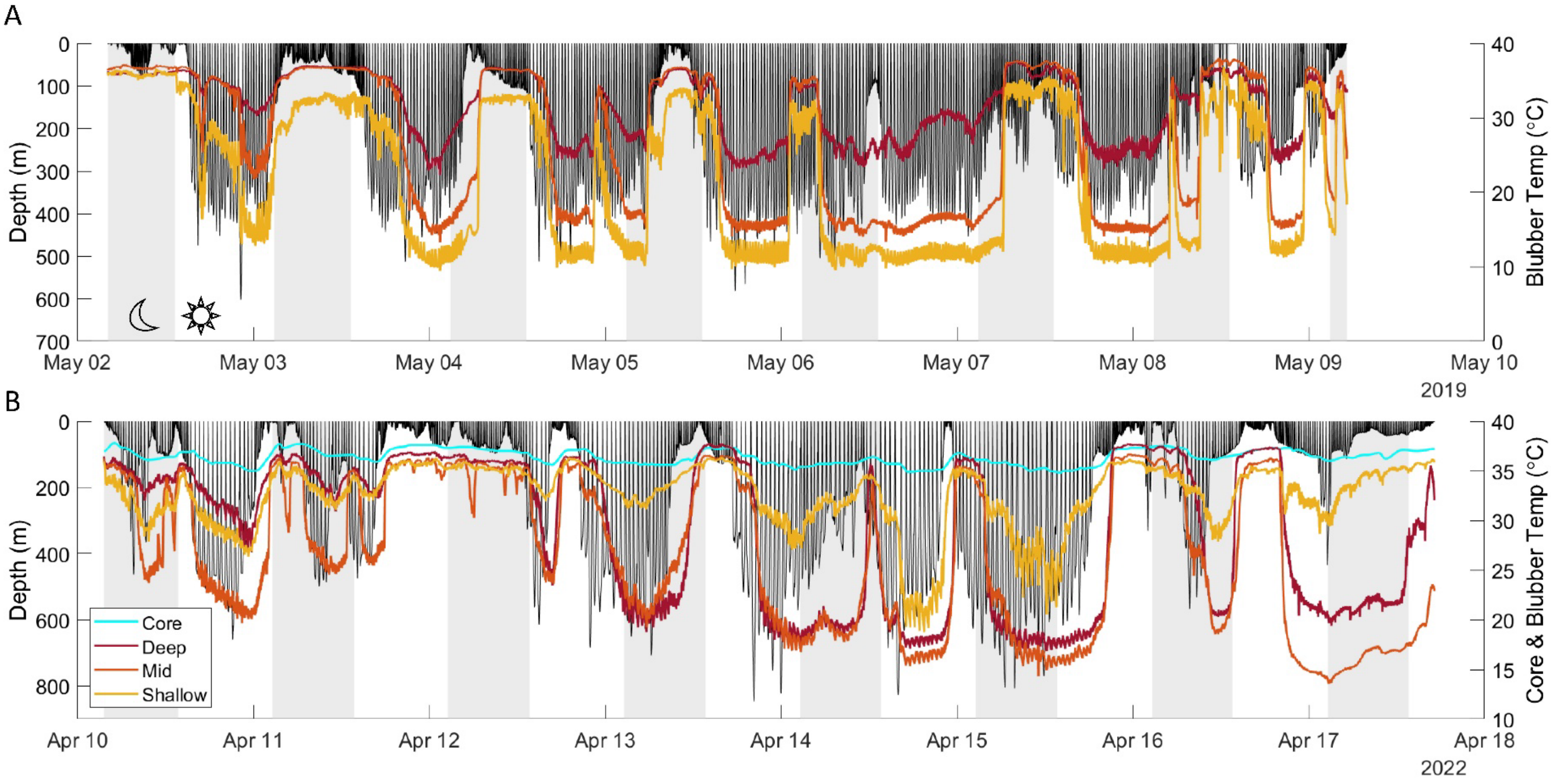


Figure 3.11 Time series depicting the bimodal nature of blubber temperatures from seals Toby (A) and Frank (B).

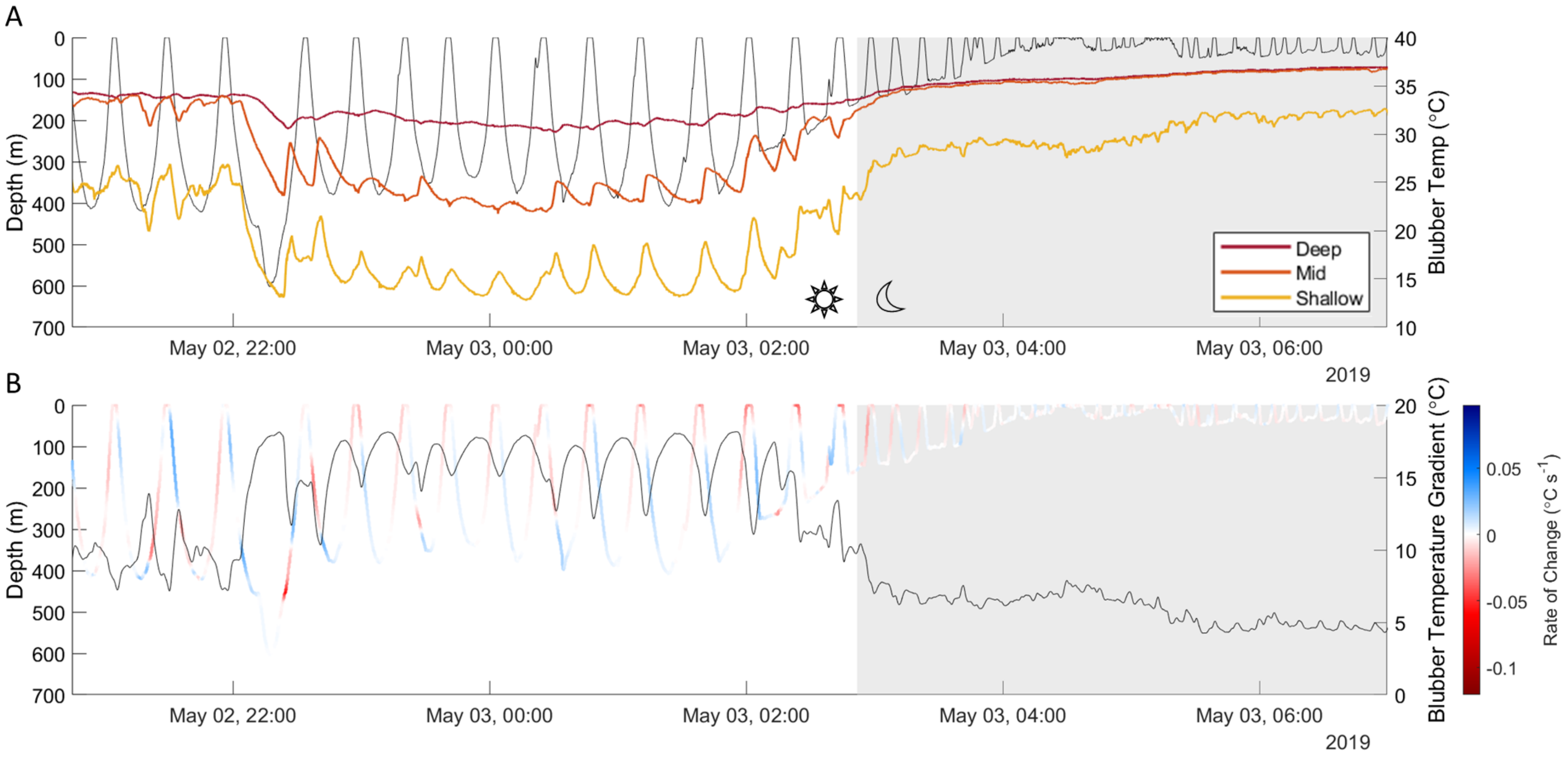


Figure 3.12 Example of within-dive vs. across-dives fluctuations in the blubber temperature (A) and blubber temperature gradient (B) of seal Toby.

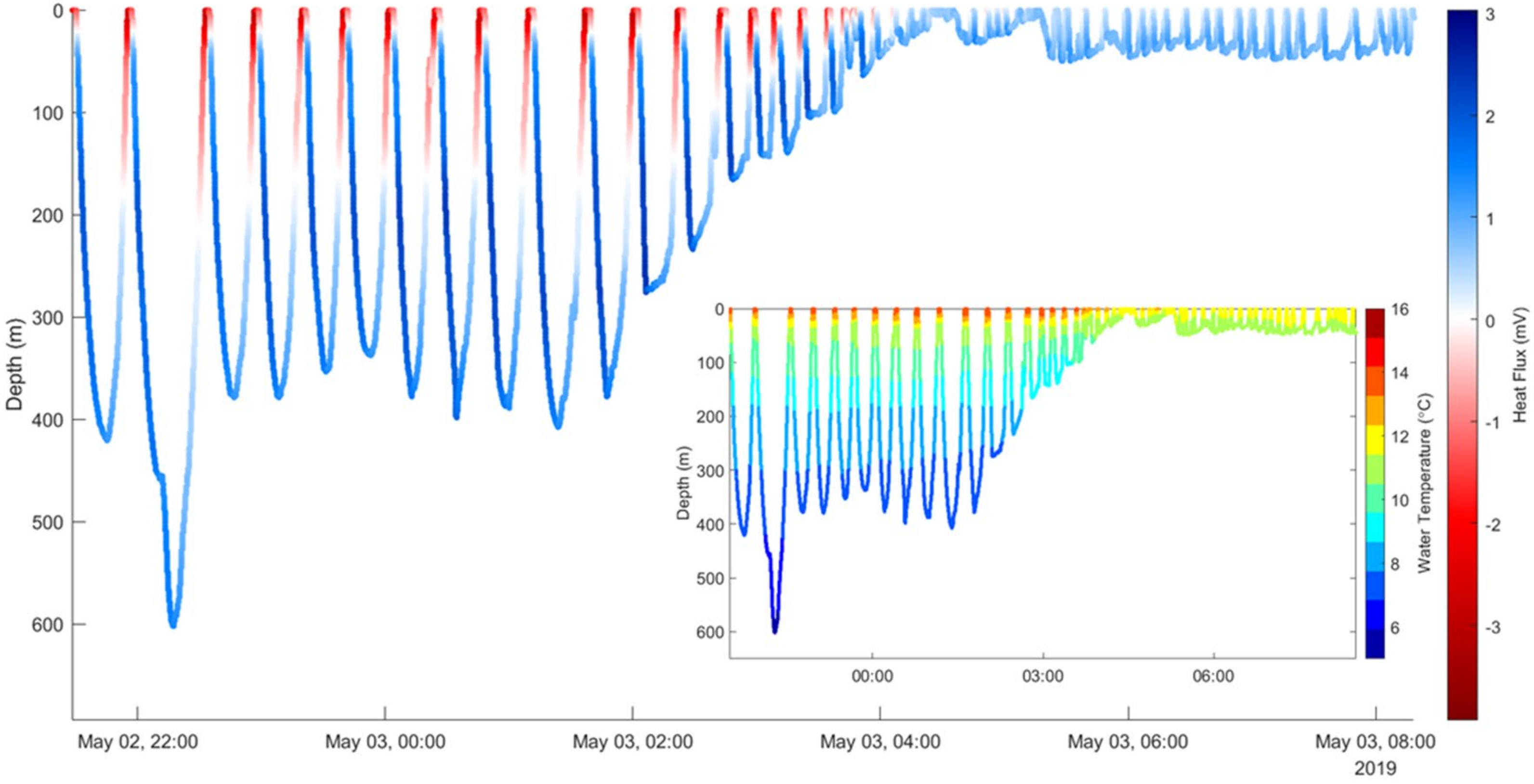


Figure 3.13 Segment of a dive profile emphasizing the differences in heat flux patterns between long-deep dives vs. short-shallow dives. The water temperature during these dives is shown in the inset.

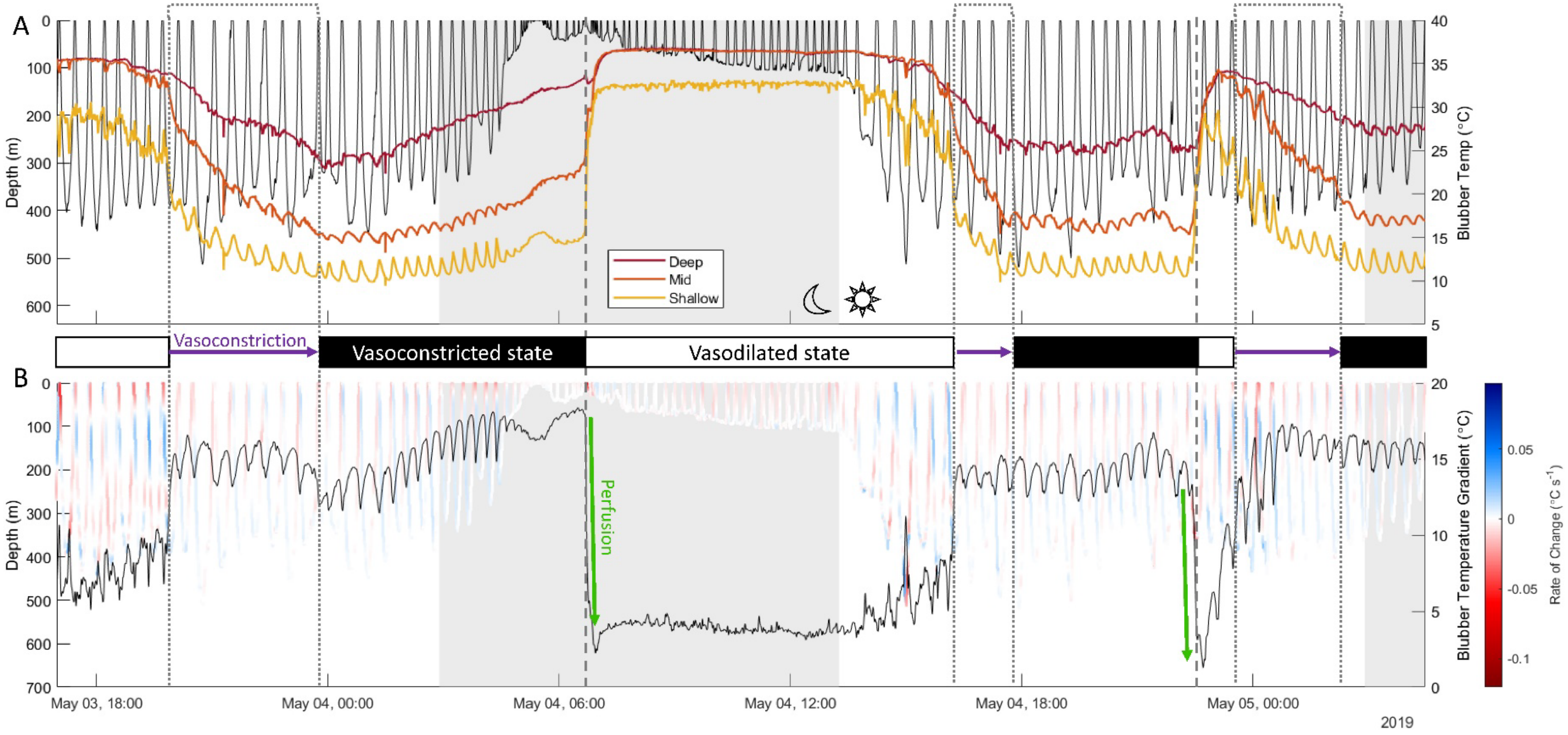


Figure 3.14 Within-dive fluctuations vs. across-dives changes in blubber temperature (A) and deep-shallow blubber gradient (B). Changes across dives are characterized by abrupt increases (dashed vertical lines) and slow decreases (area bounded by dotted lines) in blubber temperature. Hypothesized vasomotor changes (purple arrows = vasoconstriction, green arrows = peripheral perfusion) and resulting vasomotor states are indicated.

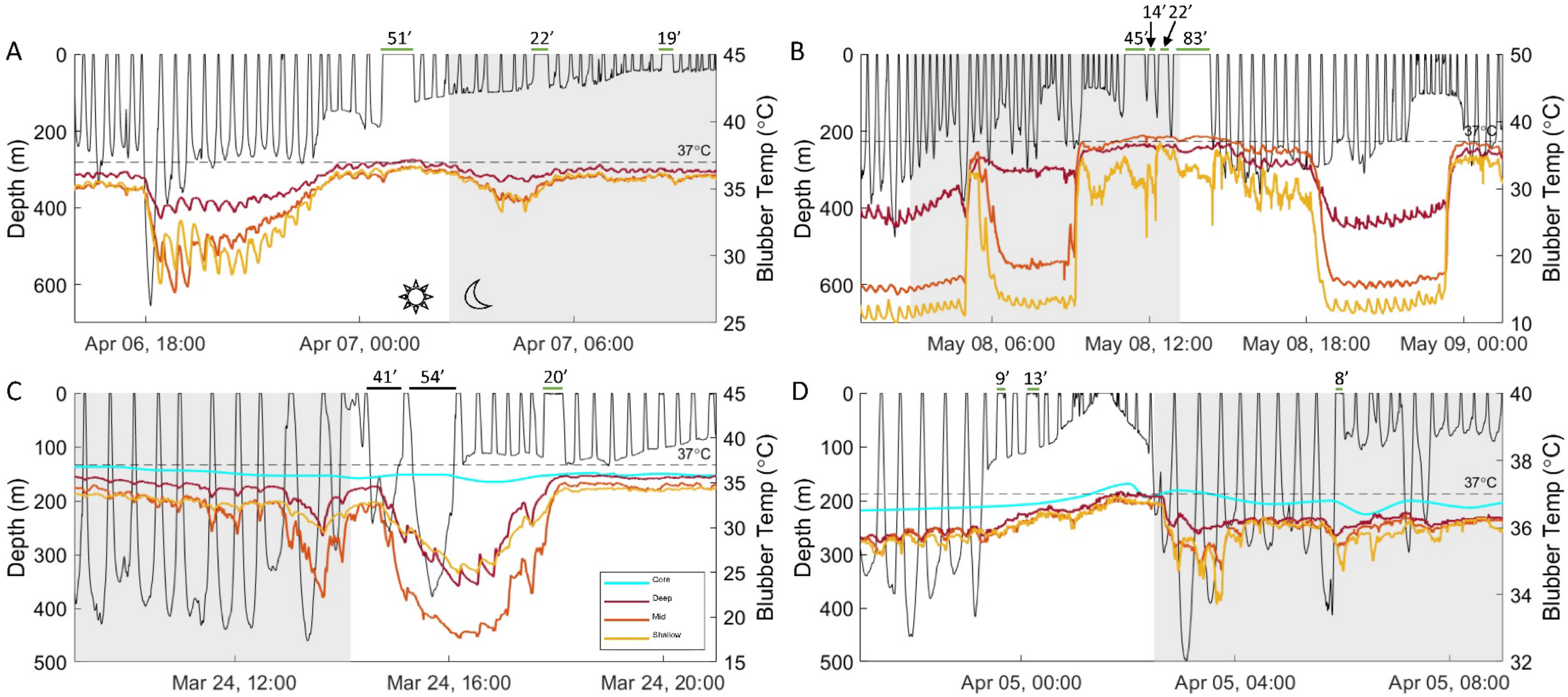


Figure 3.15 Examples of peripheral rewarming during short-shallow diving bouts and extended surface intervals (denoted by green bars, with duration in minutes on top) for seals Xena (A), Toby (B), Anisa (C), and Penny (D). Abnormally long dives are denoted by black bars with duration in minutes on top.

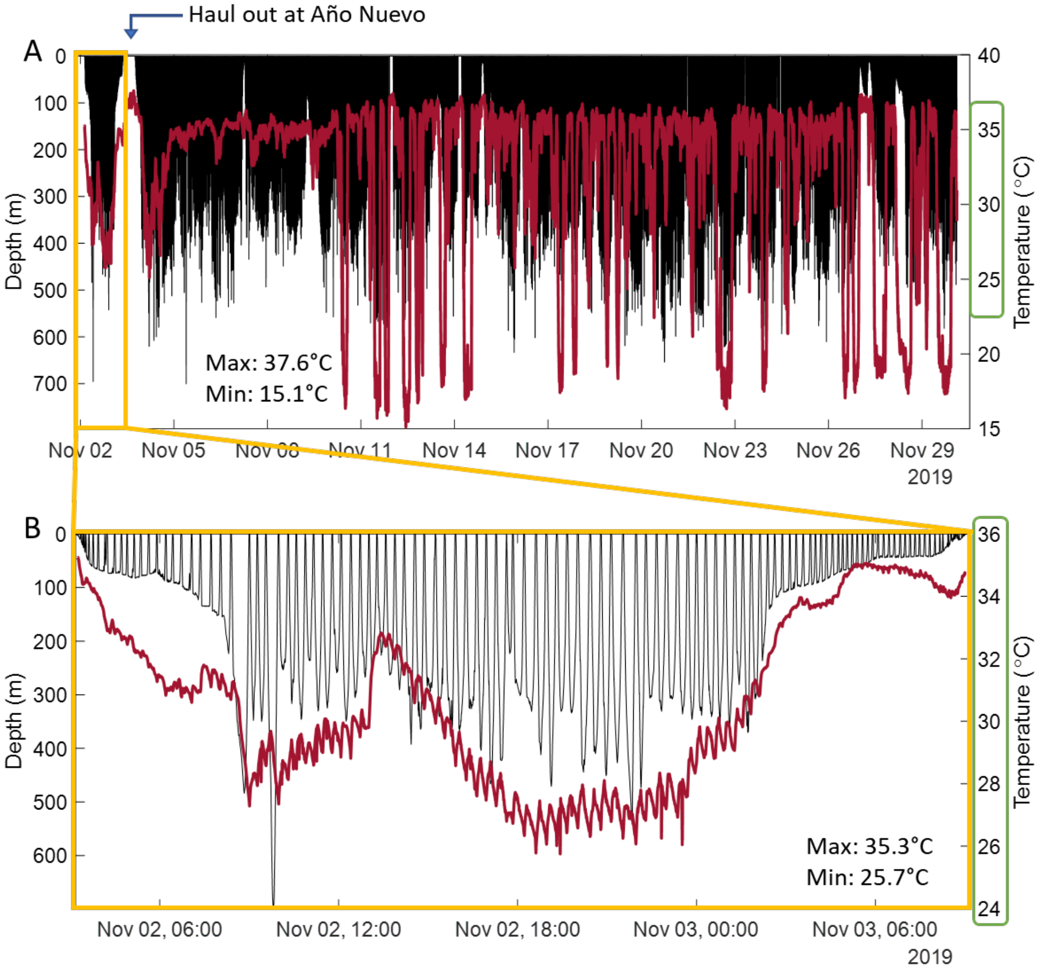


Figure 3.16 Differences in blubber temperature range during Luna's entire trip (A) vs. the first 1.3 days (B) before hauling out at Año Nuevo for ~8 hours. Comparable limits of the right y-axis are depicted with green boxes.

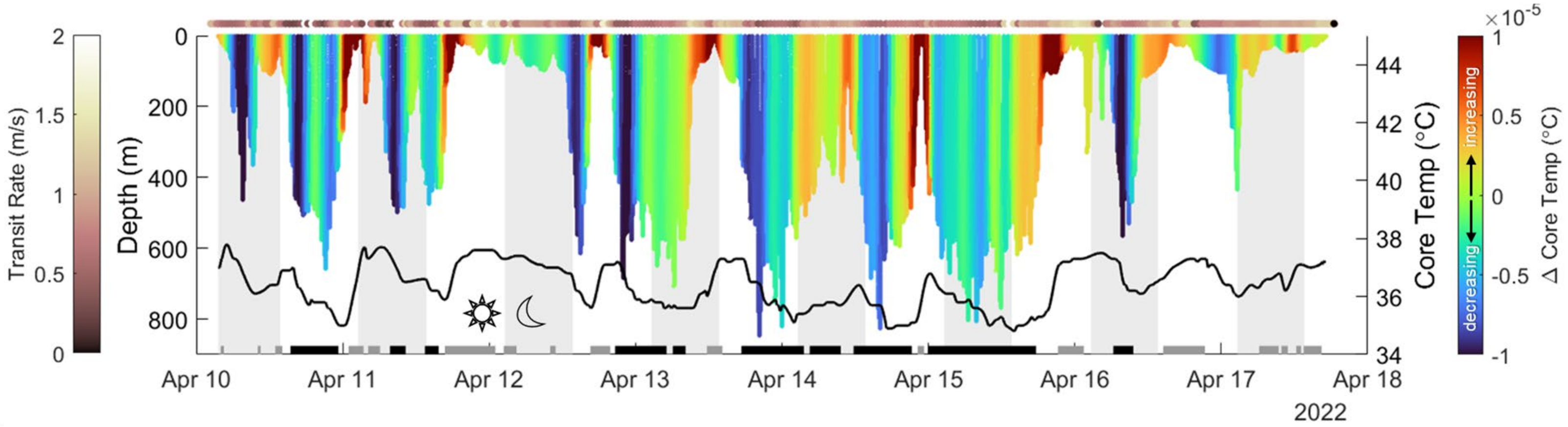


Figure 3.17 Increasing and decreasing trends in core temperature (black line) for seal Frank is depicted on the dive profile with warmer and cooler colors indicating faster increases and decreases, respectively. Black and gray bars at the bottom of the figure along the x-axis denote long-deep diving bouts and short-shallow diving bouts, respectively. Transit rate interpolated at each dive is shown above the dive profile with lighter colors indicating faster transit rates.

Table 3.S1 The percentage of time heat loss occurred on all dives, short-shallow dives vs. long-deep dives, and active vs. nonactive dives for each seal-sensor combination. The largest proportion of heat loss when comparing dive types is bolded. The remaining percentage accounts for heat gain.

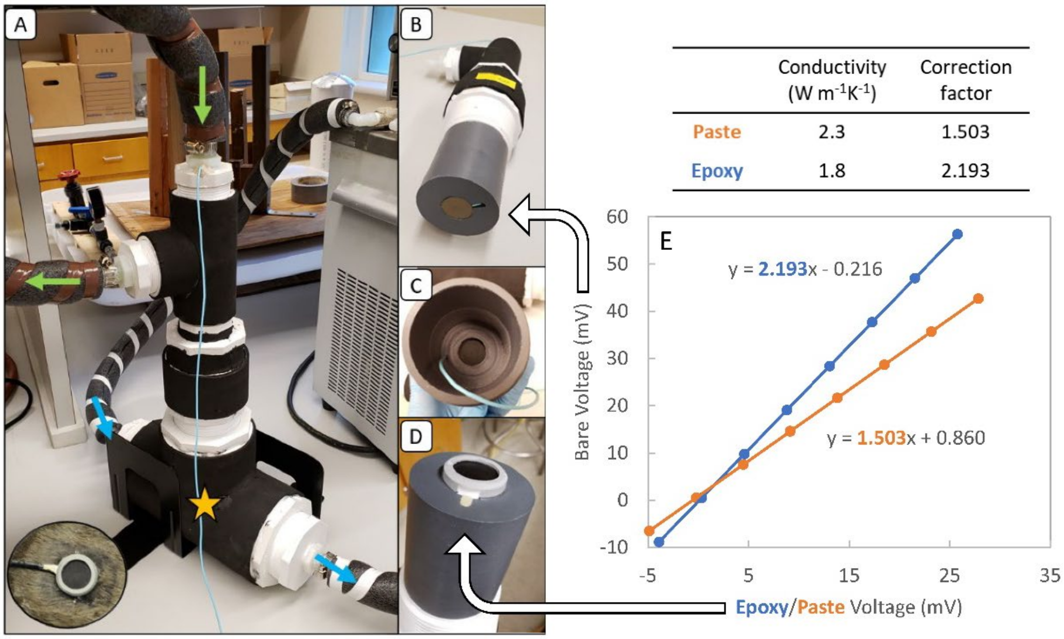
Seal	Sensor Location	No. Dives	All Dives		Short-Shallow Dives	Long-Deep Dives	Active Dives	Nonactive Dives
			Per sensor	Avg				
OJ	Ax	150	87.4	85.4	**88.5 ±13.0**	86.0 ±3.7	**89.3 ±14.9**	87.7 ±3.2
	Flank	150	83.3		82.2 ±11.1	**83.2 ±5.2**	81.3 ±13.2	**86.4 ±3.2**
CJ	Ax	613	84.0	84.7	**89.2 ±10.5**	82.0 ±4.7	**86.2 ±8.5**	85.5 ±6.0
	Flank	373	85.8		**90.5 ±11.7**	83.5 ±3.4	86.3 ±8.9	**89.0 ±5.8**
Xena	Flank	200	98.2	90.0	**99.7 ±1.0**	97.3 ±2.9	**100.0 ±0.2**	96.4 ±3.0
	LD	200	81.8		78.2 ±12.5	**83.8 ±3.1**	77.1 ±10.8	**84.6 ±3.7**
Toby	Neck	600	81.1	82.0	**81.1 ±18.9**	79.0 ±3.6	76.4 ±17.4	**83.5 ±6.3**
	Flank	37	96.5		90.5 ±15.8		78.0 ±38.6	**99.6 ±0.6**
Luna	Flank	112	90.4	90.4	**99.3 ±2.1**	85.7 ±4.7	**97.3 ±5.8**	90.6 ±7.7
Cheia	Ax	396	78.6	79.6	**84.8 ±14.9**	76.3 ±4.0	**82.3 ±12.0**	77.3 ±8.2
	Flank	396	80.5		**87.2 ±14.2**	78.0 ±4.6	**83.2 ±11.8**	80.1 ±8.9
Anisa	Ax	116	95.9	97.0	**97.8 ±4.7**	92.0 ±4.4	96.4 ±5.7	**97.8 ±3.8**
	Neck	116	95.6		**97.5 ±5.2**	90.8 ±4.5	94.6 ±6.2	**97.8 ±3.9**
	Flank	116	99.7		99.8 ±1.0	99.8 ±0.6	99.8 ±0.7	**99.9 ±0.5**
	LD	116	96.6		**96.8 ±5.6**	95.6 ±5.5	93.2 ±6.6	**98.7 ±3.1**
Snora	Ax	170	91.2	94.9	**96.3 ±7.9**	79.8 ±8.9	**99.8 ±1.3**	93.9 ±6.2
	Neck	170	93.1		**98.0 ±5.8**	81.5 ±7.7	**99.6 ±1.1**	95.9 ±6.4
	Flank	170	99.5		**100.0 ±0.0**	98.2 ±3.5	**100.0 ±0.0**	99.6 ±1.5
	LD	170	95.7		**99.4 ±3.2**	86.0 ±6.2	**100.0 ±0.0**	97.6 ±4.7
Penny	Ax	129	91.1	92.5	**94.2 ±7.2**	85.1 ±3.3	**92.0 ±7.9**	90.1 ±6.4
	Neck	129	85.4		**83.5 ±18.6**	83.1 ±6.3	81.0 ±20.3	**86.4 ±5.2**
	Flank	129	100.0		**100.0 ±0.0**	100.0 ±0.0	100.0 ±0.0	100.0 ±0.0
	LD	129	93.4		**96.4 ±4.4**	87.6 ±2.8	**95.8 ±5.1**	91.5 ±4.9
Frank	Ax	618	90.3	90.8	**91.8 ±12.1**	86.1 ±5.8	**94.0 ±9.6**	90.5 ±7.9
	Neck	618	82.6		**87.0 ±16.7**	75.1 ±7.3	**88.7 ±18.9**	82.3 ±11.2
	Flank	618	96.2		**98.7 ±4.3**	93.3 ±5.0	**99.5 ±3.9**	95.8 ±5.1
	LD	618	94.2		**96.5 ±8.3**	90.7 ±5.3	**97.6 ±6.9**	94.0 ±6.1
Overall	Ax	7 seals	88.4					
	Neck	5 seals	87.6					
	Flank	10 seals	93.0					
	LD	5 seals	92.3					

Table 3.S2 The number and percentage of heat flux transitions occurring for the most common combinations of dive phase and transition direction. For transitions from heat gain to loss, larger percentage when comparing surface interval and descent is bolded.

Seal	Sensor Location	Heat Loss to Gain		Heat Gain to Loss			
		Ascent		Surface Interval		Descent	
		#	%	#	%	#	%
OJ	Ax	122	85.3	24	16.7	112	**77.8**
	Flank	145	83.8	29	16.7	128	**73.6**
CJ	Ax	610	91.6	157	23.5	444	**66.6**
	Flank	334	95.7	82	23.4	256	**73.1**
Xena	Flank	67	94.4	58	**81.7**	1	1.4
Toby	Neck	547	96.5	54	9.5	488	**86.2**
	Flank	25	96.2	21	**80.8**	0	
Luna	Flank	71	100.0	10	14.1	54	**76.1**
Cheia	Ax	396	89.0	67	15.1	309	**69.4**
	Flank	384	95.0	57	14.1	301	**74.5**
Anisa	Ax	50	100.0	33	**66.0**	12	24.0
	Neck	55	93.2	40	**67.8**	17	28.8
	Flank	10	100.0	9	**90.0**	0	
	LD	51	100.0	34	**66.7**	13	25.5
Snora	Ax	77	97.5	42	**53.2**	29	36.7
	Neck	53	91.4	31	**53.4**	21	36.2
	Flank	6	100.0	5	**83.3**	1	16.7
	LD	30	100.0	13	43.3	16	**53.3**
Penny	Ax	99	98.0	60	**59.4**	39	38.6
	Neck	117	92.1	34	26.8	91	**71.7**
	LD	98	98.0	73	**73.0**	22	22.0
Frank	Ax	331	78.1	130	30.7	271	**63.9**
	Neck	380	71.4	108	20.3	378	**71.2**
	Flank	180	96.3	102	**54.5**	73	39.0
	LD	239	83.3	115	40.1	153	**53.3**

Table 3.S3 Average differences (± SD) in temperature (°C) between the skin (at the flank) and water per dive phase and for the entire dive (descent + bottom + ascent). Data does not incorporate the time lag for skin temperature (compare to Table 3.10). Negative values (in red) indicate that on average skin temperature was colder than the water. The dive phase that had the greatest absolute difference is bolded for each seal.

Seal	No. Dives	Descent	Bottom	Ascent	Surface	Dive
		Average ± SD	Average ± SD	Average ± SD	Average ± SD	Average ± SD
OJ	150	0.52 ±0.26	**0.59 ±0.12**	0.14 ±0.17	-0.39 ±0.31	0.52 ±0.08
CJ	613	**2.01 ±0.33**	1.54 ±0.19	0.43 ±0.40	0.34 ±0.39	1.40 ±0.14
Xena	200	**1.73 ±0.20**	1.58 ±0.28	1.15 ±0.07	1.39 ±0.46	1.53 ±0.21
Toby	36	**0.81 ±0.15**	0.74 ±0.17	0.27 ±0.19	0.33 ±0.23	0.60 ±0.11
Luna	77	2.53 ±0.27	**2.54 ±0.45**	1.73 ±0.47	1.06 ±0.75	2.36 ±0.41
Cheia	396	**0.69 ±0.34**	0.59 ±0.37	-0.04 ±0.34	-0.56 ±0.51	0.49 ±0.30
Anisa	116	2.14 ±1.62	**2.46 ±2.37**	1.91 ±2.01	1.44 ±1.51	2.30 ±2.12
Snora	170	2.55 ±1.91	**2.70 ±2.06**	2.31 ±2.16	2.03 ±2.01	2.57 ±1.91
Penny	129	2.60 ±0.78	**2.62 ±0.90**	2.04 ±0.82	1.64 ±0.85	2.51 ±0.80
Frank	618	1.31 ±0.77	**1.32 ±0.85**	0.96 ±0.92	0.64 ±0.97	1.26 ±0.83
Overall	2505	**1.59 ±1.01**	1.48 ±1.11	0.84 ±1.15	0.57 ±1.16	1.37 ±1.05



	Conductivity (W m^{-1}K^{-1})	Correction factor
Paste	2.3	1.503
Epoxy	1.8	2.193

Figure 3.S1 (A) The jury-rigged contraption used to quantify the effects of the attachment mechanism (shown on a seal in the inset), which includes a custom-made PVC ring with superglue around its edges to hold the heat flux sensor coated with a thin layer of a thermally-conductive epoxy or paste to improve contact with the skin. This attachment is replicated inside the contraption (indicated by the yellow star). Water at different temperatures flows through the contraption from two temperature-controlled water baths as indicated by the blue and green arrows, resulting in a temperature gradient across the sensor. Output values from the bare sensor (B) and bare sensor with dummy sensor attached (D) are regressed against each other as shown in (E). The slope of the regression is the determined correction factor to account for the effects of attachment mechanism.

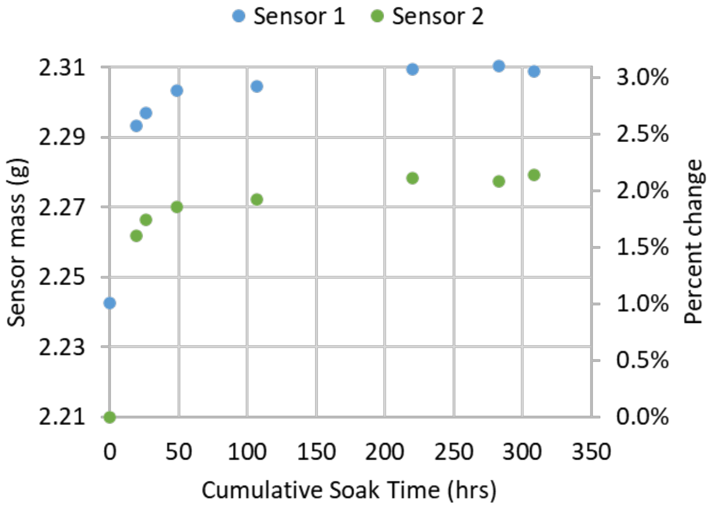


Figure 3.S2 Changes in mass of two heat flux sensors that were soaking in fresh water.

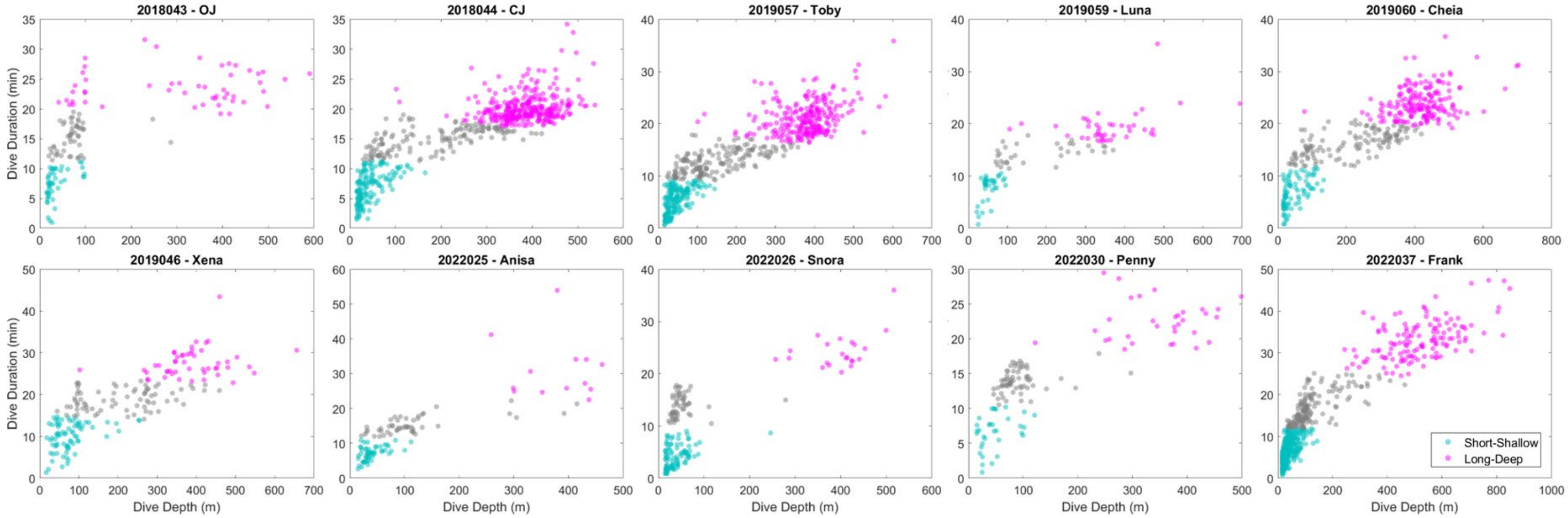


Figure 3.S3 Results of k-means clustering (k=3) for each seal were used to classify short-shallow dives (turquoise) and long-deep dives (magenta). See Table 3.3 for the dive depth and duration centroids of the two extreme clusters.

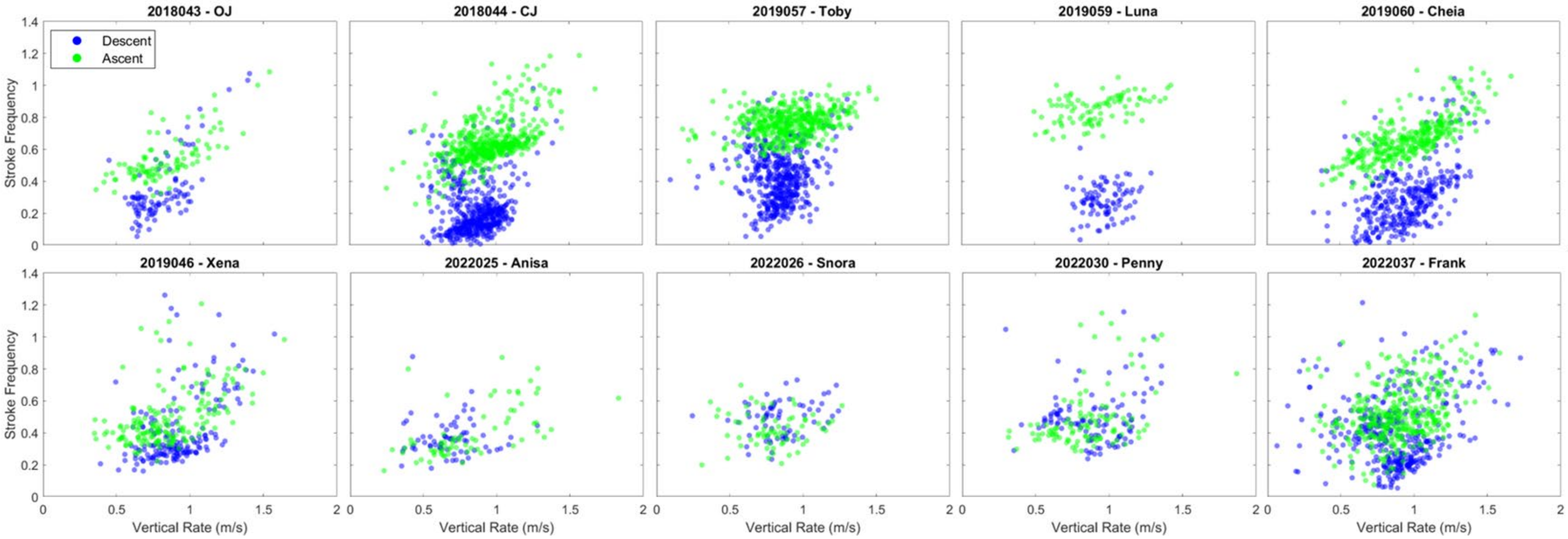


Figure 3.S4 Comparison of stroke frequency vs. vertical transit rate on the descent and ascent of dives >50 m for each seal. For a given vertical transit rate, smaller seals (top row) stroke more on the ascent suggesting they are negatively buoyant. The patterns are less clear for the larger seals, suggesting they may be closer to neutral buoyancy.

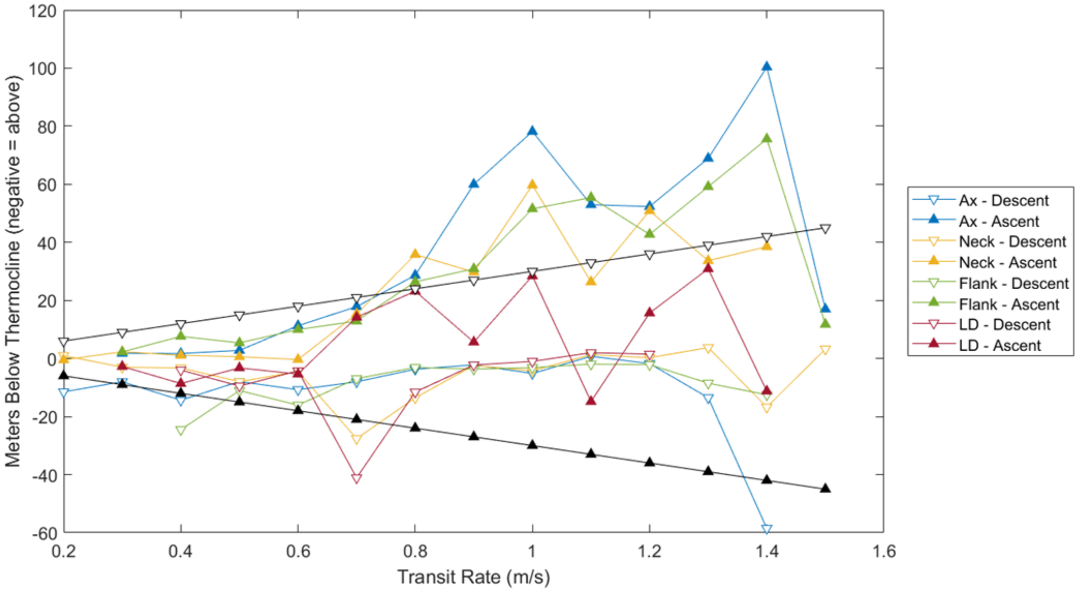


Figure 3.S5 Heat flux transition depths on descent (open triangle) and ascent (filled triangle) relative to the thermocline depth averaged across seals at binned transit rates for each sensor location. Black lines are the theoretical depth at which heat flux transition should occur relative to the thermocline on descent or ascent if the 30-second response time of the heat flux sensor was the only determinant of transition timing after passing through the thermocline. See Figure 3.9 for the adjusted values that take this response time into account.

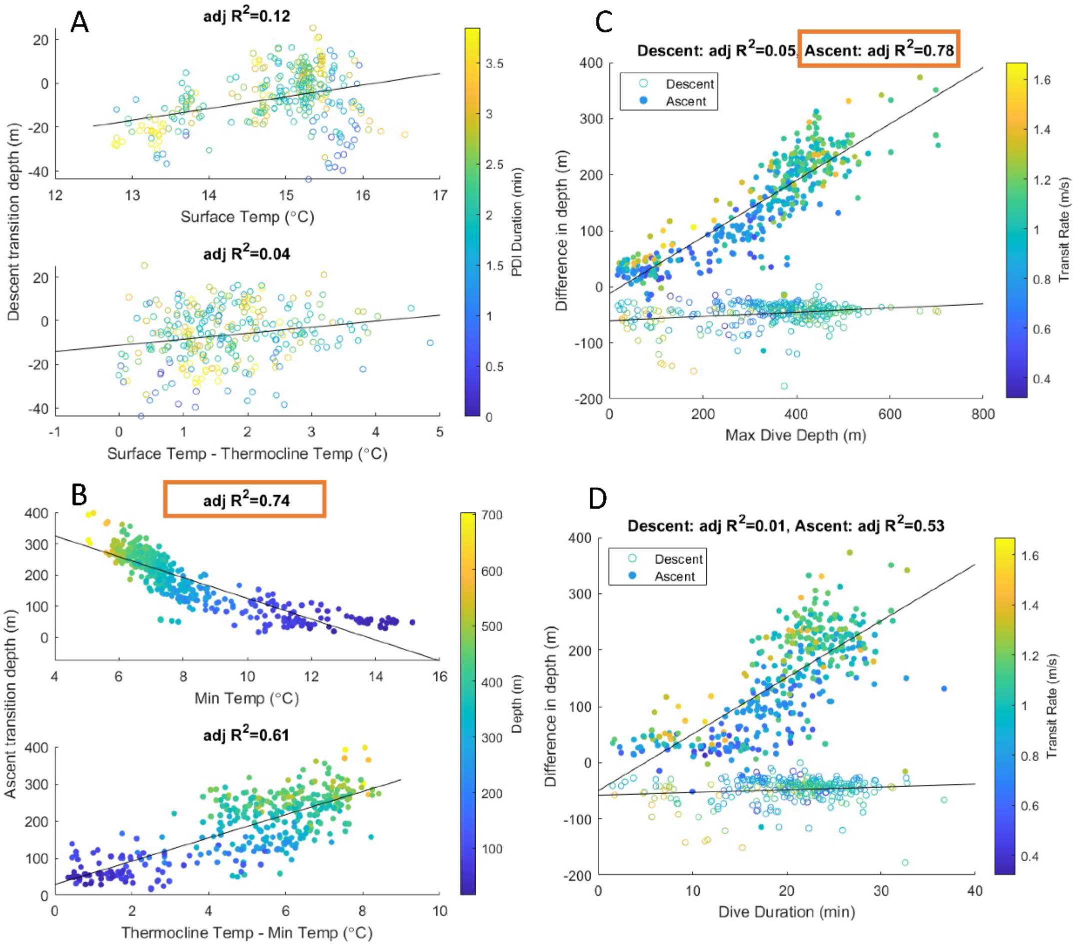


Figure 3.S6 Examples using data from seal Cheia's flank sensor of the various correlations tested to determine if heat flux transitions are due to changes in water temperature (A-B) or diving behavior (C-E). Correlations were tested using heat flux transition depths on descent (A), heat flux transition depths on ascent (B, E), or the difference between transition depth and thermocline depth (C-D). The adjusted R^2 values that are boxed in orange are the relationships that were strongest and most consistent across seals.

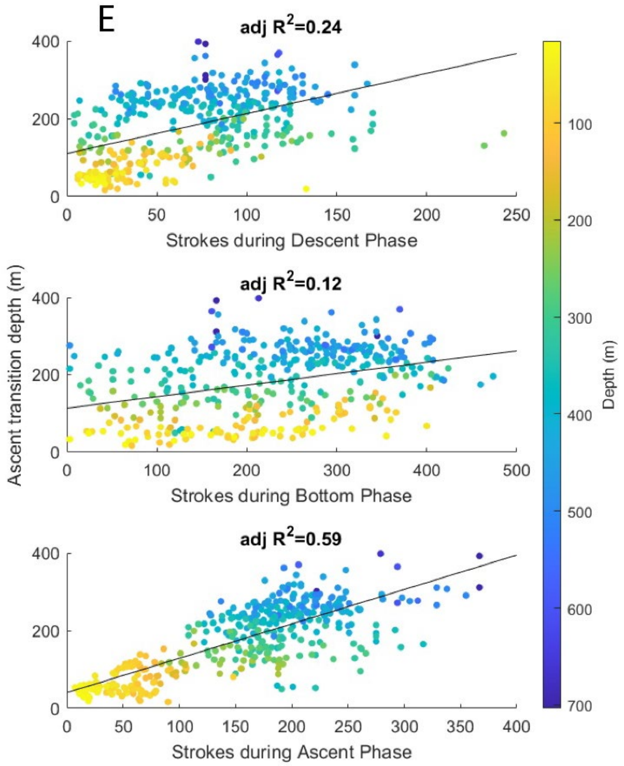


Figure 3.S6 (continued) Examples using data from seal Cheia's flank sensor of the various correlations tested to determine if heat flux transitions are due to changes in water temperature (A-B) or diving behavior (C-E). Correlations were tested using heat flux transition depths on descent (A), heat flux transition depths on ascent (B, E), or the difference between transition depth and thermocline depth (C-D). The adjusted R^2 values that are boxed in orange are the relationships that were strongest and most consistent across seals.

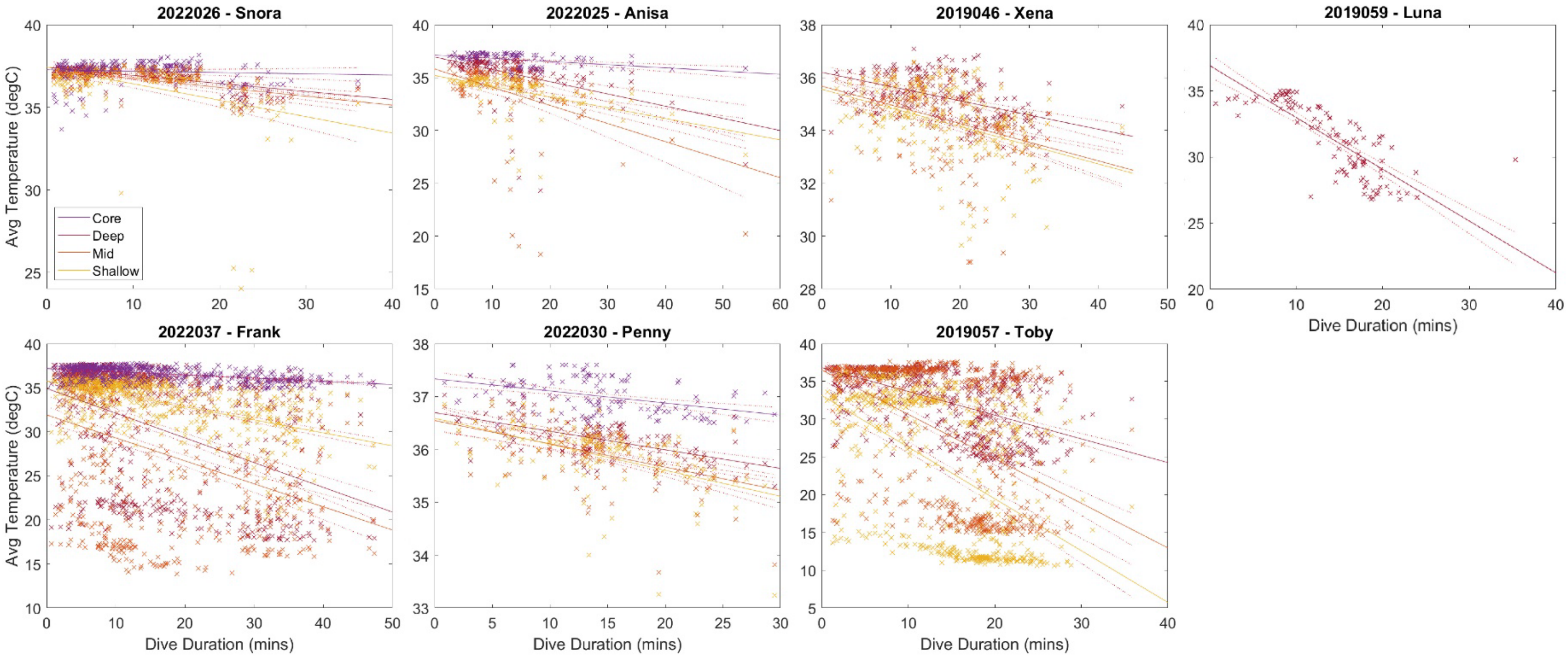


Figure 3.S7 Representative blubber and core temperature determined as the y-intercept from the regression of mean temperature vs. dive duration for each seal.

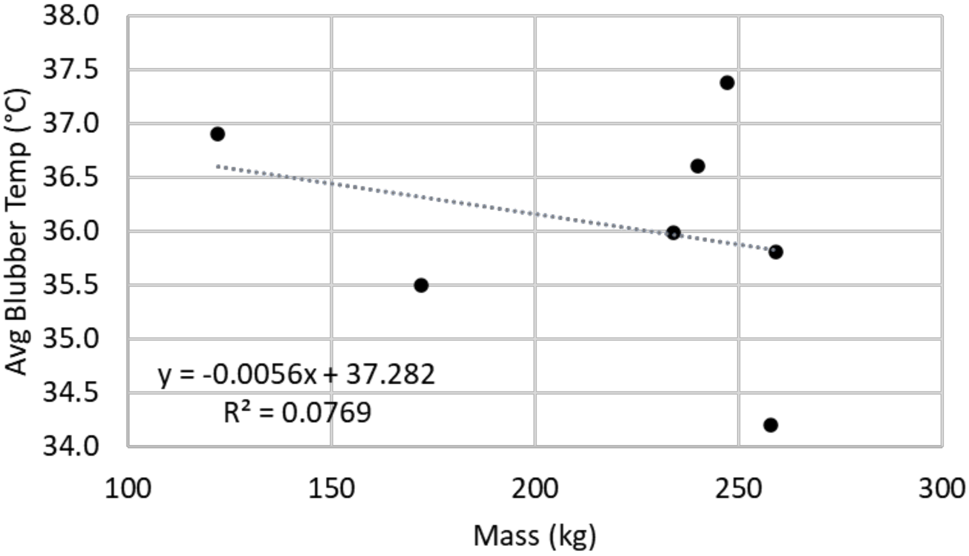


Figure 3.S8 The relationship between average representative blubber temperature and mass indicates they are not correlated.

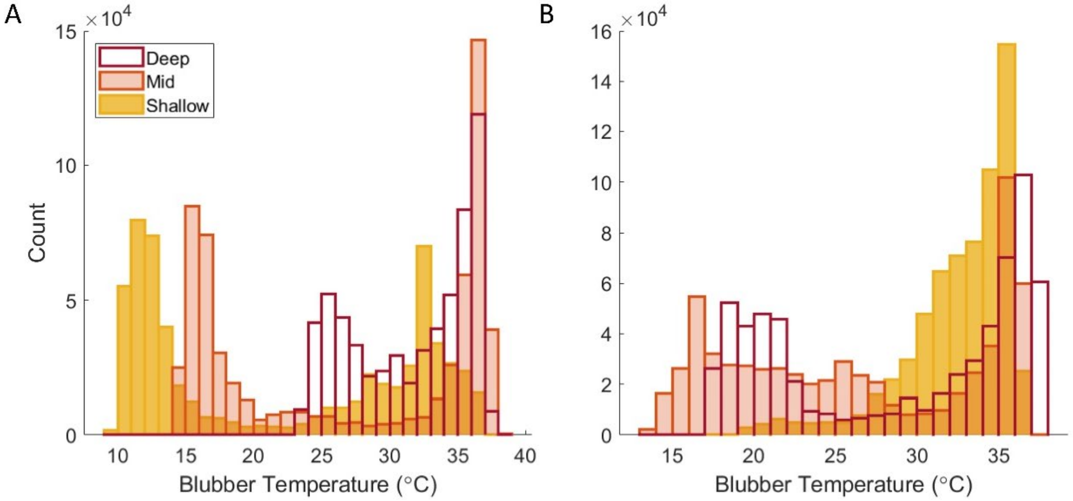


Figure 3.S9 Blubber temperature distributions for seals Toby (A) and Frank (B) shows bimodal distributions for some or all of the thermistor locations.

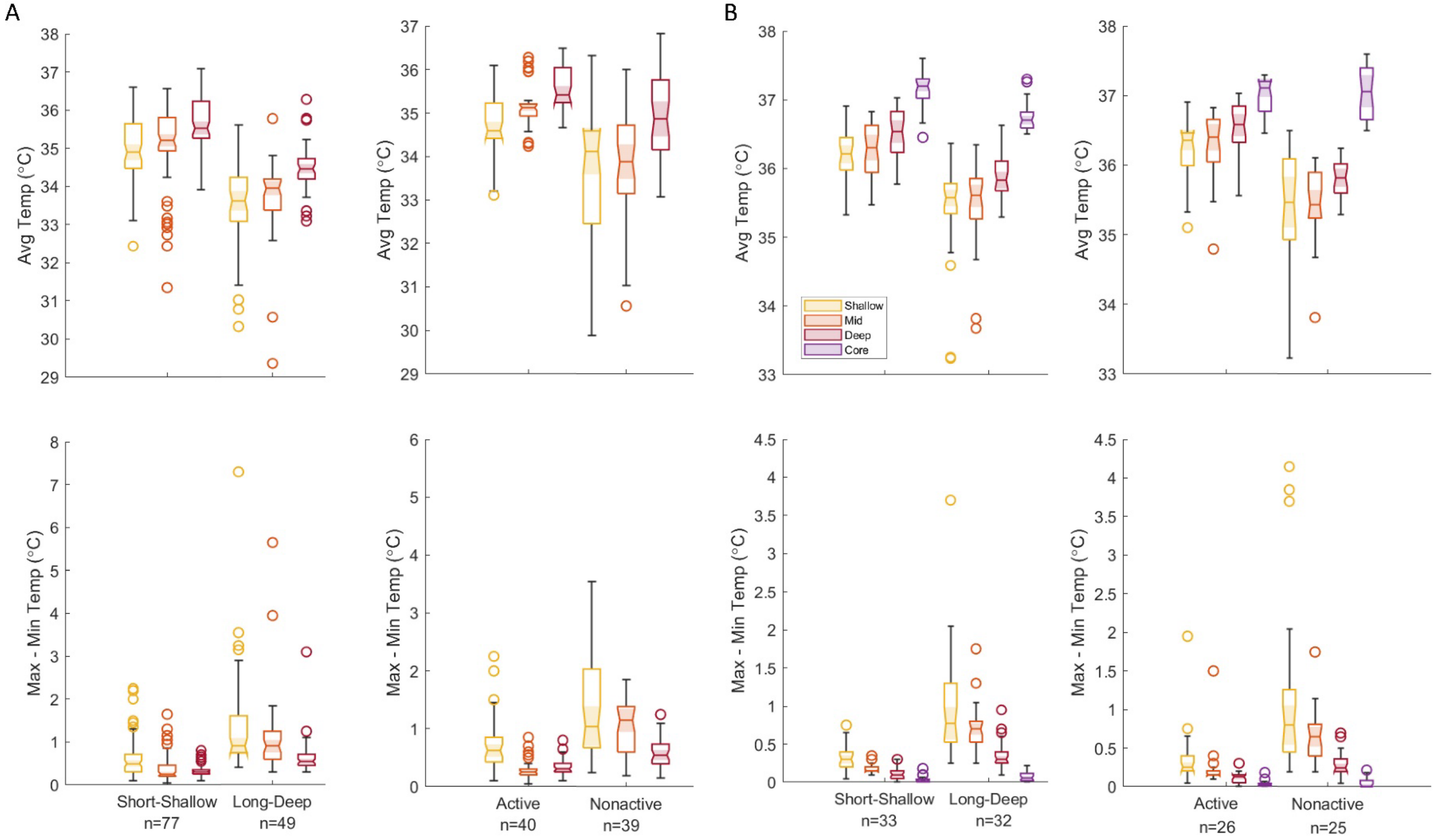


Figure 3.S10 Examples of average blubber and core temperature and temperature ranges between short-shallow and long-deep dives for seals Xena (A) and Penny (B).

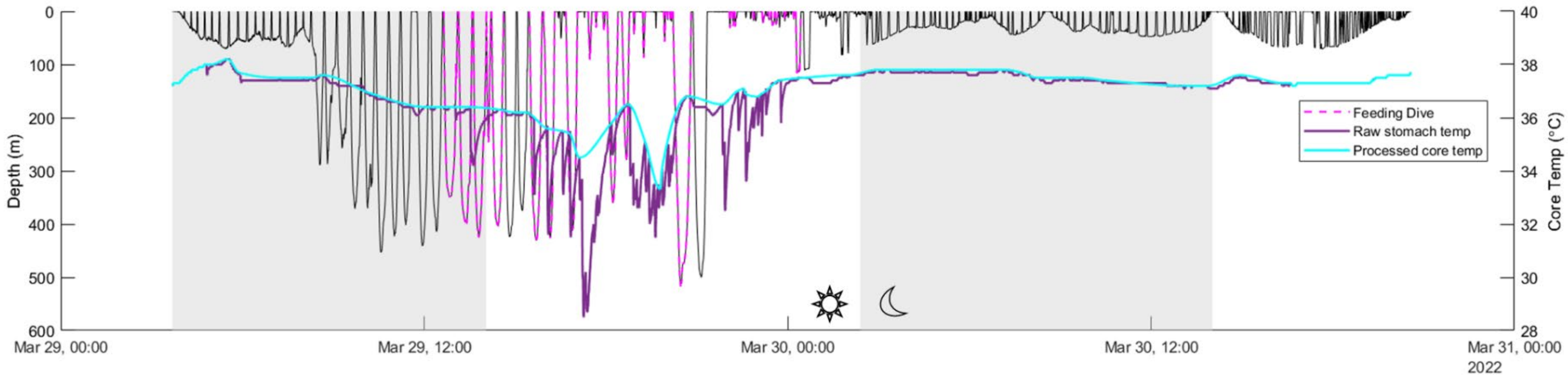


Figure 3.S11 Raw stomach temperature and processed core temperature of seal Snora. Low core temperatures are likely due to several consecutive ingestion events on successive feeding dives.

Chapter 4

Diving and foraging behavior of a mesopelagic predator, the northern elephant seal, in relation to low-oxygen zones

Arina B. Favilla, Rachel R. Holser, Akinori Takahashi, Elliott L. Hazen, Ana M. M. Sequeira, A. Marm Kilpatrick, Theresa R. Keates, Daniel P. Costa

4.1 Abstract

The mesopelagic zone provides critical foraging opportunities for large air-breathing deep-diving predators, which can pursue prey seeking refuge in low-oxygen waters from water-breathing predators. Northern elephant seals (*Mirounga angustirostris*) are mesopelagic predators that exhibit continuous, diel diving behavior across two annual foraging migrations. Recent work documented prey capture events at >800 m using animal-borne cameras and jaw accelerometers and suggested that northern elephant seals target sluggish prey in the oxygen minimum zone (OMZ). To assess their use of OMZs, we combined tracking and diving data from 364 adult female northern elephant seals as well as jaw acceleration data from 52 seals with monthly averaged modeled dissolved oxygen data from the Copernicus Marine Environment Monitoring Services to examine their diving and foraging behavior relative to the OMZ and oxygen limited zone (OLZ). Our results indicate that, at a population level, seals primarily dove into the OLZ rather than the OMZ as previously hypothesized, but diurnal, regional, and seasonal differences were found. The greatest use of the OMZ occurred in the California Current, where the OMZ is shallower. Outside the California Current, most daytime dives reached the OLZ while

nighttime dives remained in high-oxygen waters. During the post-breeding trip, seals spent more time in OMZ regions and deeper daytime dives resulted in greater use of low-oxygen zones; however, dissolved oxygen levels at their feeding depths did not affect their short-term foraging success, which contrasts with the post-molt trip. Greater foraging effort and a less selective diet may help post-breeding seals compensate for the shorter trip and regain mass necessary for the molting fast. For both trips, seals that spent more time diving in OLZ regions (where no OMZ exists) had greater energy gain. OLZ regions are further from the colony and the OMZ-OLZ boundary coincides with other important oceanographic features including the gyre-gyre boundary and, during part of the post-molt trip in the summer, the Transition Zone Chlorophyll Front, which is known to attract many migrating marine species. Although OMZs are not substantially used by the population, certain individuals could be considered OMZ specialists, but further work is needed to quantify their prevalence and whether their strategy confers energetic benefits that were masked by the population-level analyses. Dissolved oxygen plays a major role in determining mesopelagic prey composition and distribution in the entire water column; therefore, elephant seals are a sentinel species for monitoring and understanding ecosystem-level impacts of OMZ shoaling associated with climate change.

4.2 Introduction

Ocean deoxygenation is currently ranked among the most concerning changes to the marine environment. Over the past half century, the open ocean has lost ~2% of its oxygen content (~77 billion metric tons; Levin, 2018; Schmidtko et al., 2017). In the open ocean, deoxygenation is primarily caused by global warming, which increases seawater temperatures, thus leading to a decrease in oxygen solubility while simultaneously increasing organisms' oxygen consumption. Global warming also intensifies stratification which reduces ocean ventilation which is key for the drawdown of surface oxygen into deeper waters (Breitburg et al., 2018; Oschlies et al., 2018). Ocean oxygen content plays an important role in marine productivity, biodiversity, and biogeochemical cycles. Therefore, ocean deoxygenation will have a major impact on marine species and ecosystems as well as humans who depend on them.

The combination of physical processes (i.e., ventilation, circulation, transport, and mixing) and biogeochemical cycles (e.g., microbial respiration) results in low dissolved oxygen content (e.g., <63 mmol m^{-3}) in the deep ocean. The depths at which dissolved oxygen reach certain thresholds (defined for each ocean basin) have been termed the oxygen minimum zones (OMZ) and the oxygen limited zones (OLZ; the layer above the OMZ; Gilly et al., 2013; Hofmann et al., 2011; Karstensen et al., 2008). These low-oxygen zones generally occur in the mesopelagic and play an important role in ecosystem structure (Robinson et al., 2010). Due to species-specific hypoxia tolerances (Childress & Seibel, 1998; Duskey, 2023; Seibel, 2011), the vertical distribution of prey is affected by low-oxygen zones.

Despite the seemingly inhospitable conditions (i.e., dark, cold, high pressure, and lower oxygen), the mesopelagic, or twilight zone, encompasses critical oceanic habitat at depths of 200-1000 m for a diversity of species (Robison, 2004). Despite comprising ~20% of the ocean's volume, due to its inaccessibility, relatively little is known about this large ecosystem (St. John et al., 2016). Previous studies have estimated a biomass of mesopelagic fish on the order of 10^3-10^4 million tons, or roughly 90% of the ocean's fish biomass (Irigoien et al., 2014). Mesopelagic fishes, along with squid, krill and other micronekton, form aggregations known as the deep scattering layer visible to echosounders. These species remain beneath the euphotic zone during the day, and many will migrate vertically at night to feed on zooplankton in the epipelagic zone (Klevjer et al., 2016). This diel vertical migration is the largest animal migration on Earth in terms of biomass and has significant consequences on the biological pump and nutrient cycling (Bianchi et al., 2013). The most widely accepted hypothesis for this behavior is the avoidance of predators (Benoit-Bird & Moline, 2021; Hays, 2003). By ascending under the cover of darkness to feed in productive epipelagic waters at night, mesopelagic micronekton avoid visual predators. Then, by returning to deep low-oxygen zones (primarily the OLZ and upper OMZ) during the daytime, they also avoid water-breathing predators, like sharks and tunas, that depend on well-oxygenated water for active pursuit of prey. Other predators that are not hindered by low oxygen and cold temperatures, such as marine mammals, despite being constrained by their maximum dive duration, can take advantage of this abundant prey resource (Gilly et al., 2013; McMahon et al., 2019).

Due to ocean deoxygenation, OMZs have expanded by ~4.5 million km^2 over the past 50 years (Breitburg et al., 2018). This expansion has led to a shoaling of the OMZ layer as well as an increase in the horizontal extent of OMZs. Species that are intolerant to low oxygen, like billfish, are experiencing vertical habitat compression (Carlisle et al., 2017; Logan et al., 2023) and increased vulnerability to fishing pressure (Prince & Goodyear, 2006; Stramma et al., 2012; Vedor et al., 2021). On the other hand, species that target prey in the deep scattering layer may have enhanced foraging success as the depth of vertical migration reduces (Llapapasca et al., 2022; McMahon et al., 2019; Stewart et al., 2013).

Mesopelagic prey have been reported as important components in the diets of deep-diving marine mammals, including elephant seals, sperm whales, and beaked whales (Goetsch, 2018; Harvey et al., 2014; Walker et al., 2002). Northern elephant seals are the most readily studied of these mesopelagic predators because they predictably return to their colony twice a year in between their foraging trips, which allows for instrumentation and biological sampling (Robinson et al., 2012). Since 2004, biologgers have been deployed on ~20 adult females each year resulting in a long-term tracking and diving dataset (Costa et al., in prep). Additionally, elephant seals spend most of the year at-sea in the North Pacific where oxygen loss is projected to be up to 50 mmol m^{-3} by 2100 under the “business-as-usual” scenario (RCP8.5) and account for 18% of the total global change in dissolved oxygen, likely resulting in OMZ expansion (Bopp et al., 2013; Keeling et al., 2010; Schmidtko et al., 2017). Therefore, as a generalist mesopelagic predator with a long-term dataset, the northern elephant seal serves as an ideal sentinel species for understanding the ecosystem-level impacts (e.g., trophic interactions) of current and future OMZs (Braun et al., 2022; Goetsch, 2018; Hazen et al., 2019).

Female northern elephant seals (*Mirounga angustirostris*) go on two annual foraging trips—one after the breeding season in the boreal winter-spring lasting ~10 weeks and the other after the molting season in the summer-fall lasting ~7 months (Robinson et al., 2012). Like many other marine megafauna that migrate long distances because their breeding and foraging grounds are spatially separated, their foraging behavior is scale-dependent—large-scale features influence migration routes, whereas mesoscale features induce a switch in behavioral state (Hyrenbach et al., 2002; Kenney et al., 2001). Previous studies have shown that elephant seals select for certain oceanographic features, including the gyre-gyre boundary (Robinson et al., 2012) and mesoscale activity, such as eddies (Abrahms, Scales, et al., 2018; Keates et al., 2022). The different scales at which these features influence elephant seal behavior could be attributed to their spatial extents as well as their dynamic versus stable nature. Mesoscale features such as eddies and fronts are smaller, dynamic, and more temporary. In contrast, the gyre-gyre boundary is a relatively consistent and permanent feature that spans east-west between the 40-50°N latitudinal band in the North Pacific. Apart from the subset of females (~15%) that undertake a more coastal migration, female elephant seals seem to track the gyre-gyre boundary as they travel westward across the North Pacific and exhibit slower transit rates along this area suggestive of localized foraging activity (Figure 4 & 6 in Robinson et al., 2012). Similar to the gyre-gyre boundary, low-oxygen zones are semi-permanent features with some seasonal variability (Paulmier & Ruiz-Pino, 2009), and OMZs have been suggested to be important oceanographic features influencing elephant seal behavior (Naito et al., 2017), but has not yet been thoroughly investigated.

Unlike other large marine megafauna with well-defined foraging grounds (e.g., Andrews-Goff et al., 2018), elephant seals exhibit continuous diving behavior and diel patterns which suggest they are constantly searching for and following vertically migrating prey while migrating thousands of kilometers across the North Pacific (Adachi et al., 2021; Naito et al., 2013; Robinson et al., 2012). They dive deeper during the day and shallower at night, tracking the migration of the deep scattering layer. This diel diving behavior aligns with recent diet studies showing that the diet of elephant seals is comprised chiefly of vertically migrating mesopelagic fish, mainly myctophids (lanternfish), which are the most abundant and the most energy-dense prey available in the mesopelagic (~12,100 kJ/kg; Sinclair et al., 2015), followed by bathylagids (deep sea smelts), which are less energy dense but abundant in the eastern North Pacific (Goetsch et al., 2018; Yoshino et al., 2020). Non-migrating squid are a smaller component of their diet (~1/3). Although less energetically rich (2,000-4,000 kJ/kg), they are larger and slower moving, making them easier to catch (Sinclair et al., 2015). Vertically migrating squid are similar in energetic content and the second most abundant group in the mesopelagic but were not prevalent in the seals' diet, except for certain individuals (Goetsch, 2018). These squid are more agile and thus less energetically efficient to prey upon. Therefore, at a population level, the foraging strategy of elephant seals aligns with the optimal prey selection theory, which states that predators should select prey that optimizes their net energy gain (Krebs et al., 1977).

Aligning with the idea that the optimal prey would be the most energy-dense but easiest to catch, recent work documenting prey capture events at depth using animal-borne cameras and jaw accelerometers has suggested that northern elephant seals target prey in OMZs where seals may be advantaged against metabolically suppressed prey that have slower escape responses (Naito et al., 2017; Yoshino et al., 2020). However, there has yet to be a detailed examination of their diving and foraging behavior relative to OMZ depths across their expansive foraging habitat. Furthermore, the depth and thickness of OMZs differ across the North Pacific, and indeed, region-specific differences in diving and diet have been described (Goetsch, 2018). Since dissolved oxygen is a major contributor to determining the composition and vertical distribution of their prey (Robinson et al., 2010), a detailed examination of their diving and foraging behavior relative to OMZs could shed light onto how low-oxygen zones influence the foraging ecology and success of northern elephant seals.

To address this gap, we assessed to what extent adult female northern elephant seals use low-oxygen zones throughout their foraging trips and whether diurnal, seasonal, and spatial differences exist. Given how dissolved oxygen profiles change substantially across their foraging range, we also examined how the varying depth and thickness of low-oxygen zones across the North Pacific affects their utilization of these zones. Since all seals were equipped with a time-depth recorder, we analyzed their diving behavior to quantify their use of these zones. For a subset of seals with jaw accelerometers, we further refined the definition of use to include foraging behavior. Given that female seals have different foraging strategies (Adachi et al., 2021; Robinson et al., 2012), we investigated whether individual differences in the utilization of low-oxygen zones are reflected in foraging success metrics.

4.3 Methods

4.3.1 Animal behavior data

This study uses a long-term dataset of tracking and diving data from adult female northern elephant seals during their post-breeding (n = 205) or post-molting (n = 159) foraging trips during 2004-2019. Each year, ~20 female seals were chosen for tag deployment based on known or estimated age, history of consistently returning to the colony, and normal physical appearance. Animals were sedated for instrument attachment and removal following established protocols (Robinson et al., 2012) at Año Nuevo State Park, San Mateo County, California, USA (37.11°N, -122.33°W). During the deployment and recovery procedures, morphometric measurements including mass, length, girth, and blubber thickness were taken and used to calculate body composition with the truncated cones method (Gales & Burton, 1987) and calibrated to body water measurements (Webb et al., 1998). To estimate mass gain over the foraging trip, mass measurements were corrected to account for the time spent fasting on land between when the seal was weighed and its departure or arrival using an empirically derived equation (see methods in Holser et al., 2023). Energy gain was estimated based on the mass gain and body composition (i.e., relative amounts of water-free fat versus lean tissue) using energy content values of 17.99 MJ kg^{-1} for lean tissue and 39.33 MJ kg^{-1} for fat tissue, assuming 27% and 90% water-free tissue mass, respectively. All animal handling was conducted under National Marine Fisheries Service permit numbers 786-1463, 87-143, 14636, 17952, and 19108 and approved by the University of California, Santa Cruz Institutional Animal Care and Use Committee.

Each seal carried a satellite tag glued to the top of their head, which transmitted geolocations (Wildlife Computers, Seattle, WA, USA; Sea Mammal Research Unit, St. Andrews University, UK), and a time-depth recorder (if separate, glued to the seal's back; Wildlife Computers, Seattle, WA, USA) that sampled depth at least every 8 seconds at a resolution of 0.5 m with an accuracy of 1% of the pressure reading. The tags were attached to high-tension nylon mesh netting with cable ties and fishing line and glued to the fur using 5-minute quick setting epoxy (Loctite®). A subset of seals also carried an accelerometer glued to the lower jawline that recorded jaw motion events as a proxy for prey capture attempts (Kami Kami Logger, Little Leonardo Co., Tokyo, Japan). Briefly, the single-axis longitudinal jaw accelerometer samples mandible acceleration at 32 Hz and has on-board processing that detects jaw motions using an amplitude threshold of 0.3G and minimum separation of 0.5 s and records the number of these detected signals (as a count from 0 to 10) for every 5 s window (Adachi et al., 2017; Naito et al., 2013, 2017). This subset of seals, hereafter referred to as Kami seals, were used to investigate foraging behavior in association with dive profiles and low-oxygen zones. Only the jaw motion events that occurred deeper than 100 m were used to avoid noise in the acceleration data at the surface unrelated to feeding (Naito et al., 2017).

Data processing and statistical analyses were conducted in R (version 4.2.2; R Core Team, 2022) and MATLAB R2022b. Argos and GPS locations were filtered and processed using the aniMotum R package (version 1.1-04), which uses a continuous time state-space model that incorporates location error estimates when available to predict locations at evenly spaced time steps (Jonsen et al., 2023), in our instance, on an hourly basis. Geographic locations for each dive were interpolated from these hourly locations based on the start time of the dive. Solar elevation was calculated for each dive using the SolarAzEl MATLAB function (Koblick, 2023) and the start time and location of the dive and used to determine daytime (solar elevation ≥ 0°), nighttime (solar elevation < -6°), and twilight (-6° ≤ solar elevation < 0°) dives.

Depth data were zero-offset corrected and processed using a custom-written toolbox in MATLAB (Costa et al., in prep). Individual dives that were deeper than 15 m and longer than 32 s and occurred between surface intervals were detected. The bottom phase was defined by a change in the descent and ascent slope that occurs deeper than 50% of the maximum dive depth where the vertical speed (calculated as distance over time) becomes less than 20% of the vertical speed calculated from the descent and ascent portion, respectively, up to 50% of the maximum depth. The following dive summary metrics were calculated for each dive: dive start time, dive duration, maximum dive depth, descent phase duration, descent rate, bottom phase duration, ascent phase duration, ascent rate, post-dive interval duration.

Elephant seals perform drift dives in which they stop actively swimming and passively drift, which could function as time to digest food or sleep (Crocker et al., 1997; Kendall-Bar et al., 2023). Drift dives have been used to estimate changes in at-sea body condition (leaner seals are less buoyant and drift downward while fatter seals are more buoyant and drift upward) and thus foraging success across several days (Biuw et al., 2003; Robinson et al., 2010). Drift dives were identified using a stepwise filtering approach following previously used criteria (Adachi et al., 2023; Dragon et al., 2012; Gordine et al., 2015). Vertical speed was calculated from the gaussian-smoothed time-depth data by using the function gradient in MATLAB. Acceleration was calculated similarly from the vertical speed. For dives deeper than 100 m where residual air in the lungs is unlikely to affect buoyancy, drift phases within dives were isolated by finding segments where vertical speed is |0.05-0.6| m/s. If multiple segments met these criteria within a dive, the longest segment was taken to be the putative drift phase. The drift phase also had to meet the following criteria: (1) longer than 3 minutes, (2) more than 20% of the dive duration, and (3) low variance (|acceleration| < 0.05 m s^{-2} and variance < 0.005). For drift phases that met these conditions, a drift rate was calculated as the slope of the best fitting linear regression line.

To obtain a daily drift rate, a cubic spline was fit to the drift rates after filtering if the seal had at least 50 drift dives. Drift rates were retained for spline fitting if the drift phase met a combination of duration and linearity criteria. For negatively buoyant drift dives, the drift phase had to be longer than 40% of the dive duration or longer than 30% of the dive duration and the mean squared error of the linear regression was less than 5. Drift phases tend to be shorter during positively buoyant drive dives, so to retain sufficient dives for fitting a spline, the duration criteria was relaxed to 20% of the dive duration but had to have a mean squared error of less than 3. Drift rate data are inherently noisy and the quadratic relationship between drag and velocity results in discontinuities around neutral buoyancy (i.e., drift rate = 0). Prior to fitting the spline, the drift rate data were filtered further to remove noisy data and square transformed (while maintaining its original sign) to reduce the impact of this effect (Biuw et al., 2003). Median drift rates calculated from sets of 3 or more consecutive drift dives were used to calculate an overall median drift rate for negatively buoyant drift dives and positively buoyant drift dives (if present, generally for post-molt trips). Drift rates that were greater than three median absolute deviations from the overall median were flagged as outliers. If sets of 3 or more consecutive drift dives did not exist, the overall median was calculated from all the drift dives. After visually inspecting the fitted splines, outliers were excluded on a case-by-case basis by applying slight modifications to the code. These modifications included adjusting when the transition to positive buoyancy occurred and/or adjusting the overall median by only including values of the appropriate sign.

The cubic smoothing splines were fit to the filtered and square transformed drift rate data using the ss function in the R package npreg (version 1.0.9; Helwig, 2022) with knots spaced evenly at 9-day intervals starting with the timestamp of the first drift dive that met all criteria detailed above (Figure 4.1). This interval was chosen as a compromise between smoothness and overfitting and spans the temporal scale required to detect a biologically realistic change in drift rate (Biuw et al., 2003; Robinson et al., 2010). Estimated daily drift rates were calculated using the predict function on the resulting spline model and used to calculate a daily change in drift rate (Figure 4.1). The squared estimated daily drift rate values were then back-transformed for further analyses (described in section 4.3.3 and 4.3.4).

4.3.2 Oceanographic data

Based on the location and timestamp (month and year) of each dive, profiles of monthly mean dissolved oxygen at 75 depth levels between the surface and 6,000 m deep were extracted from the global biogeochemistry hindcast model (GLOBAL_MULTIYEAR_BGC_001_029, https://doi.org/10.48670/moi-00019) at a 0.25° resolution provided by the E.U. Copernicus Marine Service Information (CMEMS, downloaded on May 2022). Previously defined thresholds of 0.5 ml l^{-1} (22 mmol m^{-3}) and 1.4 ml l^{-1} (63 mmol m^{-3}) were used to determine the horizontal and vertical extent of the oxygen minimum zone (OMZ) and oxygen limited zone (OLZ), respectively (Gilly et al., 2013; Hofmann et al., 2011; Levin, 2018). Areas where oxygen levels remain above 1.4 ml l^{-1} (63 mmol m^{-3}) were considered high-oxygen (HighDO). To distinguish between horizontal and vertical analyses of dissolved oxygen (DO) levels, we will use the term “DO region” when referring to DO levels in the horizontal dimension and “DO zone” when referring to DO levels in the vertical dimension.

Due to the seals' large spatial coverage of an ocean basin with variable oceanography, the North Pacific was divided into three biogeographic ecoregions: California Current (CC), Central North Pacific (CNP), and Subarctic Pacific (SAP). Sutton et al. (2017) defined these ecoregions based on several characteristics of the mesopelagic zone, including dissolved oxygen. We characterized the average depth of the OLZ and OMZ as well as the OLZ thickness that seals encountered in each of these ecoregions based on their dive locations. Bathymetry was extracted from GEBCO's gridded bathymetry dataset (on a 1/15 arc-second interval grid) using the interpolated dive locations and error estimates to verify whether diving behavior was topographically constrained (*GEBCO 2023 Grid*, 2023).

4.3.3 Descriptive analyses

To assess how much seals are diving into DO zones, an index was calculated for each dive where the depth of the upper boundary of the OLZ is subtracted from maximum dive depth and divided by the thickness of the OLZ (defined by its upper and lower boundary, where its lower boundary is the depth of the OMZ):

$$DO\ Zonation\ Index = \frac{Max\ dive\ depth - \ OLZ\ depth}{OLZ\ thickness}$$

This index, referred to as the DO zonation index, indicates how maximum dive depth compares to the OLZ and OMZ depths since the depth and thickness of the OLZ will determine the depth of the OMZ while also accounting for the variable depths of these layers across the North Pacific. Index values are less than 0 if the dive is above the OLZ (or in HighDO), between 0 and 1 if the dive is within the OLZ, and greater than 1 if the dive reaches the OMZ (Figure 4.2). Oxygen levels sometimes increase after reaching a minimum, resulting in a second OLZ layer beneath the OMZ. In these situations, a DO zonation index of 1.5, for example, would indicate the dive is within the OMZ but the dissolved oxygen levels would suggest OLZ. We quantified the discrepancy between DO zones categorized to match the index versus actual oxygen levels and found that the difference was nonexistent or negligible for most seals (Figure 4.S1). Only 3 PB seals and 5 PM seals had >25 dives where the categorization differed between the two methods, which accounts for a small proportion of total dives.

The absence of an OMZ layer in OLZ regions makes it difficult to determine a comparable OLZ thickness; therefore, the DO zonation index was only used to analyze the use of low-oxygen zones when OMZs are present. To determine if seals are also foraging in these zones, an index was calculated using the same approach for the Kami seals but the max dive depth was replaced by either the median depth of jaw motion events per dive or the depth of each jaw motion event. We also determined the average proportion of Kami signals in each DO zone per ecoregion and individual to compare individual foraging effort and strategies across ecoregions.

The density distributions of the DO zonation index at a population level were compared across the three ecoregions. To separate seals with different foraging migration strategies (Kienle et al., 2022; Robinson et al., 2012), we determined the number of seals with dives in each ecoregion using the VennDiagram package (version 1.7.3; Chen, 2022) in R (sample sizes provided in Table 4.S2). For the subset of seals in each overlapping area of the Venn-diagrams, density distributions of the

DO zonation index were estimated using a gaussian kernel with a bandwidth of 0.1 and weighted by each seal's total number of dives within each region to equalize the contribution from each seal.

To examine the temporal and spatial patterns in their use of OMZs, heat maps were created by averaging the index values across all the seals for each hour on each day of the year. This was done for all ecoregions combined and each ecoregion separately. Maps depicting the 2D kernel density distributions of dives in each oxygen region and zone were created using the MATLAB function kde2d (Botev, 2023) to provide more spatially explicit visualizations.

4.3.4 Statistical analyses

Statistical analyses were conducted separately for the post-breeding and post-molt foraging trips because the different physiological demands and timing constraints imposed on each trip, in addition to the different oceanographic conditions, will influence foraging effort and thus foraging success (Robinson et al., 2012). For the trip level model, we excluded seals that were skip-breeders (i.e., not seen with an offspring during the breeding season after returning from the PM trip; n = 15, or 12% of PM seals) because their physiological demands during the trip and energy gain are not comparable to breeders (in part due to shorter trip, Figure 4.S2). Since northern elephant seals exhibit diel diving patterns, daytime and nighttime dives were also considered separately when analyzing at a finer resolution than the daily level. When calculating average metrics across dives (e.g., average DO at depth of Kami signals), we excluded dives occurring during civil twilight ($-6 \leq$ solar elevation < 0) when seals are likely transitioning from their deep daytime diving to shallow nighttime diving as they follow the diel scattering layer or use that time to digest and rest (Beltran et al., 2021; Crocker et al., 1997; Kendall-Bar et al., 2023). To focus our analyses on putative foraging dives that occur in the mesopelagic, drift dives were excluded as well as dives <200 m over the continental shelf (where the bathymetry was <200 m) at the beginning and end of the trip. For most ecoregion-DO region combinations, over 80% of dives were retained for analysis (Table 4.S1). The exception was CC dives that were either in HighDO or OLZ regions because these occur close to the coast.

For all statistical modeling, the data were checked for collinearity using diagnostic plots and for extreme outliers ($Q_{1,3} \pm 3\times$IQR) by first using the identify_outliers function in the rstatix package (version 0.7.2; Kassambara, 2023) in R and then visually inspecting before deciding to remove them. For example, most of the extreme outliers identified and excluded for the 6-day bout-level model were due to the discontinuity that occurs in their drift rate when seals approach neutral buoyancy. Data points identified as outliers by q-q plots or with standardized residuals > |3| were examined and removed if determined to be an outlier or influential data point.

We fit separate linear models to examine foraging effort and foraging success. Foraging effort was compared across DO regions and ecoregions at a daily level while controlling for the differing availability of OMZ in each ecoregion. Foraging success was modelled at the trip level and at a finer scale (6-day period) to investigate the influence of the oxyscape at two spatiotemporal scales. After fitting each model (further described below), the model residuals were inspected for normality, homoscedasticity, and linearity. When diagnostic plots revealed heteroscedasticity, we tested different variance structures to account for different variances across groups and used the variance structure whose model had the lowest corrected Akaike Information Criteria (AICc). When comparing candidate models with the same variance structure (if any) and different fixed effects, we refit the models using maximum likelihood estimation. Candidate models containing all or a subset of the covariates with or without interactions were selected *a priori* based on ecological interpretability and compared using AICc to find the highest ranked model. If the ΔAICc < 2, we selected the best model by taking the AICc weight, R^2, and parsimony into account.

For the daily foraging effort model, we used the subset of seals with Kami Kami loggers and fitted a linear model to the number of dives per day with Kami signals as a metric of foraging effort. For each Kami seal, we quantified the number of dives per day with Kami signals that occurred in each ecoregion-DO region combination. The model included two categorical variables—Ecoregion and DO region—and a continuous variable that quantified the proportion of dives in OMZ regions for each ecoregion to account for the differing availabilities of OMZ and OLZ regions in each ecoregion (e.g., CC has relatively little OLZ regions). Model diagnostic plots suggested heteroscedasticity for the PB trip, so we refit this model using generalized least squares estimation with the nlme package (version 3.1.160;

(Pinheiro et al., 2022) in R and included the variance structure varIdent with each categorical covariate separately and together and compared models using the AICc. For both PB and PM models, we compared models with and without interactions for the fixed effects using AICc to select the highest ranked model (Table 4.S3).

To determine if individual differences in the utilization of OMZs are reflected in the seals' foraging success, we modelled two metrics of body condition at different spatiotemporal scales. First, we focused on the trip level and used energy gain (in MJ) as the response variable in a linear model. Although the estimation of energy gain across the trip has more potential sources of error, we chose this metric over mass gain as the better measure of body energy reserves and net success of foraging because energy gain takes into account the relative proportions of lean and fat tissue while mass gain does not. To examine if and how their horizontal use of DO regions affects their energy gain, we used the proportion of dives in OMZ regions as a predictor variable. We also included as predictors percent adipose at departure, number of days at sea, and daily distance traveled (sum of both horizontal and vertical distances) to account for other factors that may influence energy gain. Predictor variables were scaled to account for the large range in magnitudes. We limited the analyses to 307 complete diving records from 270 seals with mass data (from which energy gain was calculated). Due to a subset of seals with repeat deployments in the same foraging trip in different years (30 PB seals and 7 PM seals), we ran the model twice and randomly selected one of the deployments in the first run and used the other deployment (or randomly selected one of the two other deployments if a seal had three) for the second model run to confirm that the results were not dependent on the deployments used in the model and gauge the amount of variability among years (since resampled seals were insufficient to include year as a random effect).

Second, we did a finer-scale analysis and modelled short-term foraging success using as the response variable the change in drift rate across a 6-day window, which is the time required to detect a biologically significant change in drift rate (Biuw et al., 2003; Robinson et al., 2010). Positive changes in drift rate indicate enhanced body condition since a seal with more body reserves will become more buoyant. However, because a negative change in drift rate could result from either a loss of adipose tissue or a gain of lean tissue (Robinson et al., 2010), we only interpreted positive changes in drift rate. We used the subset of seals with Kami Kami loggers (n = 52) and identified 6-day periods spent in a DO region within an ecoregion. For each 6-day period, the average DO level at the depth of all the Kami signals was included as the primary variable of interest with DO region and ecoregion as categorical covariates. We used a linear mixed model to examine the relationships between the change in drift rate and the DO levels at the depths of their foraging behavior with individual seal as a random effect. To account for changes in foraging effort throughout the trip, we also included the average number of Kami signals per dive and when during the trip the 6-day period occurred (as a percentage of total trip). A linear and a quadratic term for the percent of trip was included since a nonlinear relationship was observed with the change of drift rate (Figure 4.S3). Only one Kami seal had a repeat deployment in the same season, so the shorter of its two deployments (in terms of percent of total trip duration) was excluded.

For both foraging success models, we compared the highest ranked model to the model without the variable associated with DO region or levels (i.e., proportion of dives in OMZ in the trip-level model and average DO at Kami signals for the finer-scale model) to test for main effects. We also compared the highest ranked model to the null model, which for the short-term foraging success model, would provide the relative explanatory power of individual differences.

4.4 Results

4.4.1 Oxyscape encountered by seals

The OMZ was shallowest in the CC, followed by the SAP, and deepest in the CNP (Table 4.1 & Figure 4.3). The same pattern existed for OLZ depths. The OLZ layer in OMZ regions was the thinnest in the CC and thickest in the SAP. These patterns across ecoregions were consistent for both seasons. When comparing between seasons within an ecoregion, OLZ and OMZ depths were deeper (on the order of tens of meters) during the post-molt trip, with the exception of the OLZ depth in OLZ regions in the CC. Some interannual variability in OLZ and OMZ depths was present, and some shoaling of the OLZ is apparent in the CNP in OLZ regions across 2004-2020 (Figure 4.S4). Maps depicting the OMZ depth and OLZ depth and thickness across the North Pacific for a particular month during each foraging trip show these patterns in a more spatially explicit visualization (Figure 4.4).

4.4.2 Three-dimensional use of low-oxygen zones

All seals examined in both post-breeding (n = 205) and post-molt trips (n = 159) spent part of their trip in OMZ regions (Figure 4.5). A total of 768,648 dives for the PB seals and 1,414,781 dives for the PM seals were analyzed as putative foraging dives, of which 74.7% and 47.2% were in OMZ regions, respectively (Table 4.S1). Most dives in OMZ regions occurred in the CC followed by the CNP. Dives in OLZ regions (where no OMZ zone was present) occurred mostly in the SAP followed by the CNP. Kernel density maps of dives in DO regions and DO zones depict that they dive into OLZ zones throughout most of their spatial range. However, dives into the OMZ occur mainly in the CC (Figure 4.6), in part due to the availability of OMZs across their range (Figure 4.5).

Dive depth distributions across ecoregions and DO regions showed strong diel patterns with deeper daytime dives except for OLZ regions in the CC (Figure 4.7). Both daytime and nighttime dives in OLZ regions in the CC were much shallower than those in the SAP and CNP. Unlike the CC, median dive depths in the CNP and SAP were similar. Median dive depths in HighDO regions were much shallower in all ecoregions, ranging between 94-279 m for daytime dives and 70-235 m for nighttime dives (Table 4.S2). Although HighDO regions only occur coastally (Figure 4.6), these dives are unlikely to be constrained bathymetrically because we excluded all dives over the continental shelf. Dives were consistently deeper in the CNP with daytime median depths of 641-699 m and nighttime median depths of 463-581 m. In the SAP, median daytime and nighttime dive depths were 613-619 m and 452-527 m, respectively (excluding shallower dives in HighDO regions). Dives were slightly deeper during the PB trip except for daytime dives in the SAP (Table 4.S2).

Bimodal depth distributions were common with one main peak and a second smaller peak. The two peaks were of more comparable densities for the PB trip for the following: nighttime dives in the SAP, daytime dives in HighDO regions in the SAP, nighttime dives in the CNP, and daytime dives in OLZ regions in the CNP. The distribution of nighttime dives in OLZ regions in the CNP during the PB trip was the only clear trimodal distribution. Dive depth distributions of dives reaching each DO zone show that, as expected, dives reaching the OLZ zone are generally shallower than dives reaching the OMZ zone in each ecoregion. Interestingly, in the SAP, the peak depth densities for dives reaching the OLZ and OMZ zones have high overlap (Figure 4.7), which could be attributed to the spatially variable oxyscape in the SAP (Figure 4.4).

The density distributions of the DO zonation index for each overlapping area of the ecoregion Venn-diagrams for each season were similar for seals that went into all three ecoregions and for seals that went into two ecoregions—the CC and either the CNP or SAP (Figure 4.S5). Therefore, these were combined into one figure. The seals that only had dives in the CC (PB: 7 seals, PM: 1 seal) were plotted separately. All the seals with dives only in the CC had complete records, so their sole use of the CC is not due to missing data. The distributions show that seals dive into the OMZ mainly while in the CC, and slightly more during the daytime; however, dives into the OLZ in OMZ regions are just as common in this ecoregion (Figure 4.8). This contrasts with the CC seals where most dives reach the OMZ during both daytime and nighttime. When in OMZ regions of the SAP and CNP, seals mostly remained in HighDO zones during the nighttime. More nighttime dives reached the upper OLZ during the PB trip compared to the PM trip. Nighttime dives in the CNP during the PB trip have a bimodal distribution with the shallower peak matching the peak of the PM trip. Compared to the CNP, a greater density of dives reached the OLZ in the SAP, especially during the daytime where peak densities occur just beneath the OLZ boundary for both trips.

Heat maps of the DO zonation index match the patterns of the density distributions and provide greater detail of the temporal patterns (hourly and daily across the entire year) but, unlike the density distributions, relative densities are not represented. The heat map with all ecoregions combined depicts that, at a population level, seals use low-oxygen zones more during the daytime than nighttime, and this diel difference is especially true for the post-molt trip (Figure 4.9). PB seals use the OMZ during the daytime but generally at the beginning and end of the trip whereas PM seals primarily use the upper OLZ during the daytime throughout the trip. Slight deviations from this occur during late June when fewer dives in the early morning reach the OLZ as well as during December when daytime dives reach deeper into the OLZ and more nighttime dives reach the upper OLZ.

To better examine spatial patterns alongside temporal patterns, heatmaps were created for each ecoregion. Most dives reaching the OMZ occur in the CC, where seals primarily use the OMZ during the daytime and OLZ during the nighttime. However, not many seals remain in the CC resulting in low sample sizes for portions of the trips as denoted by the grayed-out days in the heatmaps. The temporal patterns in the CNP and SAP are similar—most daytime dives reach the OLZ while nighttime dives remain in HighDO. However, more use of the OLZ zone occurs in the SAP.

During the PM trip, there is an increasing trend in the use of low-oxygen zones as the trip progresses in all ecoregions. In the CNP, this results in daytime dives transitioning from using HighDO waters during the first 1-2 months to the OLZ for the rest of the trip. In the SAP, seals transition to using the OLZ zone more during nighttime dives in the last 1-2 months of the trip. Thus, the deviations that were apparent in the combined heatmap (described above) occur in the CNP and SAP, respectively.

These spatiotemporal patterns in the use of low-oxygen zones could be either due to the seals changing their diving behavior relative to the low-oxygen zones, or alternatively, due to the changing DO profiles throughout the North Pacific. To gain insight into which may be more important, we created similar heatmaps for dive depth and OLZ depth across the three ecoregions (Figure 4.9). Across all ecoregions, the progression of greater low-oxygen zone use during the PM trip aligns with the progression of deeper diving as shown in the equivalent heatmaps of dive depth. In the CNP, the OLZ depth is constant, which suggests the temporal patterns in the DO zonation index for this region are primarily driven by the seal's diel diving behavior.

In contrast, the OLZ depth in the SAP transitions from shallower to deeper and back to shallower during the PM trip. The deeper nighttime diving during the last 1-2 months of the trip noted earlier coincides with a shallower OLZ depth and results in greater use of the OLZ. In this instance, both factors seem to be contributing to the observed index values.

In addition to the depth of the OLZ, its thickness will determine whether the OMZ is easily reachable by the seals given their physiological capacity for diving. Scatterplots of individual dives plotted against the OLZ depth and thickness at each dive location suggests that seals used OMZ zones when the OLZ is shallower than ~500 m and less than 400 m thick, with a negative relationship between OLZ thickness and depth (Figure 4.10A). When the OLZ is deeper than ~500 m, most dives remain in HighDO waters and there is a positive relationship between OLZ depth and thickness. The trend is similar for both daytime and nighttime dives, but a shift to using more low-oxygen zones, mainly the OLZ, when the OLZ is >500 m deep is apparent during daytime. By overlaying the ecoregions on these scatterplots (Figure 4.10C), we again find that most OMZ dives occur in the CC while most HighDO dives are in the CNP. Dives in the SAP are clustered at intermediate OLZ depths where the OLZ is generally thicker.

Similar scatterplots were made denoting dive depth instead of the DO zonation index (Figure 4.10B). While no clear patterns emerged for nighttime dives, daytime dives are deeper when the OLZ is deeper (mostly in the CNP) and shallower when the OLZ is shallower (mostly in the CC). PM dives also tend to be shallower than PB dives, especially at night. By plotting the expected DO zonation index values determined using the overall average dive depth of all seals in OMZ regions across realistic combinations of OLZ depth and thickness (Figure 4.11), we found the same general pattern as the DO zonation index scatterplots show, which indicates that, at a population level, the seals use low-oxygen zones when they are reachable considering their routine diving behavior.

4.4.3 Foraging behavior relative to low-oxygen zones

Kami seals (n = 52) exhibited similar patterns in their diving behavior relative to low-oxygen zones, indicating that this subset of seals is representative of the entire population (Figure 4.S6). Scatterplots of the median depth of Kami events during each dive against OLZ depth and thickness were similar to the patterns of maximum dive depth except median Kami depths were slightly shallower overall (Figure 4.12). The number of Kami signals per dive were also examined against OLZ depth and thickness. No clear patterns emerged except for slightly fewer Kami signals per dive during PB nighttime dives where the OLZ is shallow and thin (i.e., in the CC) and easier for the seals to reach.

Bar plots of the proportion of Kami signals in each DO zone by individual seal and ecoregion showed that the seals' foraging behavior in the SAP and CNP are more similar compared to the CC for both trips (Figure 4.13). Across all seals, the majority of daytime Kami signals in the SAP and CNP occurred in the OLZ followed by HighDO for both trips. However, the proportion was more evenly split between OLZ and HighDO for the CNP, particularly for the PM trip. The majority of nighttime

Kami signals in the SAP and CNP occurred in HighDO, except for during the PB trip in the SAP where a larger proportion of nighttime Kami signals occurred in the OLZ (Table 4.2). The patterns were different in the CC with the majority of daytime Kami signals occurring in the OMZ while nighttime Kami signals were in the OLZ for both trips. All seals while in the CC had Kami signals in the OMZ and generally a higher proportion during the daytime (Figure 4.13). In the SAP, only 2 of 13 PM seals had Kami signals in the OMZ compared to 16 of 32 PB seals (Figure 4.13), but this difference could be due to the smaller sample size. Within an individual seal, the proportions of Kami signals in each DO zone varied across ecoregions. However, seals that had higher proportions in the OMZ while in the CC also tended to have higher proportions in the SAP and CNP (e.g., PB TOPPIDs 2011018, 2012006, 2013008, and PM TOPPID 2013029).

The models focusing on foraging effort for each trip and the parameter estimates are shown in Table 4.3. For the PM trip, there was no statistical difference in the number of Kami dives per day between ecoregions and DO regions ($F_{4,47} = 0.57$, $p = 0.687$, adj. $R^2 = -0.035$; Figure 4.14). In contrast for the PB trip, both ecoregion and the interaction between ecoregion and DO region were significant predictors of the number of Kami dives per day. The CC had fewer Kami dives per day ($\beta = -12.00$, $p < 0.001$) compared to the SAP, while the CNP was not significantly different from the SAP ($\beta =-0.96$, $p = 0.606$). OLZ regions had slightly higher but nonsignificant number of Kami dives per day than OMZ regions ($\beta = 3.08$, $p = 0.146$). The relationship between number of Kami dives per day and the proportion of dives in OMZ regions (Figure 4.15) was positive for the PB trip ($\beta = 4.62$) and negative for the PM trip ($\beta = -2.96$), but both were nonsignificant ($p = 0.068$ and $p = 0.610$, respectively).

4.4.4 Foraging success relative to low-oxygen zones

Trip-level summary statistics relevant to energy expenditure and foraging success are provided in Table 4.4. The resulting patterns for the two trip-level foraging success models using the same individual seals but different deployment years for those with repeat deployments were comparable for the DO-relevant variable, indicating that the overall conclusions are not dependent on which individual trips are used in the model. We report results from the first model run (Table 4.5) and the second model's results are provided in Table 4.S4. Model comparison using the AICc suggested retaining all variables with no interactions for the PM trip model and dropping *DaysAtSea* for the PB trip model (Table 4.S5). Both models had some explanatory power (adjusted R^2 of 0.230 and 0.234 for the PB and PM models, respectively). The proportion of dives in an OMZ region as well as the percent adipose at departure had significant and negative effects on energy gain for both trips (Table 4.5). The other predictors were not consistently significant across both model runs. Models with *propOMZdives* had more support than the reduced model and null models for both trips (Table 4.S6).

In contrast, the variable related to dissolved oxygen in the vertical dimension in the finer-scale model (i.e., average dissolved oxygen levels at the depth of the Kami signals) was not an important predictor of their short-term foraging success for the PB trip ($p = 0.881$) but was marginally important for the PM trip ($p < 0.05$; Table 4.6). However, comparing the highest ranked model determined for each trip (Table 4.S7) to the reduced model without the variable *AvgDOatKami* supported dropping the term for both trips (Table 4.S8). DO region had a significant effect on change in drift rate, with OLZ regions having slightly greater changes in drift rate for both trips ($p < 0.05$ for both trips). Both models had similar explanatory power (PB: marginal $R^2 = 0.307$, conditional $R^2 = 0.337$; PM: marginal $R^2 = 0.245$, conditional $R^2 = 0.299$). A reduced model with only the percent of trip terms and individuals as a random effect explained 28% of the variance for the PB trip, which accounts for the majority of the marginal R^2, but only 11% of the variance for the PM trip. This aligns with the percent of trip variables being significant for the PB trip ($p < 0.001$) but not for the PM trip ($p > 0.5$). For the PM trip, the number of Kami signals per dive also helped explain some of the variance ($\chi^2 = 3.977$, $p < 0.05$).

4.5 Discussion

4.5.1 Availability vs. use of low-oxygen zones

We found that at a population level, female northern elephant seals are not consistently using OMZs throughout their foraging migrations. Rather, their use of OMZs is dependent on seasonal and spatial influences. OMZ regions extend westward from the California Current region until ~180°W, but the latitudinal range decreases (Figure 4.4). The SAP and CNP have proportionally more regions without OMZs and deeper OMZs, when present, compared to the CC. Therefore, the similarity in the seals' low use of OMZs in the SAP and CNP can be partly attributed to the similarity in oxyscapes in these ecoregions as opposed to the CC, where OMZs are present and shallow throughout most of the ecoregion. Seasonal differences in OLZ depth are negligible in the CNP, while seasonal shoaling of the OLZ occurs in the SAP and CC during the PB trip (Figure 4.S7; Paulmier & Ruiz-Pino, 2009). This aligns with the increased use of low-oxygen zones in the SAP and CC during the PB trip (Figure 4.9 & Table 4.3).

In addition to the spatial differences in seasonal changes of the oxyscape, differences in the duration of the two trips influence the oxyscape that seals encounter. PM seals are at-sea for over twice as long as PB seals (Table 4.4). They travel much further west into the North Pacific, where there are fewer OMZ regions and thus have access to OMZ regions for a smaller proportion of their trip than the PB trip (Figure 4.5; Table 4.S1). In contrast, PB seals spent more of their trip in OMZ regions because the PB trip is shorter (Table 4.4), but their vertical behavior also showed greater use of low-oxygen zones. PB seals generally dove deeper, resulting in greater use of OMZs in the CC and OLZs in the SAP or CNP, particularly during the daytime when they dive deeper to reach the deep scattering layer (Figure 4.7). Deeper dives should be easier for seals at the beginning of the trip as they have less body fat and are negatively buoyant (Adachi et al., 2014; Holser, 2020). Unlike the PM trip, seals remain negatively buoyant throughout the entire PB trip (Figure 4.1; Adachi et al., 2014). Therefore, their greater use of low-oxygen zones during the PB trip could result in adopting a more efficient diving strategy. However, seals also had more dives with Kami signals per day during the PB trip than the PM trip, except for in the CC (Figure 4.14). This enhanced foraging effort could compensate for the shorter trip to regain mass lost while fasting during the breeding season. The observation that seals are less selective and have a more variable diet during the PB trip (Goetsch, 2018) supports this hypothesis—they prioritize quantity over quality (i.e., greater energetic content), adopt a generalist approach, and consume prey opportunistically to meet their energetic requirements.

In contrast, seals are less time constrained to forage and regain mass during the PM trip. Yet, females have the additional physiological demand of growing a fetus (if implantation was successful), which has both behavioral and physiological consequences. For example, dive duration increases throughout the PM trip as females increase their body condition and oxygen stores (Hassrick et al., 2007). In the latter half of the trip, dive duration declines in pregnant females compared to non-pregnant females resulting in shorter dives by the end of the trip (Hückstädt et al., 2018). In addition to shorter dive durations, their positive buoyancy at the end of the PM trip would make reaching the depth of the OMZ energetically expensive. Given that their foraging effort steadily declines after the first third of the PM trip (Figure 4.S8), we hypothesize that the PM trip is long enough for seals to regain their mass and have surplus energy to support the growth of their fetus, precluding the need to work harder for prey towards the latter portion of their trip.

Interestingly, we found that seals dove deeper during the night towards the end of the PM trip (Nov-Dec), coinciding with a shallower OLZ in the SAP (Figure

4.9). Thus, seals transitioned from using HighDO zones to the upper OLZ during that time of night. This may be an instance where seals adjusted their diving behavior to preferentially target non-migrating prey in low-oxygen zones when these zones were reachable at their routine diving depths. However, these examples were rare, and generally, the temporal patterns (daily and seasonal) observed in the DO zonation index reflected their diel-diving behavior across a changing oxyscape. As further support, we showed that if the seals dove to a constant dive depth (equivalent to their overall mean dive depth) across varying OLZ depths and thickness, the general patterns we observed in the data are to be expected (Figure 4.11).

4.5.2 Re-examining diet and foraging behavior relative to low-oxygen zones

We found that seals in OLZ regions had higher foraging success—both at the local scale and trip level—than OMZ regions. A diet study using quantitative fatty acid analysis has previously described and attributed regional differences in their diet to the spatial differences in low-oxygen zones across the North Pacific. For example, the study found that seals foraging in the CNP during either trip have the highest ratio of fish to squid but also the lowest degree of diet specialization (Goetsch, 2018). In the CNP, the OLZ is deep (>650 m) and thick (>200 m); therefore, migrating prey that aggregate in the upper OLZ during the day have a longer distance to travel each night to their shallow foraging depths. Seals could dive deep to target slower-moving prey in the upper OLZ during the daytime and/or forage opportunistically on shallower prey, given how deep the OLZ is in this region. The former is consistent with our findings that in the CNP, a greater density of dive depths occurred in the upper OLZ during daytime compared to nighttime (Figure 4.8). Furthermore, a greater proportion of daytime Kami signals occurred in the OLZ (Table 4.2). The latter is consistent with a greater proportion of nighttime Kami signals in HighDO (Table 4.2). This is consistent with video footage of prey capture events showing that seals consumed a higher proportion of cephalopods at shallower depths (up to 400 m) and in offshore waters south of 50°N (Yoshino et al., 2020).

Despite having a greater proportion of energy-rich fish in their diet in the CNP, we found that seals in the CNP did not have greater foraging success. In fact, for the PB trip, no significant difference in short-term foraging success was found between ecoregions. During the PB trip, elephant seals feed (1000-2000 times/day) to attain a positive energy balance (Adachi et al., 2021) and sustain these high foraging rates for most of the trip (Figure 4.S8). Given that this requires spending 80-100% of the day foraging (Adachi et al., 2021), they may be approaching a maximum foraging rate. Seals in the CC had a lower foraging effort (Figure 4.14, Table 4.3), but this may be compensated by a greater proportion of larger non-migrating squid in their diet. Interestingly, most of the variance in short-term foraging success for the PB trip could be explained by the timing of the 6-day period during the trip (Table 4.S8). In addition to the low variability among individuals, this would further support our hypothesis that PB seals function at a physiological ceiling to recover their body condition during this shorter trip.

In contrast, for the PM trip, we found that seals in the SAP had the greatest short-term foraging success (Table 4.6). PM seals foraging in the CC and CNP had lower foraging success, although the difference was not significant for the CNP. This aligns with the fact that PM seals can travel further west into the SAP and CNP and spend more time in OLZ regions, which seems to have the greatest and most consistent effect on short-term and trip-level foraging success. Interestingly, a marked transition to bimodal diving behavior with increased deep nighttime dives and slower transit rates is evident when seals transition into the SAP (Figure 4.16). We hypothesize that a strong association between prey and DO levels in this area leads to a more predictable prey patch for seals to exploit. Although less common, we also found examples where a seal's diving behavior tracked the OLZ as it became shallower (around early October in Figure 4.16). This aligns with our modelling results showing that DO levels at their foraging depths account for some, albeit a small amount, of the variance in their foraging success during the PM trip. The effect of DO levels was positive in OMZ regions (i.e., higher oxygen predicted greater foraging success) and negative in OLZ regions (Figure 4.S9). Therefore, under less time constraints, PM seals may adopt different foraging strategies in different DO regions based on how prey are vertically distributed.

For example, targeting non-migrating prey that seek refuge in low-oxygen zones (Roberts et al., 2020) would be easier when the low-oxygen zones are shallower (e.g., in the CC). Indeed, Goestch (2018) showed that the elephant seals' diet in each ecoregion differed during the PM trip, with non-migrating prey driving those differences. As expected, we found that in the CC the majority of Kami signals occurred in the OMZ during daytime (Table 4.2). However, seals foraging in CC had lower foraging success on average than in SAP or CNP during the PM trip (Table 4.6). Therefore, the relative ease of reaching non-migrating prey in the OMZ in the CC did not enhance their foraging success. This is further supported by Kami seal 2013029, which, compared to other PM Kami seals, had the largest proportion of Kami signals in the OMZ while in the CC but had the third lowest energy gain (Figure 4.13) despite having similar or greater number of Kami signals per day (Figure 4.S10). The greater number of Kami signals could be interpreted as more prey capture attempts or more effort required to ingest larger prey. The former would explain this seal's low energy gains, while the latter would suggest non-migrating prey in the CC are less energetically rich than those in SAP and CNP, although both are plausible (i.e., not mutually exclusive explanations).

Interestingly, a PB Kami seal (2014015) who spent its entire trip in the CC had the highest energy gain of all Kami seals (Figure 4.13). This aligns with Adachi et al. (2021), who found that three females who foraged coastally, likely on demersal prey, had greater foraging success. Unlike PM seal 2013029 who foraged mostly in the OMZ zone while in the CC, PB seal 2014015 foraged primarily in the OLZ zone. Unexpectedly, seal 2014015 had fewer Kami signals per day compared to other PB seals (Figure 4.S10). These differences in energy gain could also be attributed to the time spent in the SAP by seal 2013029. Performing a diet analysis on such seals with different strategies in the same ecoregions could reveal whether different prey or a high degree of specialization in their diets could explain their differing foraging success. Such differences in foraging strategy would not be observable when analyzing population-level patterns, thus emphasizing the need to investigate individual variability in future work.

4.5.3 Role of oceanographic features for top predators

Given the hypothesis that OMZs should aggregate prey seeking refuge from water-breathing predators and that seals would be advantaged targeting these metabolically suppressed prey, we expected to find higher foraging success in OMZ regions. Surprisingly, we found that seals in OLZ regions had higher foraging success—both at the local scale and trip level—than OMZ regions. At the trip level, energy gain was negatively correlated with the proportion of dives in OMZ regions for both trips (Table 4.5), suggesting that spending a greater proportion of time in OLZ regions is energetically beneficial despite having to travel further to reach these regions. When examining foraging success at a local scale, seals foraging in OLZ regions also had greater short-term foraging success, and there was a weak but significant effect of DO levels at feeding depths but only for the PM trip. For the PB trip, most of the variance explained by the model was accounted for by the day of the trip, suggesting that the scale at which low-oxygen zones influence foraging success differs for the two trips. For the PB trip, the effects are only at the landscape scale (i.e., oxyscape), while for the PM trip, they are at the patch or regional (i.e., ecoregions) scale (*sensu* Senft et al., 1987).

Interestingly, the gyre-gyre boundary is located near the OMZ-OLZ boundary (i.e., where the horizontal extent of the OMZ ends). It is unclear what happens to vertical prey distribution at such a boundary. While the gyre-gyre boundary and low-oxygen zones are more stable features with only slight seasonal variability, the Transition Zone Chlorophyll Front (TZCF) shifts substantially across seasons. During the summer months of the PM trip, the TCZF is at its northernmost extent (Ayers & Lozier, 2010) and coincides with the gyre-gyre and OMZ-OLZ boundaries. Thus, changes in foraging success at this location are likely due to the interaction of all these features and their influence on prey distribution and patchiness. During the PB trip, there is less overlap between the TCZF and gyre-gyre boundary because the TCZF migrates southward (Ayers & Lozier, 2010). The PB trip is too short for seals to reach the gyre-gyre boundary, which also limits the time they can spend in OLZ regions. In contrast, the TCZF is more reachable since it has shifted further south into the CNP. The sharp chlorophyll gradient at this front, along with the mixing of waters from the subarctic and subtropical gyres, creates a productive area known as the North Pacific Transition Zone that is a hotspot for several migratory marine megafauna, including tunas, turtles, albatross, and seals (Nishizawa et al., 2015; Polovina et al., 2001, 2017). This could explain why seals foraging in the CNP had slightly greater foraging success during the PB trip.

Understanding how prey distribution and abundance change at the gyre-gyre boundary with the shifting TCZF would provide greater insight into the features that impact their foraging success at the landscape level (Saijo et al., 2017). Examining prey distribution at the OMZ-OLZ boundary could also provide foresight into what may happen at boundaries where OMZs are expanding. Is there horizontal displacement of species across this boundary that are seeking more favorable oxygen conditions? Or, perhaps this boundary attracts species that seek refuge in OMZs but would have the option of migrating horizontally or vertically to higher oxygenated waters to reoxygenate.

4.5.4 Population patterns vs. individual strategy

In this study, we focused on describing adult female northern elephant seals' use of low-oxygen zones at the population level. We found that seals do not dive into the OMZ as much as we expected across their foraging migration. We predicted that seals would take advantage of larger non-migrating prey or metabolically suppressed prey in the OMZ; however, the costs of diving deep to reach the OMZ and the relative densities of prey at their daytime and nighttime depths determine the most energetically efficient foraging strategy at the patch level. Variability among individuals in diving capabilities and energetic requirements must also be considered when determining the most efficient strategy and explaining differential foraging success. Given the low variance explained by our foraging success models ($R^2 < 0.35$), investigating other intrinsic and extrinsic predictors is warranted.

Given the individual variability, we suspect that intrinsic factors, like age and body size, affect how much an individual uses low-oxygen zones. Naito et al. (2017) hypothesized that larger seals forage and depend on larger prey in the OMZ. They found that larger seals had a greater number of dives >800 m with higher feeding rates at depths >700 m compared to smaller seals and lower feeding rates at shallower depths (500-700 m). Although that study did not compare dissolved oxygen levels at the depths of individual dives, they determined that dives >800 m were in OMZs throughout most of the spatial extent of the PB trip. These deep foraging dives were V-shaped with little to no bottom time, suggesting that seals search for prey vertically rather than horizontally in this zone. Naito et al.’s study focused on 15 PB elephant seals. A quick examination of the larger dataset across both seasons reveals this deep-diving behavior is more common among PB seals than PM seals (Figure 4.17), but the relationship with body mass is less clear (Figure 4.S11) and warrants further investigation. Furthermore, we caution the use of a depth threshold as a metric of OMZ utilization given the variable oxyscape across the North Pacific. As an example, seal TOPPID 2011018 used the OMZ consistently along the coast (43% of dives) but only 5% of dives were >800 m (Figure 4.18). In contrast, seal TOPPID 2016002 had 12% of dives >800 m but did not use the OMZ as much (<5%) during its pelagic migration (Figure 4.18). Interestingly, seal TOPPID 2011018 had over 8 times the number of dives >1000 m (42 dives vs. 5 dives for seal TOPPID 2016002). Expanding Naito et al.’s study to a larger sample size and incorporating dive-specific dissolved oxygen levels may reveal what proportion, if any, of the population are OMZ specialists, and what intrinsic factors may be driving that strategy.

In addition to further investigating individual variability in the vertical dimension, examining the consistency of low-oxygen zone use within individuals would further support whether individuals could be considered OMZ specialists. Some seals that have been tracked multiple times have demonstrated high migration route fidelity (Costa et al., 2012; Horton et al., 2017). The degree of this fidelity varies among the population and leads to divergent strategies—high-fidelity individuals have a moderate reward with low risk. In contrast, low-fidelity individuals take greater risks for possibly greater rewards (Abrahms, Hazen, et al., 2018). In stable environmental conditions, high-fidelity individuals will do better on average, whereas low-fidelity individuals do better during unpredictable conditions due to their plastic behavior. If this fidelity translates into a consistent use of low-oxygen zones, this could result in different implications for these seals as the ocean's oxyscape changes.

4.5.5 Consequences of future deoxygenation

The results of this chapter establish a baseline understanding of their current use of low-oxygen zones on both foraging trips and how it differs across the North Pacific. The ocean is projected to lose 3-4% of its oxygen by 2100, primarily in the top 1000 m where most life occurs (Bopp et al., 2013). The consequences will not be straightforward—some regions will be more impacted than others. Some species will experience direct effects, while others will be indirectly affected. Northern elephant seals forage in the North Pacific, where oxygen loss is predicted to be significant. As ocean deoxygenation continues, we will be able to track changes in their use of these zones and how it impacts their foraging success since their prey will be directly affected by lower oxygen levels. If the OMZ continues to shoal, the depth at which the deep scattering layer resides during the daytime will become closer to the surface. This may increase elephant seals' foraging success as they could reach the same prey at shallower depths. On the other hand, our results suggest that if OMZs continue to expand horizontally, their foraging success may decrease when fewer OLZ regions are available. These changes in the location and volume of OMZs will alter prey composition and vertical distribution, and thus change species interactions since different species have different low-oxygen tolerances.

Since higher trophic levels are important indicators of ecosystem health (Hazen et al., 2019), assessing how northern elephant seals are affected by OMZ shoaling could lead to better predictions of the ecological implications of ocean deoxygenation. Our findings suggest that elephant seals are a great species to deploy animal-borne dissolved oxygen loggers (e.g., Bailleul et al., 2015; Coffey et al., 2020; Coffey & Holland, 2015; Logan et al., 2023) to track changing oxygen levels since their diving behavior is not directly hindered or altered by low-oxygen zones. Due to the many societal benefits that derive from these OMZ regions (e.g., fisheries, aquaculture, biodiversity and tourism, carbon sequestration), we must enhance our ability to predict the magnitude and effects of ocean deoxygenation in an attempt to better mitigate its impacts (Garçon et al., 2019; St. John et al., 2016).

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Table 4.1 Median values for the OLZ depth, OMZ depth, and OLZ thickness encountered by seals on their dives during the post-breeding (PB) and post-molt (PM) trips for each DO region-ecoregion combination. Dives on the continental shelf were excluded. MAD = median absolute deviation.

Trip	DO region	Ecoregion	No. Dives	OLZ depth (m)		OMZ depth (m)		OLZ thickness (m)	
				Median	MAD	Median	MAD	Median	MAD
PB	OLZ	CC	4673	147	20			1369	22
		CNP	48503	664	28				
		SAP	170204	553	80				
	OMZ	CC	310607	323	124	539	87	211	64
		CNP	173699	661	50	915	134	256	81
		SAP	175799	562	120	852	116	302	95
PM	OLZ	CC	3728	90	30			1371	30
		CNP	213302	683	35				
		SAP	696009	579	95				
	OMZ	CC	284561	339	140	543	97	207	65
		CNP	285766	681	38	954	123	281	81
		SAP	225766	571	120	860	126	303	97

Table 4.2 The average percentage of Kami signals in each DO zone during the day and night for each ecoregion and trip. The highest percentage for each ecoregion and time of day is bolded.

Trip	Ecoregion	No. Seals	Time of Day	OMZ	OLZ	HighDO
PB	SAP	32	Day	6.9 ± 12.3	**75.4 ± 16.7**	17.7 ± 17.2
		31	Night	3.2 ± 6.9	**52.9 ± 25.0**	43.9 ± 27.9
	CC	40	Day	**63.6 ± 19.8**	31.2 ± 16.5	5.3 ± 7.2
			Night	37.8 ± 23.3	**42.4 ± 14.8**	19.9 ± 18.0
	CNP	17	Day	12.6 ± 21.0	**56.5 ± 14.5**	30.9 ± 19.3
			Night	1.7 ± 2.7	22.9 ± 17.6	**75.4 ± 20.0**
PM	SAP	13	Day	3.0 ± 10.2	**63.6 ± 21.1**	33.4 ± 20.5
			Night	0.8 ± 2.6	33.6 ± 28.1	**65.6 ± 27.7**
	CC	13	Day	**55.9 ± 15.2**	40.0 ± 15.3	4.1 ± 3.5
			Night	31.4 ± 18.1	**40.8 ± 15.4**	27.8 ± 19.0
	CNP	8	Day	5.9 ± 10.2	**48.1 ± 21.9**	46.0 ± 27.1
			Night	0.2 ± 0.3	12.6 ± 13.7	**87.2 ± 14.0**

Table 4.3 Model outputs comparing the number of Kami dives per day in each ecoregion and DO region. The proportion of OMZ dives (*propOMZdives*) was included as a continuous covariate to account for the different availability of OMZ regions in each ecoregion. Each trip was modeled separately. The final, highest-ranked model is provided at the top.

Post-Breeding Trip	**No. Kami Dives Per Day**		
*gls(NoKamiDivesPerDay ~ Ecoregion * DOregion + propOMZdives, weights = varIdent(form = ~1|Ecoregion * DOregion))*			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	51.00 ***	47.08 – 54.91	**<0.001**
SAP	*Reference*		
CC	-12.00 ***	-15.93 – -8.07	**<0.001**
CNP	-0.96	-4.64 – 2.72	0.606
EcoregionCC:DOregionOLZ	-12.21 ***	-19.31 – -5.11	**0.001**
OMZ	*Reference*		
EcoregionCNP:DOregionOLZ	-2.37	-8.15 – 3.40	0.418
OLZ	3.08	-1.09 – 7.26	0.146
propOMZdives	4.62	-0.35 – 9.59	0.068
Observations	137		
R^2	0.511		

* $p<0.05$ ** $p<0.01$ *** $p<0.001$

Post-Molt Trip	**No. Kami Dives Per Day**		
lm(NoKamiDivesPerDay ~ Ecoregion + DOregion + propOMZdives)			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	47.31 ***	42.24 – 52.37	**<0.001**
SAP	*Reference*		
CC	2.03	-8.93 – 12.98	0.711
CNP	3.29	-3.31 – 9.90	0.321
OMZ	*Reference*		
OLZ	-2.50	-7.28 – 2.27	0.297
propOMZdives	-2.96	-14.58 – 8.66	0.610
Observations	52		
R^2 / R^2 adjusted	0.046 / -0.035		

Table 4.4 Summary statistics (mean ± SD) of trip-level metrics that are relevant to foraging success. Sample size excludes skip-breeders and includes seals with repeat deployments.

	Post-Breeding Trip		Post-Molt Trip	
	All seals	Kami seals	All seals	Kami seals
No. seals	202	41	137	11
Days at Sea	74.6 ±10.1	75.7 ±11.6	222.8 ±5.4	221.6 ±4.2
Dives per Day	59.8 ±5.7	59.9 ±4.9	51.1 ±7.2	48.5 ±8.5
Horizontal Distance Traveled (km)	4933.3 ±1104.3	4716.0 ±1300.0	10081.6 ±2167.3	10957.9 ±1430.4
Total Daily Distance Traveled (km)	129.4 ±14.8	125.3 ±16.6	96.7 ±12.8	99.3 ±7.5
Depart Mass (kg)	317.2 ±38.5	309.5 ±37.5	282.2 ±33.4	288.1 ±24.5
Mass Gain (kg)	87.9 ±21.5	90.2 ±25.1	315.3 ±38.9	341.8 ±24.8
Mass Gain Rate (kg/day)	1.2 ±0.3	1.2 ±0.4	1.4 ±0.2	1.5 ±0.1
Depart Adipose (%)	28.1 ±2.1	28.3 ±2.0	30.3 ±2.5	28.3 ±2.6
Energy Gain (MJ)	1688.7 ±509.4	1762.1 ±522.6	5734.8 ±940.1	5995.1 ±802.5
Energy Gain Rate (MJ/day)	22.7 ±7.5	23.4 ±7.9	25.6 ±4.3	26.9 ±3.6
	Subset with full trip			
No. seals	200	38	110	0
Days at Sea	74.8 ±9.8	75.2 ±11.9	223.0 ±5.4	
Dives per Day	60.1 ±5.1	59.6 ±4.9	53.2 ±4.3	
Horizontal Distance Traveled (km)	4956.8 ±1084.3	4618.0 ±1300.4	10268.7 ±2164.3	
Total Daily Distance Traveled (km)	129.8 ±14.0	124.1 ±16.7	99.6 ±10.6	
Depart Mass (kg)	316.6 ±38.1	308.5 ±37.4	282.0 ±34.1	
Mass Gain (kg)	87.9 ±21.5	88.0 ±24.6	313.2 ±41.5	
Mass Gain Rate (kg/day)	1.2 ±0.3	1.2 ±0.4	1.4 ±0.2	
Depart Adipose (%)	28.1 ±2.1	28.4 ±1.9	30.3 ±2.5	
Energy Gain (MJ)	1686.2 ±511.3	1722.4 ±521.8	5669.6 ±971.1	
Energy Gain Rate (MJ/day)	22.6 ±7.4	23.1 ±8.1	25.3 ±4.5	

Table 4.5 Model outputs testing the influence of the proportion of dives in OMZ regions (*propOMZdives*) on energy gain (MJ). Predictor variables were scaled. Each trip was modeled separately. The final, highest-ranked model is provided at the top.

Post-Breeding Trip	**Energy Gain**		
lm(EnergyGain ~ propOMZdives + DepartAdipose + DailyTotalDist)			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	1676.11 ***	1611.03 – 1741.18	**<0.001**
DailyTotalDist	-64.43	-131.82 – 2.96	0.061
DepartAdipose	-204.55 ***	-272.05 – -137.06	**<0.001**
propOMZdives	-94.92 **	-163.52 – -26.32	**0.007**
Observations	167		
R^2 / R^2 adjusted	0.244 / 0.230		

Post-Molt Trip	**Energy Gain**		
lm(EnergyGain ~ propOMZdives + DepartAdipose + DailyTotalDist + DaysAtSea)			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	5685.94 ***	5516.49 – 5855.40	**<0.001**
DailyTotalDist	-210.87 *	-397.06 – -24.69	**0.027**
DaysAtSea	-178.26 *	-351.01 – -5.50	**0.043**
DepartAdipose	-348.04 ***	-521.79 – -174.29	**<0.001**
propOMZdives	-315.47 **	-503.66 – -127.27	**0.001**
Observations	103		
R^2 / R^2 adjusted	0.264 / 0.234		

* *p<0.05* ** *p<0.01* *** *p<0.001*

Table 4.6 Model outputs testing the influence of the dissolved oxygen levels at foraging depths (*AvgDOatKami*) on short-term foraging success calculated as the change in drift rate over 6 days in the same ecoregion and DO region. Each trip was modeled separately. The final, highest-ranked model is provided at the top.

<table>
<tr><th>Post-Breeding Trip</th><th colspan="3">Change In Drift Rate</th></tr>
<tr><td colspan="4"><i>lme(ChangeInDriftRate ~ AvgDOatKami + AvgDOatKami:DOregion + KamiNoSumPerDive + Ecoregion + DOregion + PctOfTrip + I(PctOfTrip^2), weights = varIdent(form = ~1|Ecoregion * DOregion), random = (~1|TOPPID))</i></td></tr>
<tr><td><i>Predictors</i></td><td><i>Estimates</i></td><td><i>CI</i></td><td><i>p</i></td></tr>
<tr><td>(Intercept)</td><td>-0.0069</td><td>-0.0164 – 0.0027</td><td>0.158</td></tr>
<tr><td>AvgDOatKami</td><td>-0.0000</td><td>-0.0001 – 0.0001</td><td>0.881</td></tr>
<tr><td>AvgDOatKami:DOregionOLZ</td><td>-0.0002</td><td>-0.0004 – 0.0000</td><td>0.073</td></tr>
<tr><td>OMZ</td><td><i>Reference</i></td><td></td><td></td></tr>
<tr><td>OLZ</td><td>0.0176 *</td><td>0.0017 – 0.0336</td><td>0.030</td></tr>
<tr><td>SAP</td><td><i>Reference</i></td><td></td><td></td></tr>
<tr><td>CC</td><td>-0.0051</td><td>-0.0114 – 0.0012</td><td>0.110</td></tr>
<tr><td>CNP</td><td>0.0032</td><td>-0.0004 – 0.0067</td><td>0.078</td></tr>
<tr><td>I(PctOfTrip^2)</td><td>-0.0000 ***</td><td>-0.0000 – -0.0000</td><td><0.001</td></tr>
<tr><td>KamiNoSumPerDive</td><td>0.0000</td><td>-0.0002 – 0.0002</td><td>0.918</td></tr>
<tr><td>PctOfTrip</td><td>0.0008 ***</td><td>0.0005 – 0.0012</td><td><0.001</td></tr>
<tr><td colspan="4">Random Effects</td></tr>
<tr><td>σ^2</td><td colspan="3">0.0002</td></tr>
<tr><td>τ_{00} TOPPID</td><td colspan="3">0.0000</td></tr>
<tr><td>ICC</td><td colspan="3">0.0435</td></tr>
<tr><td>N TOPPID</td><td colspan="3">38</td></tr>
<tr><td>Observations</td><td colspan="3">251</td></tr>
<tr><td>Marginal R^2 / Conditional R^2</td><td colspan="3">0.307 / 0.337</td></tr>
</table>

* *p<0.05* ** *p<0.01* *** *p<0.001*

Table 4.6 (continued) Model outputs testing the influence of the dissolved oxygen levels at foraging depths (*AvgDOatKami*) on short-term foraging success calculated as the change in drift rate over 6 days in the same ecoregion and DO region. Each trip was modeled separately. The final, highest-ranked model is provided at the top.

Post-Molt Trip	**Change In Drift Rate**		
lme(ChangeInDriftRate~AvgDOatKami + AvgDOatKami:DOregion + KamiNoSumPerDive + KamiNoSumPerDive:Ecoregion + Ecoregion + DOregion + PctOfTrip + I(PctOfTrip^2),weights = varIdent(form = ~1|Ecoregion),random = (~1|TOPPID))			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-0.0082	-0.0223 – 0.0059	0.251
AvgDOatKami	0.0001 *	0.0000 – 0.0003	**0.039**
AvgDOatKami:DOregionOLZ	-0.0001	-0.0003 – 0.0000	0.086
OMZ	*Reference*		
OLZ	0.0198 *	0.0037 – 0.0358	**0.016**
SAP	*Reference*		
CC	-0.0286 ***	-0.0448 – -0.0124	**0.001**
CNP	-0.0078	-0.0215 – 0.0059	0.264
I(PctOfTrip^2)	-0.0000	-0.0000 – 0.0000	0.639
KamiNoSumPerDive	0.0001	-0.0002 – 0.0003	0.500
KamiNoSumPerDive:EcoregionCC	0.0009 ***	0.0004 – 0.0014	**<0.001**
KamiNoSumPerDive:EcoregionCNP	0.0003	-0.0001 – 0.0007	0.174
PctOfTrip	-0.0000	-0.0004 – 0.0003	0.834
Random Effects			
σ^2	0.0002		
$\tau_{00\ \mathrm{TOPPID}}$	0.0000		
ICC	0.0715		
N_{TOPPID}	13		
Observations	255		
Marginal R^2 / Conditional R^2	0.245 / 0.299		

* *p<0.05* ** *p<0.01* *** *p<0.001*

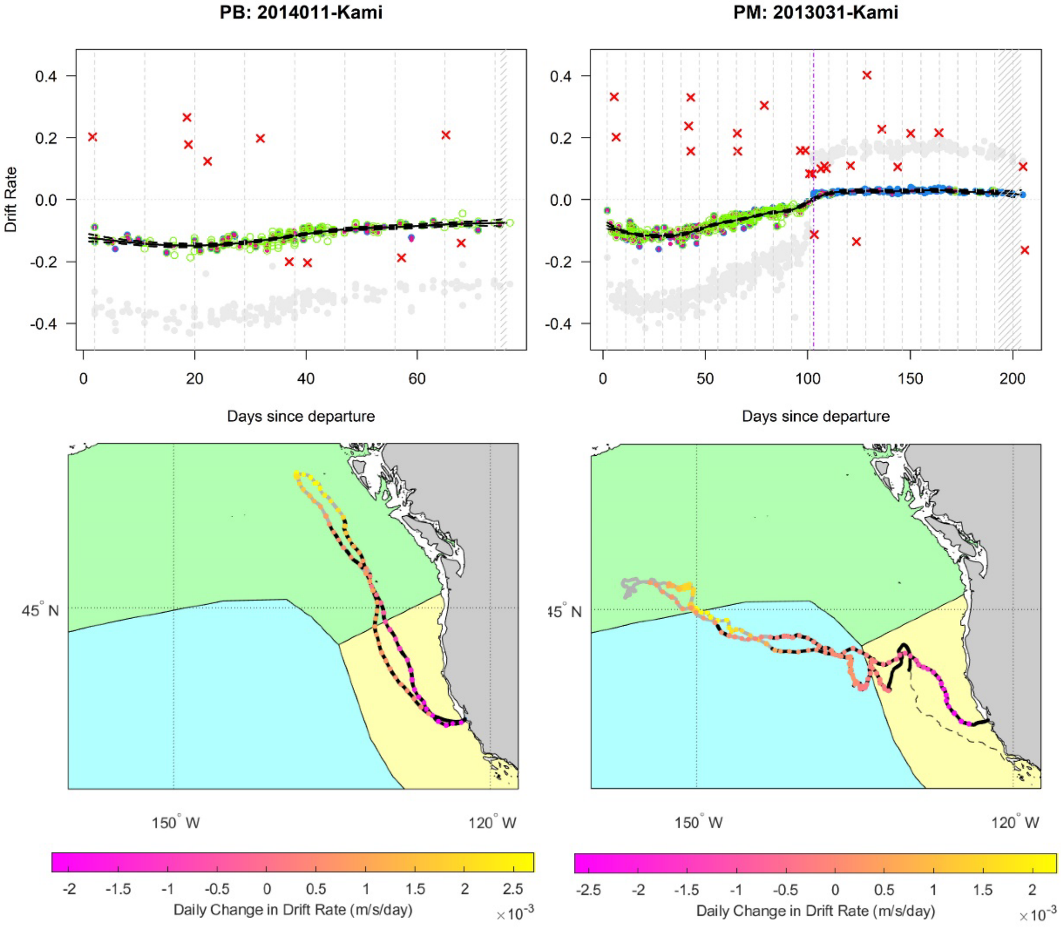


Figure 4.1 Representative examples using data from a post-breeding seal (left) and post-molt seal (right) showing how drift rates were filtered and transformed before fitting a cubic smoothing spline from which daily drift rate values were estimated. Original drift rates (light gray points) were square-transformed and drift dives that met various duration and linearity thresholds (see methods, distinguished by different colors in the plots) were retained while the rest were excluded (red crosses). A knot interval of 9 days (gray vertical dashed lines) was used to fit the spline (black line). Hatched days on the graph had too few drift dives and were not used in analyses. Daily changes in drift rate (shown on map) were calculated from the daily drift rates estimated from the spline. Dashed portions of the track do not have associated dive data due to an incomplete dive record.

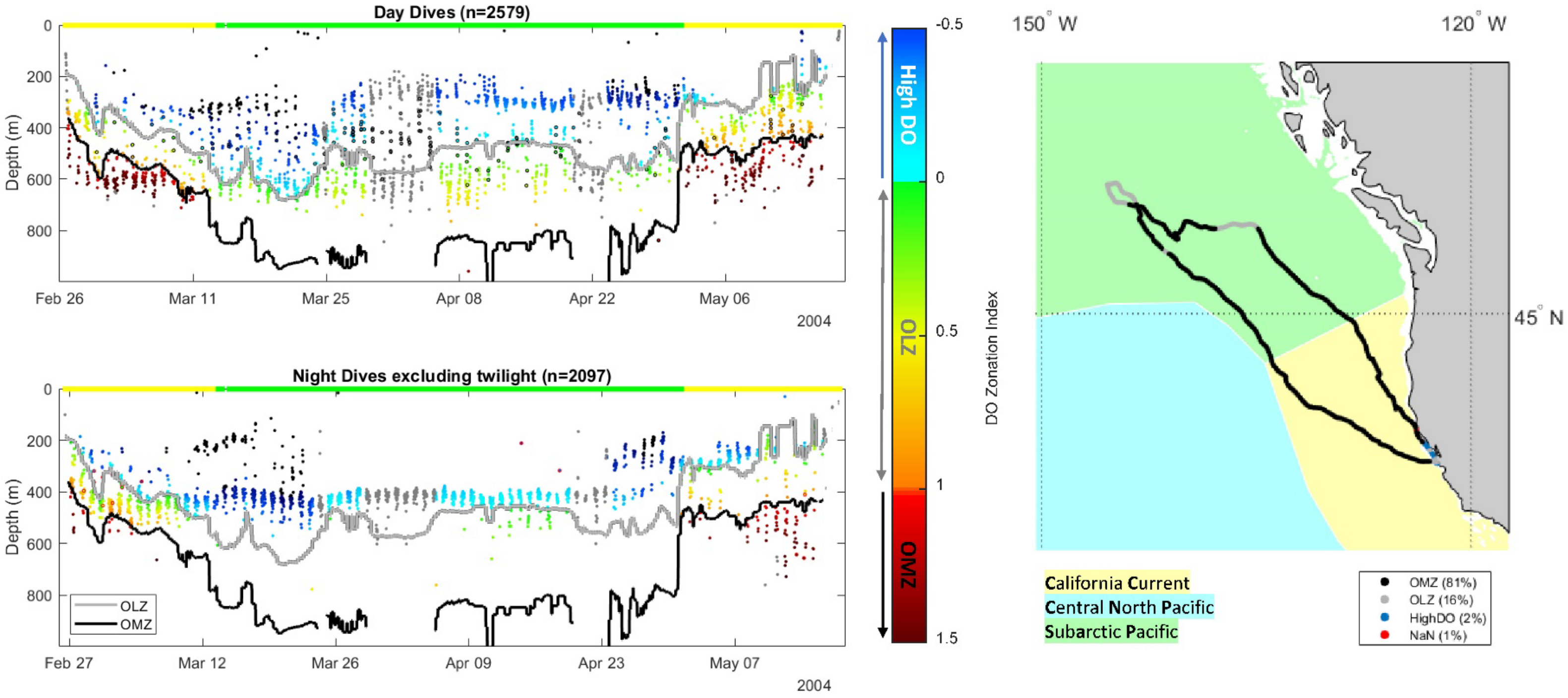


Figure 4.2 Depiction of what the DO zonation index values represent relative to the OLZ (gray) and OMZ (black). Each colored point represents a daytime (top) or nighttime (bottom) dive. The DO zonation index was not calculated for dives in OLZ regions (gray points). The color coding across the top of each graph matches the ecoregion shown on the map (right).

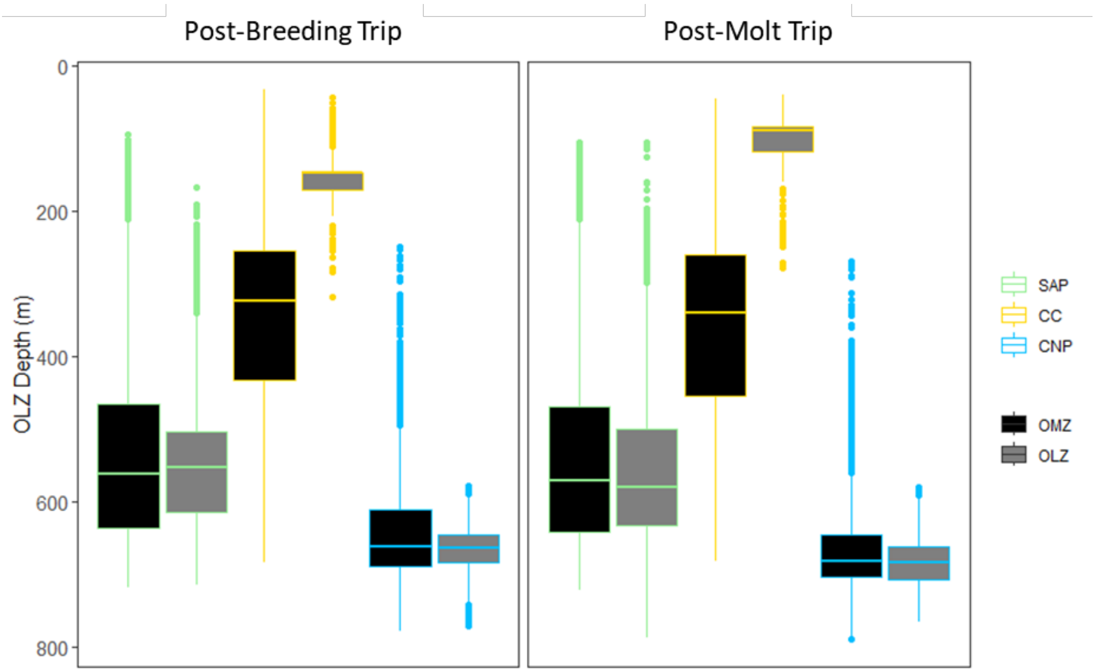


Figure 4.3 Boxplots of the OLZ depth encountered by seals on their dives for each ecoregion-DO region combination during each trip.

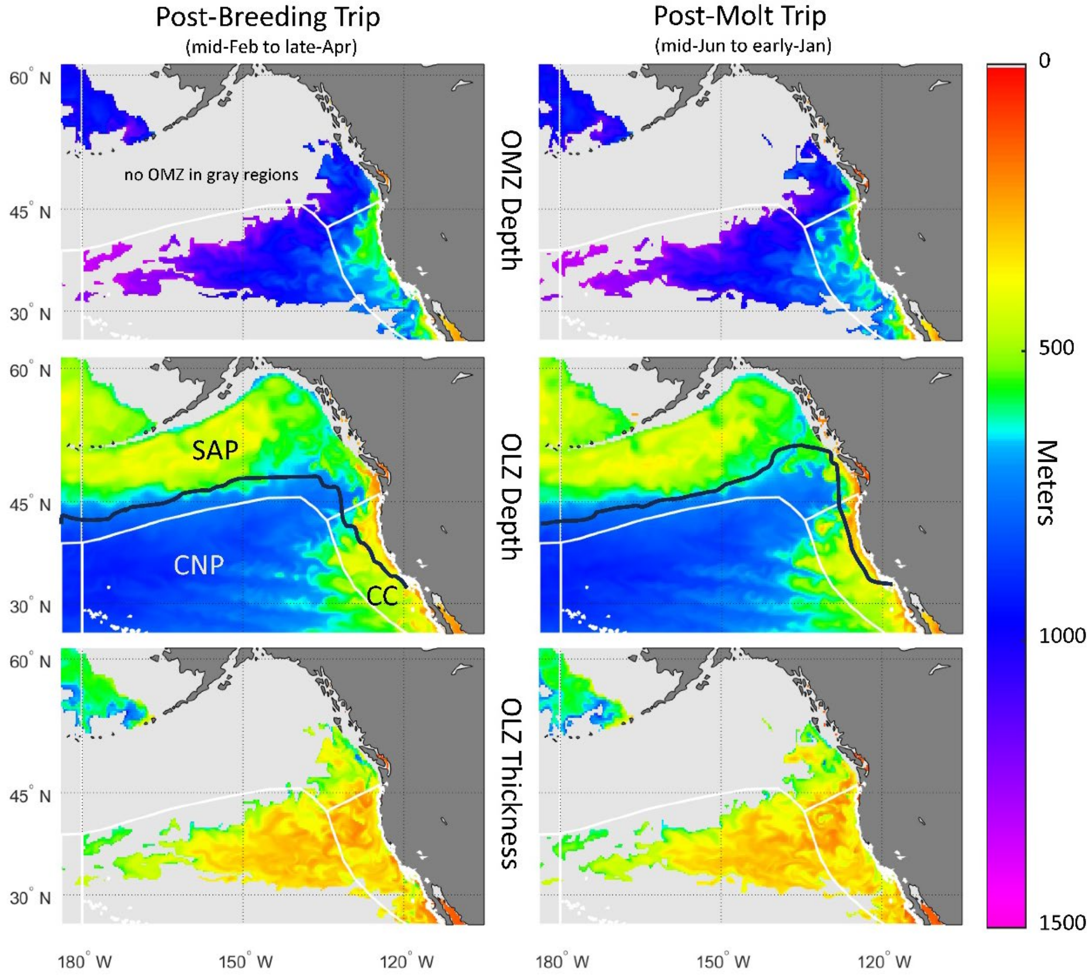


Figure 4.4 Representative maps of OMZ depth (top), OLZ depth (middle), and OLZ thickness (bottom) across the North Pacific for the post-breeding and post-molt trips. Approximate location of the gyre-gyre boundary is drawn in black on the OLZ depth map. Dissolved oxygen data are monthly averages in March (left) and September (right) of 2012.

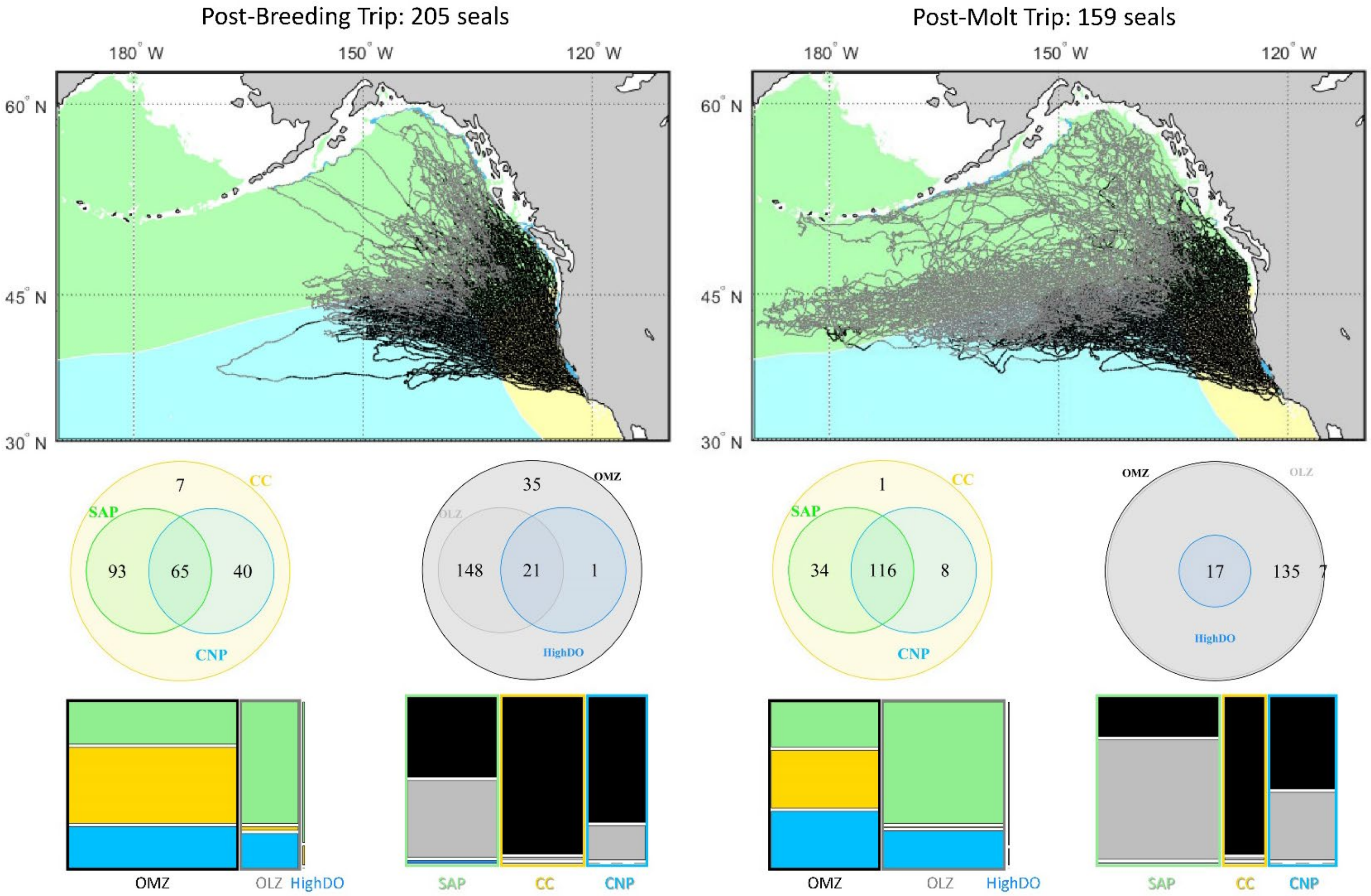


Figure 4.5 Maps show all seal tracks for each trip and the portions of the tracks that overlap with OLZ (gray) or OMZ (black) regions. Venn-diagrams provide the sample size of seals with dives in each ecoregion (left) and DO region (right). Mosaic plots show the relative proportions of dives in ecoregions in each DO region (left) and DO regions in each ecoregion (right).

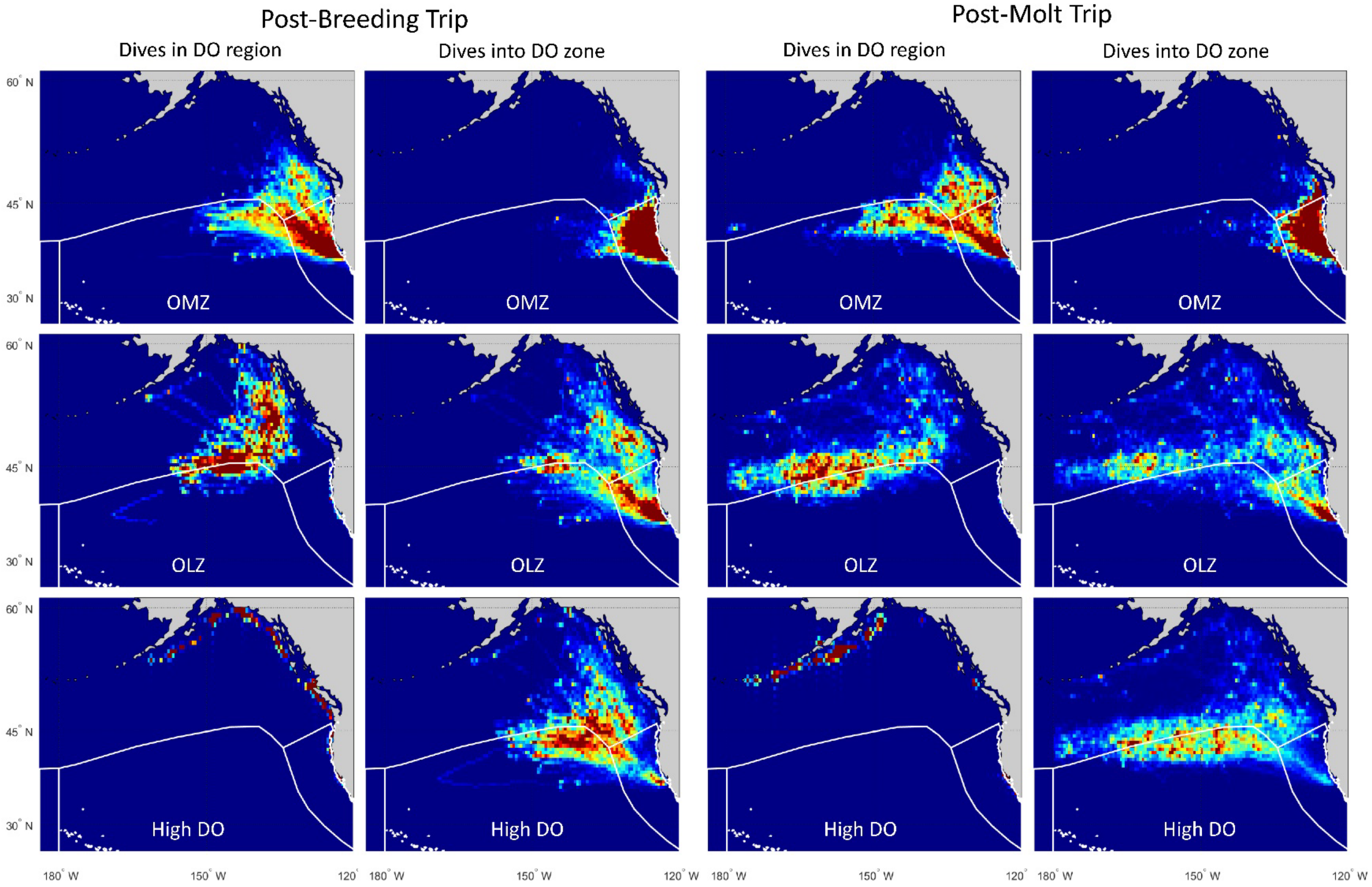


Figure 4.6 Spatial kernel density distributions for each trip showing the density of dive locations in each DO region (left column) and the density of dives reaching each DO zone (right column). Warmer colors represent higher densities.

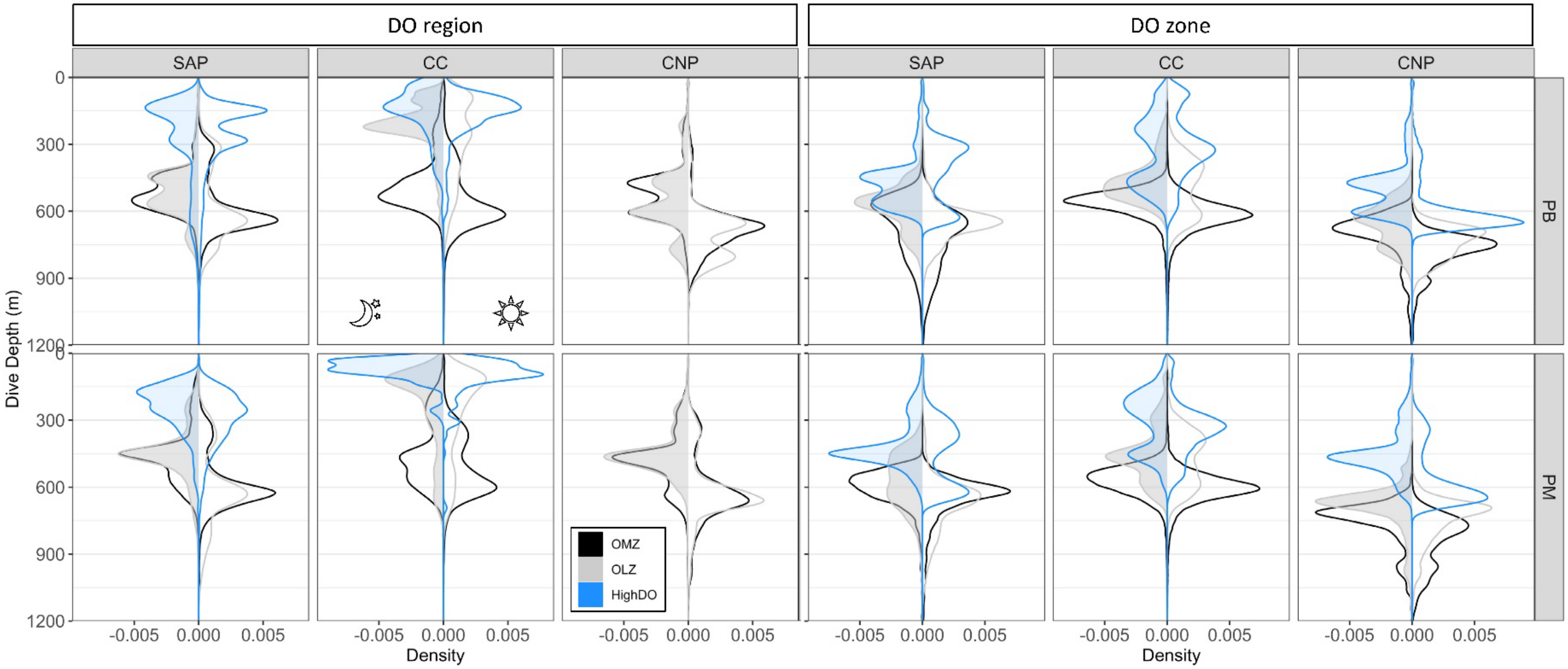


Figure 4.7 Daytime (positive values) and nighttime (negative values) density distributions of dive depths in each DO region (left) or reaching each DO zone (right) for each ecoregion (columns) and trip (rows). Sample sizes are provided in Table 4.S2.

Figure 4.8 Daytime (positive values) and nighttime (negative values) density distributions of the DO zonation index for each ecoregion calculated for the dives of the seals that belong in the sections of the Venn-diagram indicated by an orange circle. Density distributions were weighted by the number of dives for each seal.

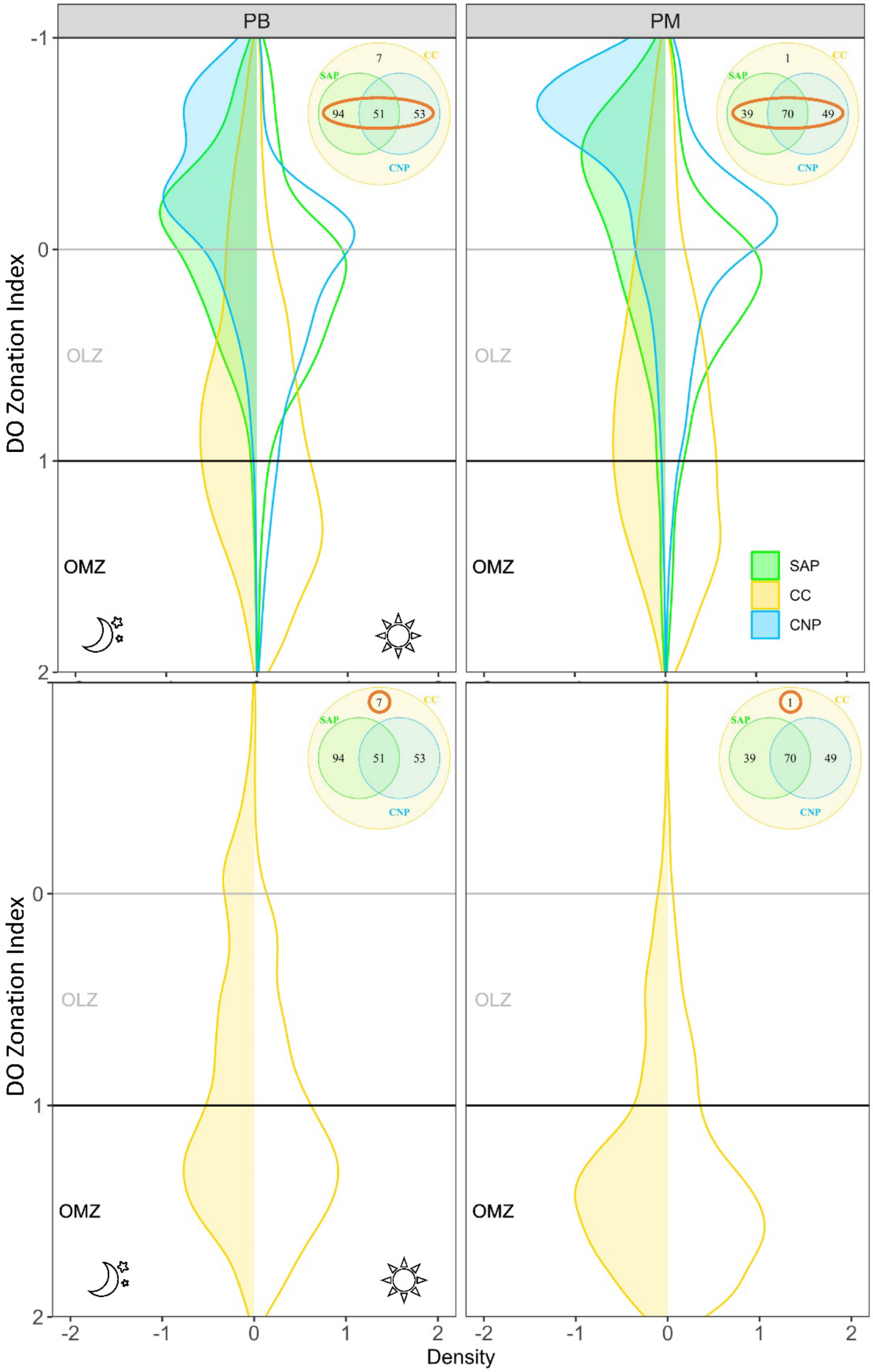

PB
PM
DO Zonation Index
-1
0
1
2
OLZ
OMZ
CC
SAP
CNP
7
94
51
53
1
39
70
49
SAP
CC
CNP
-2
-1
0
1
2
Density

Figure 4.9 Heatmaps showing temporal patterns of (from left to right) the OLZ depth, dive depth, and DO zonation index for (from top to bottom) all ecoregions, the California Current, the Central North Pacific, and the Subarctic Pacific. The white or black lines indicate when solar elevation is 0. Grayed out columns in the DO zonation index heatmaps are days for which sample sizes were small and excluded (number of days indicated in each heatmap).

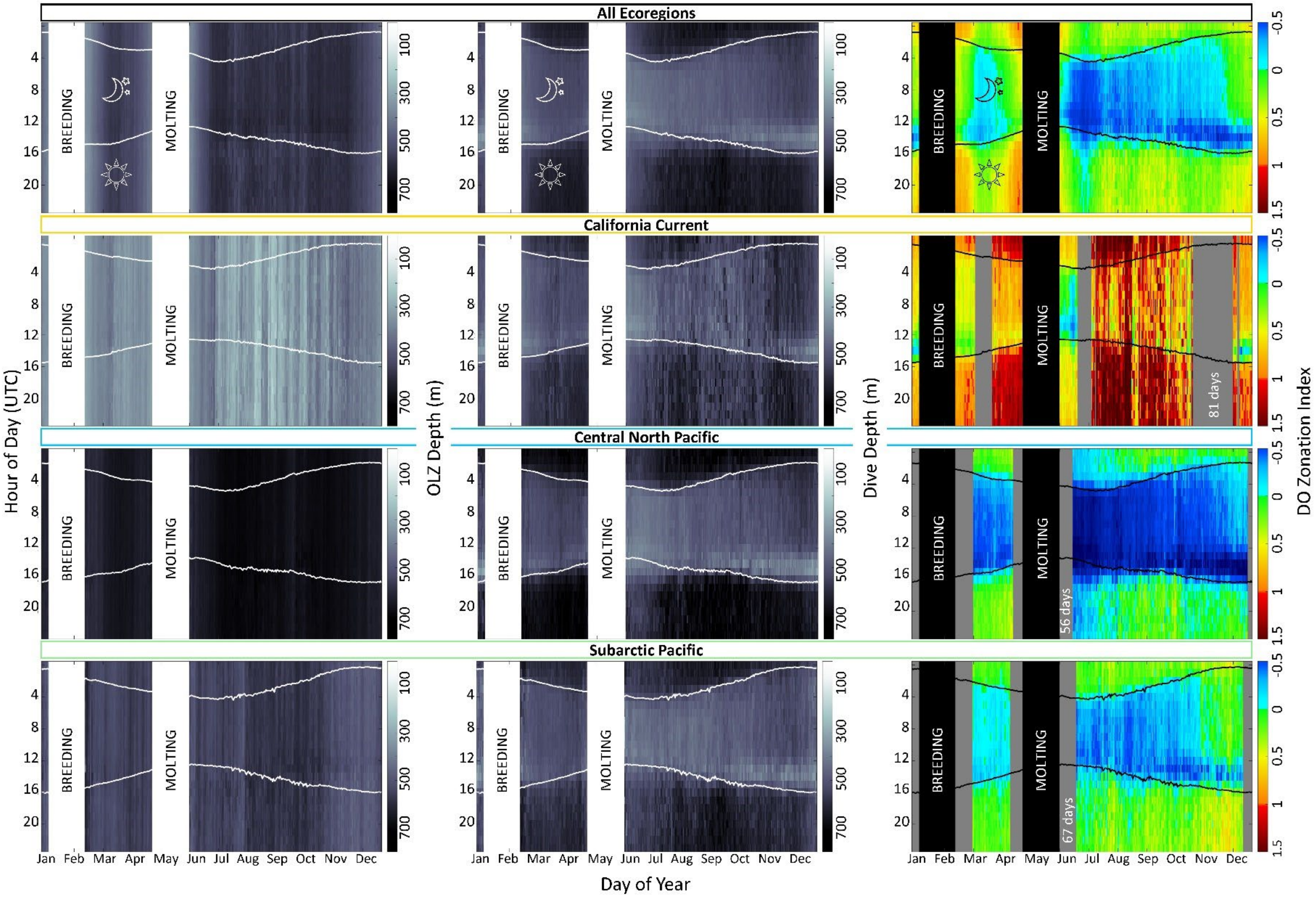
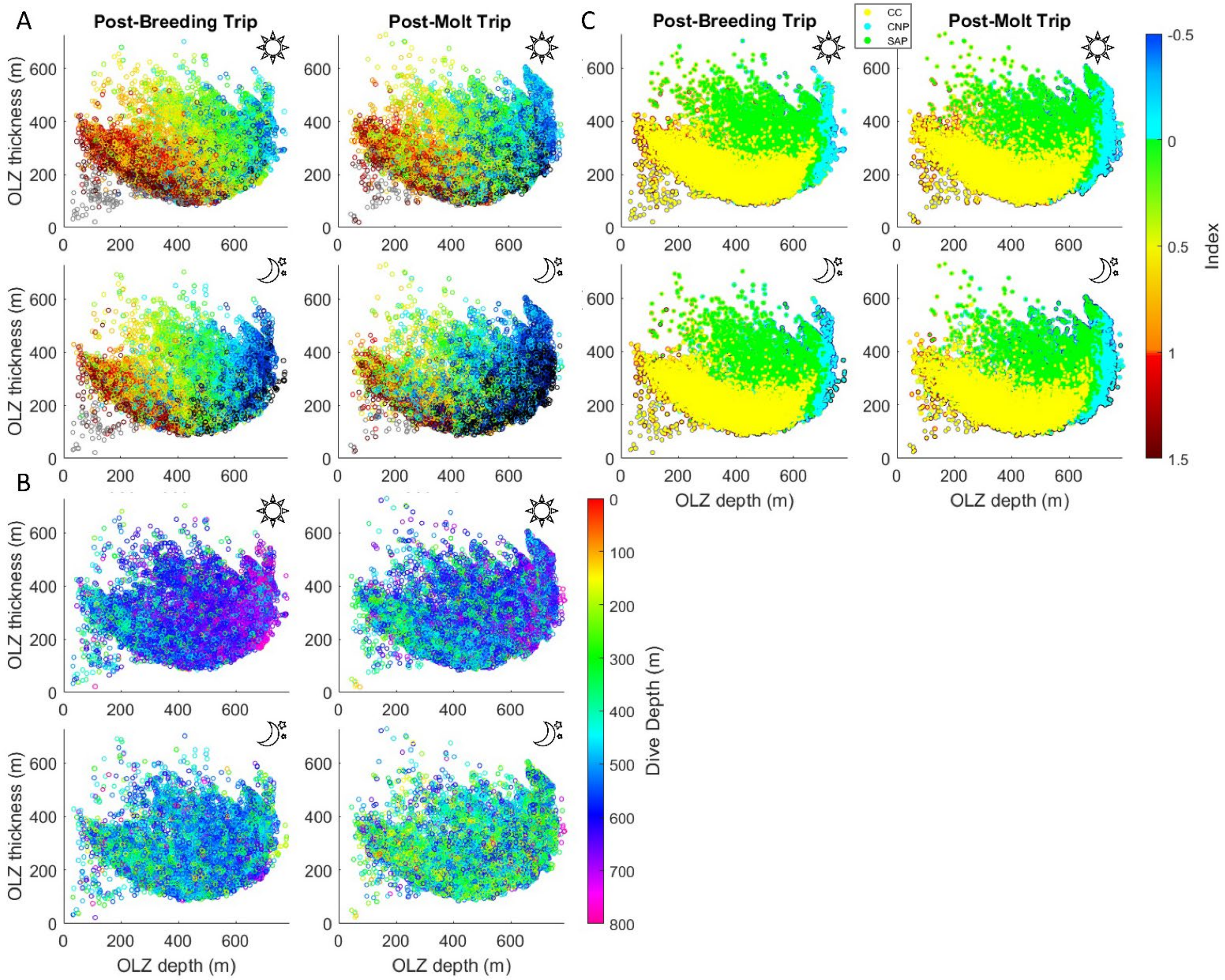

All Ecoregions
California Current
Central North Pacific
Subarctic Pacific
BREEDING
MOLTING
81 days
56 days
67 days
Hour of Day (UTC)
4
8
12
16
20
OLZ Depth (m)
Dive Depth (m)
100
300
500
700
DO Zonation Index
-0.5
0
0.5
1
1.5
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Day of Year

Figure 4.10 Scatterplots depicting the patterns in the DO zonation index (A) and dive depth (B) across a varying oxyscape (OLZ depth and thickness). The ecoregion where each dive occurred is depicted in (C). In each panel of figures, the left and right columns are dives in the post-breeding and post-molt trips, respectively, while the top and bottom rows are daytime and nighttime dives, respectively.


A
Post-Breeding Trip
Post-Molt Trip
C
Post-Breeding Trip
Post-Molt Trip
CC
CNP
SAP
B
OLZ thickness (m)
OLZ depth (m)
0
200
400
600
Index
-0.5
0
0.5
1
1.5
Dive Depth (m)
0
100
200
300
400
500
600
700
800

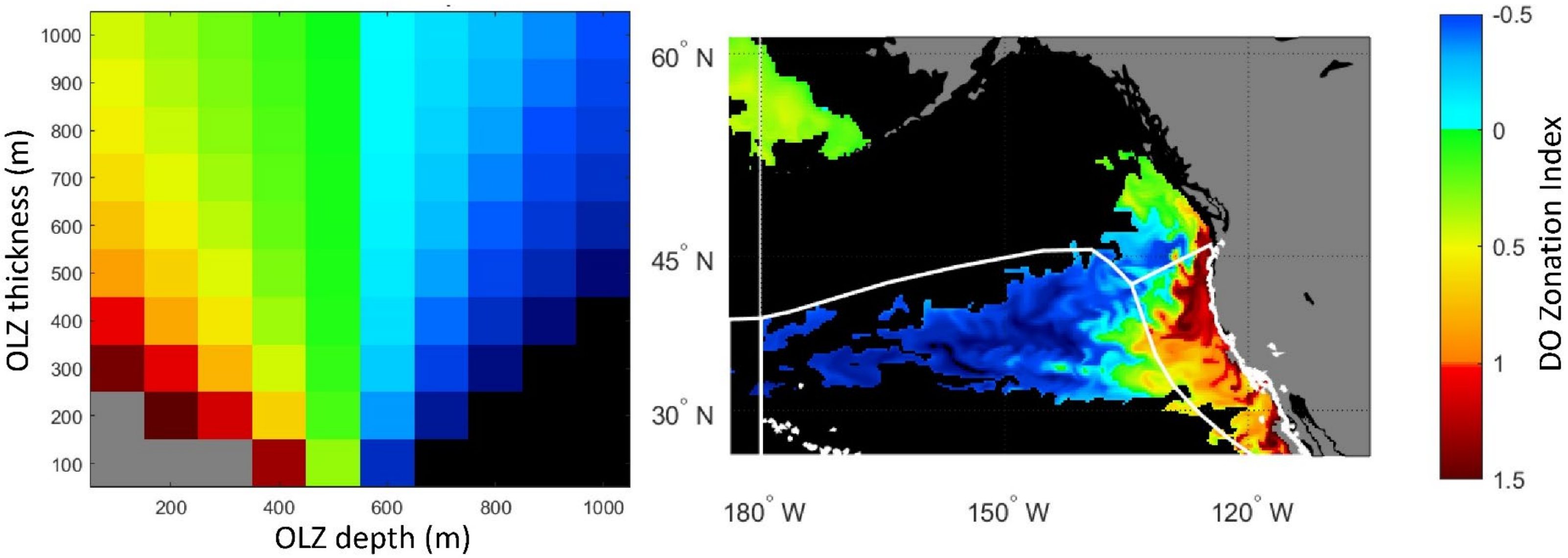
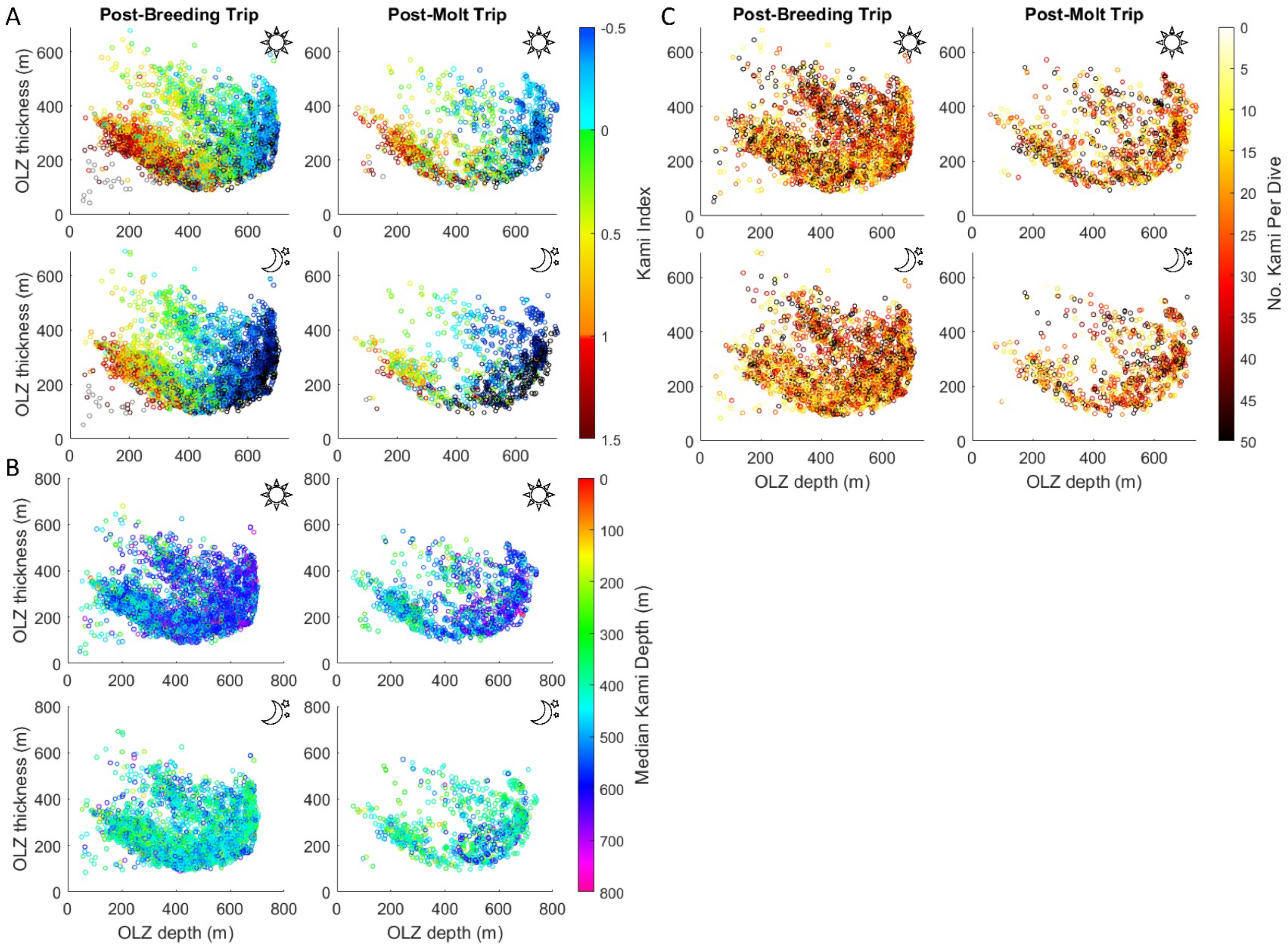


Figure 4.11 Heatmap showing the theoretical values for the DO zonation index for a constant dive depth of 531 m (overall mean) across a range of OLZ depths and thicknesses (100-1000 m). Using the same dive depth, the DO zonation index was determined for a spatially explicit oxyscape using dissolved oxygen values from March 2012. The gray and black areas on the heatmap are due to the limits set on the colormap.

Figure 4.12 Scatterplots depicting the patterns in the DO zonation index calculated for each Kami signal (A), the median depth per dive of the Kami signals (B), and number of Kami signals per dive (C) across a varying oxyscape (OLZ depth and thickness). In each panel of figures, the left and right columns are dives in the post-breeding and post-molt trips, respectively, while the top and bottom rows are daytime and nighttime dives, respectively.


A
Post-Breeding Trip
Post-Molt Trip
OLZ thickness (m)
0
200
400
600
Kami Index
-0.5
0
0.5
1
1.5
B
OLZ thickness (m)
OLZ depth (m)
0
200
400
600
800
Median Kami Depth (m)
0
100
200
300
400
500
600
700
800
C
Post-Breeding Trip
Post-Molt Trip
OLZ depth (m)
No. Kami Per Dive
0
5
10
15
20
25
30
35
40
45
50

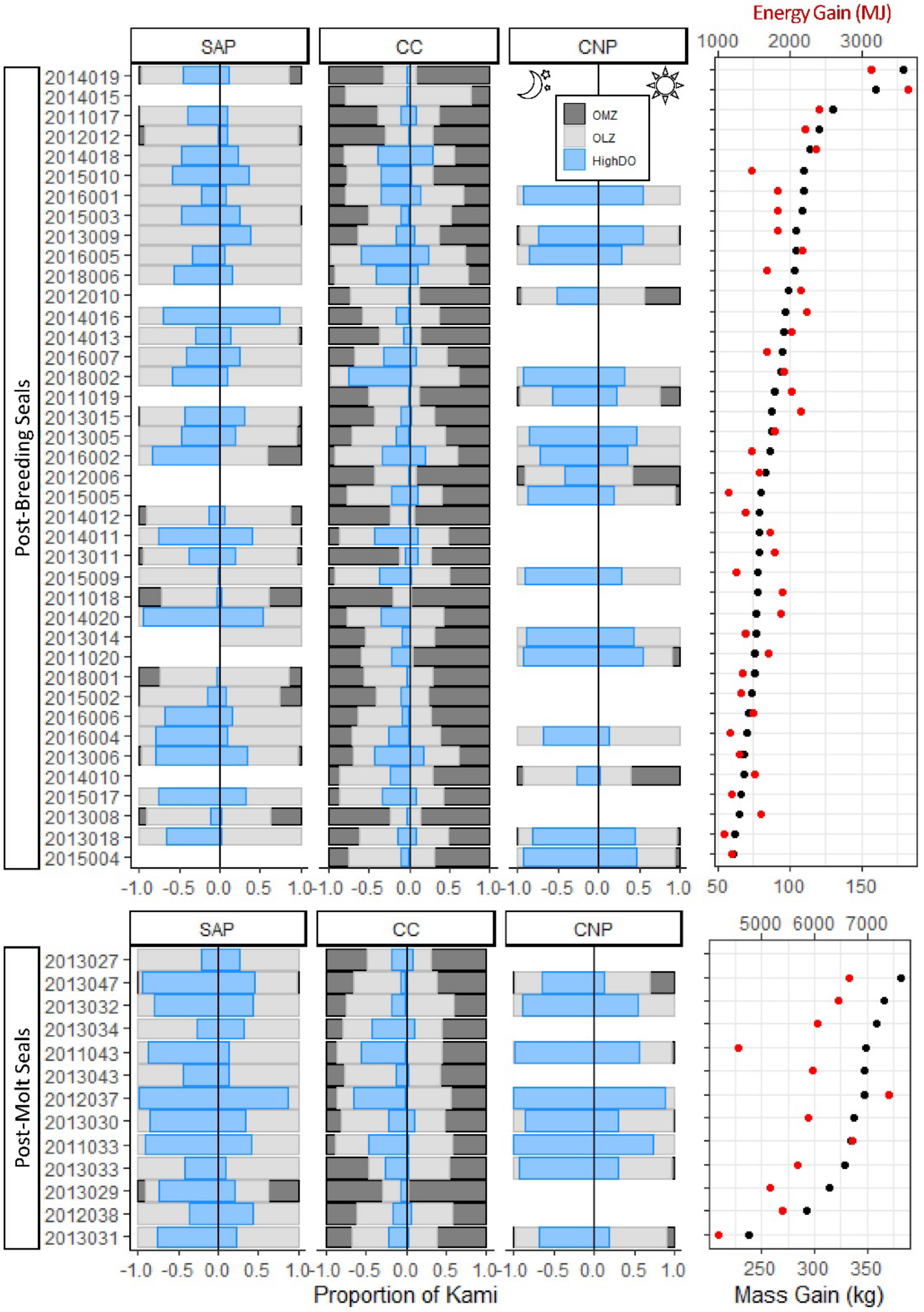


Figure 4.13 The proportion of Kami signals in each DO zone during the day (positive values) and night (negative values) for each seal for dives in each ecoregion. Mass and energy gain are shown in the rightmost panel. Seals are ordered by increasing mass gain (from bottom to top). Seal TOPPIDs 2015002 & 2018001 are the same individual. TOPPID 2013027 was not weighed.

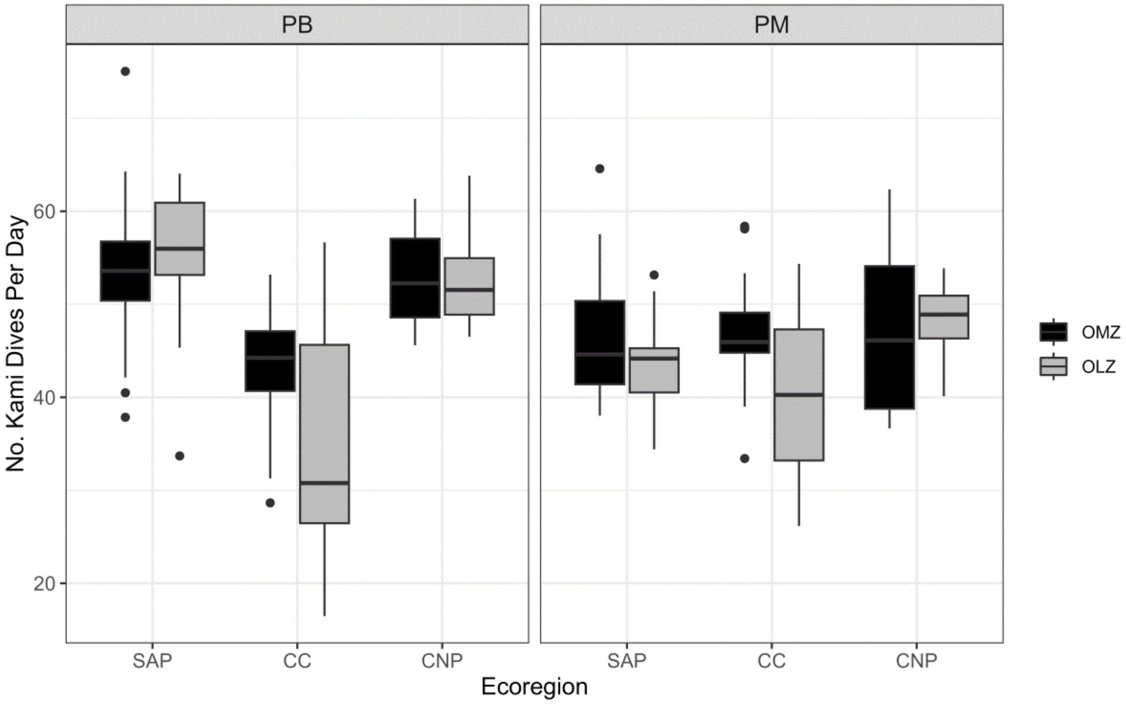


Figure 4.14 Boxplots of the number of dives per day with Kami signals in each DO region-ecoregion combination for each trip.

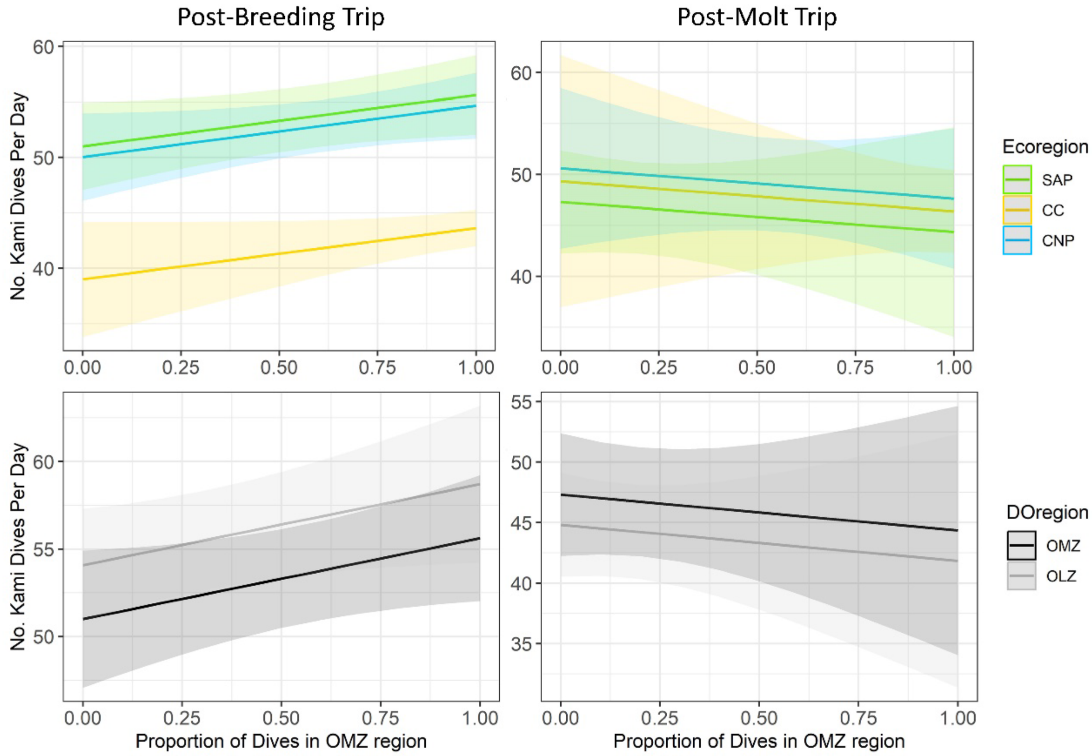


Figure 4.15 Marginal effects plots for each ecoregion (top row) and DO region (bottom row) for each trip. Predicted values of the number of Kami dives per day are plotted against the proportion of dives in OMZ regions.

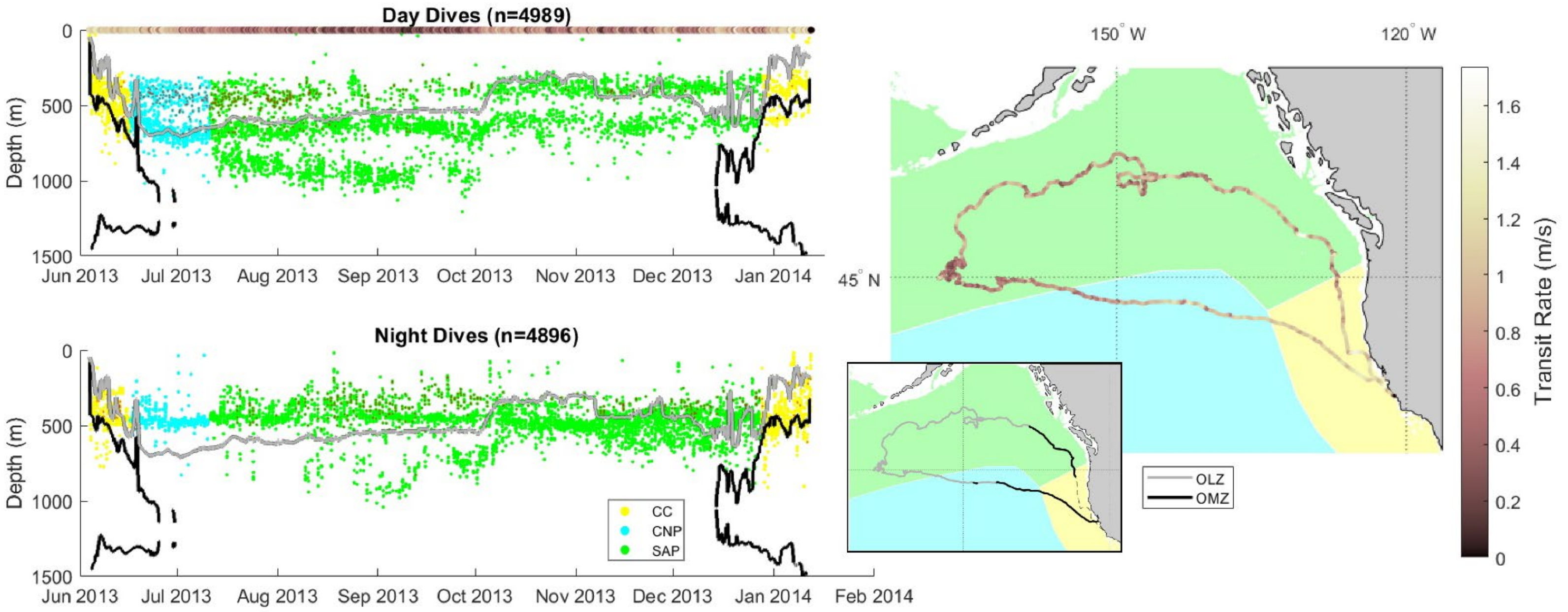


Figure 4.16 Example from seal TOPPID 2013033 of a shift in diving behavior and transit rate upon entering the SAP as well as when the OLZ depth changes around October. Each point in the time series plot represents a dive color-coded by the ecoregion. Smaller dark red points are drift dives. The depth of the OLZ and OMZ are indicated by gray and black lines, respectively. The smaller inset map shows where along its track the seal encounters OLZ and OMZ regions. Transit rate interpolated at each dive is shown above the dive profile and along the track with lighter colors indicating faster transit rates.

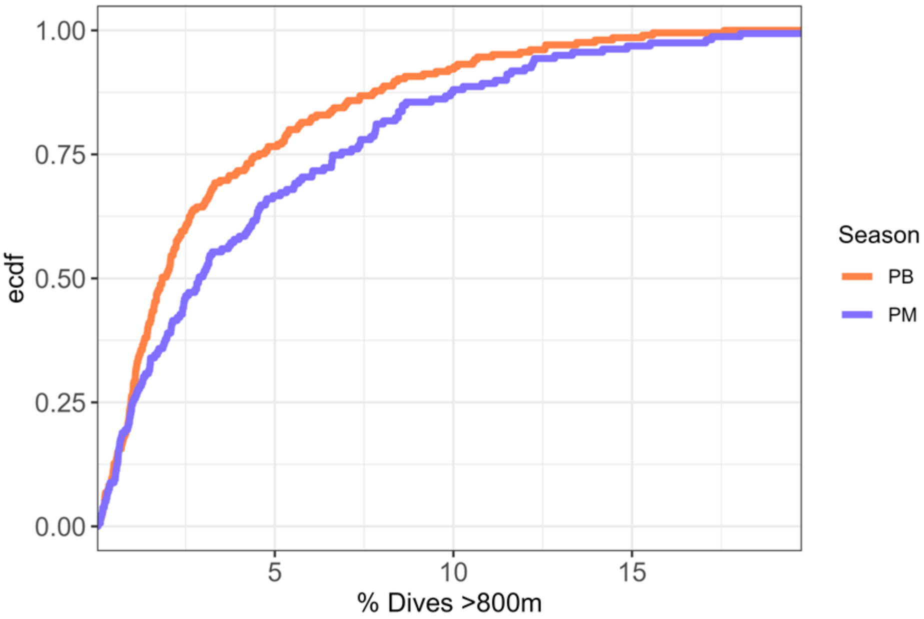


Figure 4.17 Empirical cumulative distribution function showing the proportion of seals that have a certain percentage of dives >800m.

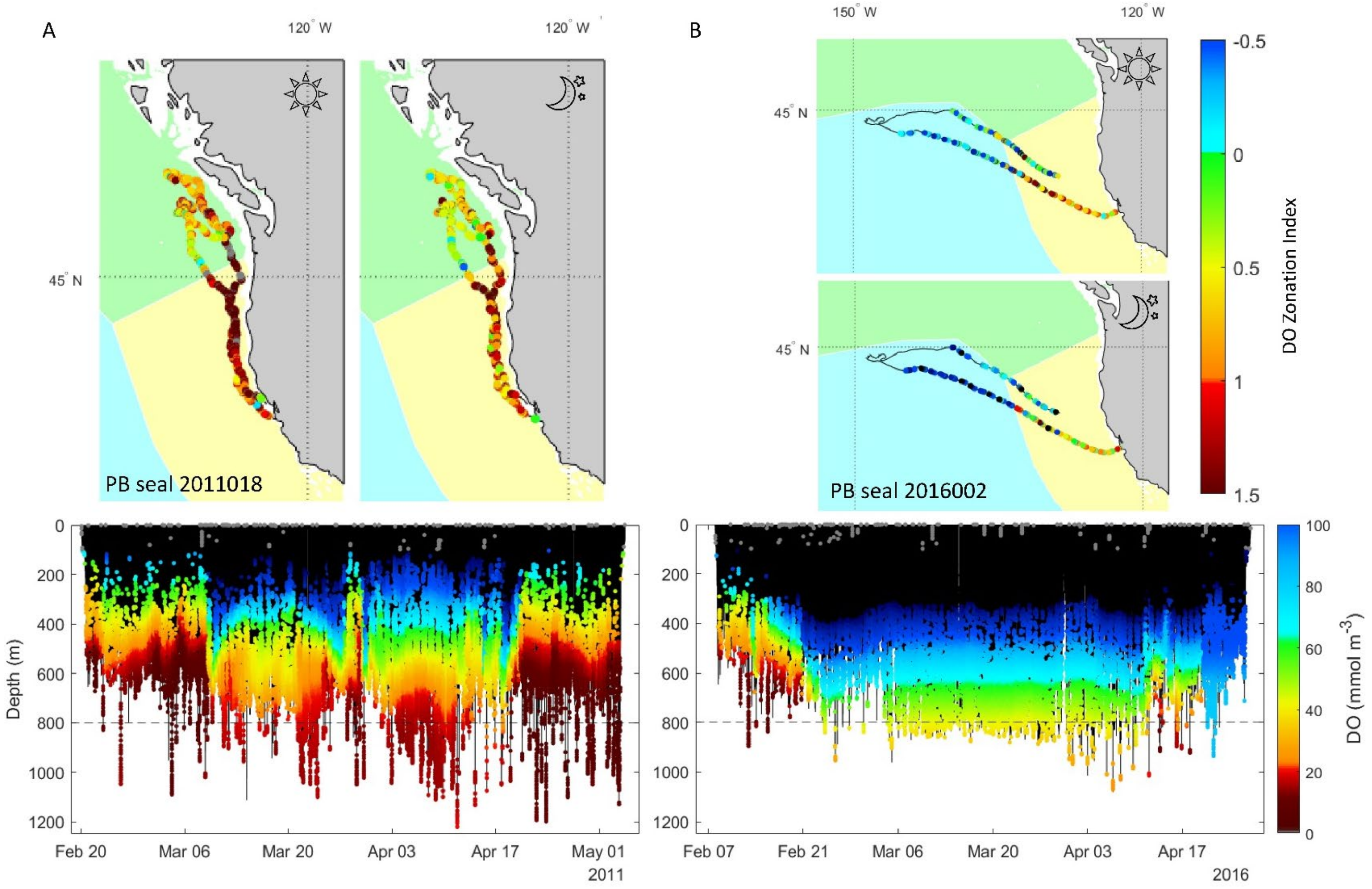


Figure 4.18 A comparison of low-oxygen zone utilization by two post-breeding seals (A: 2011018, B: 2016002). Tracks are color coded by the DO zonation index of each dive (except where no OMZ exists as is the case for part of seal 2016002's track). Bottom panels show depth record (black) with Kami signals color coded by the dissolved oxygen level.

Table 4.S1 Sample sizes of dives for each trip across DO regions and ecoregions after shelf dives, drift dives, and twilight dives were excluded.

Trip	DO region	Ecoregion	Dives analyzed	% of total dives	% in DO region	% Shelf Dives	% Drift Dives	% Twilight Dives
PB	HighDO	CC	750	5.8	0.8	93.7	1.8	49.0
		SAP	5246	85.5		0.0	2.6	12.5
	OLZ	CC	4161	35.1	24.5	60.6	1.1	9.0
		CNP	41424	85.4		0.0	5.7	9.9
		SAP	142774	83.9		0.0	6.0	11.4
	OMZ	CC	272967	84.8	74.7	3.5	3.3	9.4
		CNP	151057	87.0		0.0	4.4	9.6
		SAP	150269	85.5		0.0	4.8	10.6
		Total	768648					
PM	HighDO	CC	371	0.8	0.2	99.1	5.4	91.5
		SAP	2936	80.0		0.0	4.5	16.1
	OLZ	CC	3270	35.6	52.6	59.4	1.6	9.5
		CNP	175428	82.2		0.0	7.6	11.0
		SAP	565453	81.2		0.0	8.4	11.7
	OMZ	CC	242188	82.6	47.2	2.9	4.9	10.6
		CNP	239795	83.9		0.0	6.3	10.7
		SAP	185340	82.1		0.0	6.8	12.0
		Total	1414781					

Table 4.S2 Median depths of daytime and nighttime dives for each trip across each ecoregion-DO region combination with sample sizes provided. MAD = median absolute deviation.

Trip	Ecoregion	DO region	Daytime Dives				Nighttime Dives			
			No. Seals	No. Dives	Median Depth (m)	MAD (m)	No. Seals	No. Dives	Median Depth (m)	MAD (m)
PB	CC	OMZ	205	141201	587	103	205	131766	504	88
		OLZ	70	2293	267	212	52	1868	217	74
		HighDO	14	469	147	74	8	281	141	97
	CNP	OMZ	104	75356	679	76	104	75701	528	106
		OLZ	63	22072	699	121	64	19352	581	129
	SAP	OMZ	142	77529	619	79	141	72740	527	87
		OLZ	123	77283	619	162	123	65491	528	109
		HighDO	11	3349	260	153	11	1897	235	149
PM	CC	OMZ	159	129000	545	133	159	113188	475	142
		OLZ	45	1301	217	170	41	1969	165	110
		HighDO	9	174	94	55	8	197	70	45
	CNP	OMZ	119	115574	642	100	119	124221	479	94
		OLZ	113	89313	641	78	113	86115	463	71
	SAP	OMZ	108	92159	613	81	107	93181	465	88
		OLZ	144	298913	619	151	144	266540	452	81
		HighDO	9	2107	279	118	7	829	228	92

Table 4.S3 Model selection was performed first for the best random structure using the most complete model fitted with REML. Then, candidate models with different combinations of the fixed effects were fitted with ML and compared using AICc, its weight based on AICc, and parsimony.

*NoKamiDivesPerDay ~ Ecoregion * DOregion + propOMZdives * Ecoregion*

	PB Trip				PM Trip			
	K	AICc	ΔAICc	AICcWt	K	AICc	ΔAICc	AICcWt
varIdent(~1|Ecoregion * DOregion)	15	892.33	**0.00**	0.65	15	331.47	7.78	0.01
varIdent(~1|Ecoregion)	12	899.25	6.62	0.02	12	329.24	5.55	0.04
varIdent(~1|DOregion)	11	894.33	**1.70**	0.28	11	325.97	2.27	0.23
None	10	897.73	5.10	0.05	10	323.69	**0.00**	0.71

NoKamiDivesPerDay ~ Fixed Effects

	PB Trip				PM Trip			
	K	AICc	ΔAICc	AICcWt	K	AICc	ΔAICc	AICcWt
Random structure	*varIdent(form=1 | Ecoregion * DOregion)*							
~ Ecoregion + DOregion + propOMZdives	11	931.25	5.77	0.03	6	368.69	**0.00**	0.71
~ Ecoregion + DOregion + propOMZdives * Ecoregion	13	930.31	4.84	0.04	8	371.52	2.83	0.17
~ Ecoregion * DOregion + propOMZdives	13	925.48	**0.00**	0.49	8	372.59	3.90	0.10
~ Ecoregion * DOregion + propOMZdives * Ecoregion	15	925.69	**0.21**	0.44	10	376.11	7.43	0.02

Table 4.S4 Model outputs testing the influence of the proportion of dives in OMZ regions (*propOMZdives*) on energy gain (MJ) using a randomly selected trip for repeat seals that were different than those used in the first model run presented in Table 4.5. Predictor variables were scaled. Each trip was modeled separately.

Post-Breeding Trip		**Energy Gain**	
lm(EnergyGain ~ propOMZdives + DepartAdipose + DailyTotalDist)			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	1666.33 ***	1598.77 – 1733.90	**<0.001**
DailyTotalDist	-90.87 *	-161.16 – -20.58	**0.012**
DepartAdipose	-222.46 ***	-291.97 – -152.95	**<0.001**
propOMZdives	-97.17 **	-167.67 – -26.66	**0.007**
Observations	167		
R^2 / R^2 adjusted	0.251 / 0.237		

** p<0.05 ** p<0.01 *** p<0.001*

Post-Molt Trip		**Energy Gain**	
lm(EnergyGain ~ propOMZdives + DepartAdipose + DailyTotalDist + DaysAtSea)			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	5678.27 ***	5508.61 – 5847.93	**<0.001**
DailyTotalDist	-164.34	-350.02 – 21.34	0.082
DaysAtSea	-154.78	-327.62 – 18.06	0.079
DepartAdipose	-356.00 ***	-529.43 – -182.58	**<0.001**
propOMZdives	-291.43 **	-479.13 – -103.73	**0.003**
Observations	103		
R^2 / R^2 adjusted	0.253 / 0.222		

Table 4.S5 Performance of candidate models. Model selection was based on AICc and its weight. Bolded numbers are models with ΔAICc < 2 for which adjusted R^2 were also used for comparison. The model selected for each trip has its ΔAICc shaded.

	PB Trip				
	K	AICc	ΔAICc	AICcWt	Adj. R^2
EnergyGain ~ 1	2	2542.77	40.42	0.00	
+ propOMZdives	3	2532.73	30.38	0.00	
+ propOMZdives + DaysAtSea	4	2534.82	32.48	0.00	
+ propOMZdives + DepartAdipose	4	2503.83	**1.49**	0.14	0.218
+ propOMZdives + DailyTotalDist	4	2533.39	31.05	0.00	
+ propOMZdives + DaysAtSea + DepartAdipose	5	2505.04	2.70	0.07	
+ propOMZdives + DaysAtSea + DailyTotalDist	5	2535.49	33.15	0.00	
+ propOMZdives + DepartAdipose + DailyTotalDist	5	2502.34	**0.00**	0.28	0.230
+ propOMZdives + DaysAtSea + DepartAdipose + DailyTotalDist	6	2504.04	**1.70**	0.12	0.228
+ propOMZdives + DaysAtSea:DepartAdipose	4	2529.21	26.86	0.00	
+ propOMZdives + DaysAtSea:DepartAdipose + DailyTotalDist	5	2528.38	26.04	0.00	
+ propOMZdives + DaysAtSea:DepartAdipose + DaysAtSea + DepartAdipose	6	2505.39	3.05	0.06	
+ propOMZdives + DaysAtSea:DepartAdipose + DaysAtSea + DepartAdipose + DailyTotalDist	7	2503.59	**1.25**	0.15	0.235
+ propOMZdives + DaysAtSea:DailyTotalDist	4	2534.70	32.36	0.00	
+ propOMZdives + DaysAtSea:DailyTotalDist + DepartAdipose	5	2503.99	**1.64**	0.12	0.223
+ propOMZdives + DaysAtSea:DailyTotalDist + DaysAtSea + DailyTotalDist	6	2537.58	35.23	0.00	
+ propOMZdives + DaysAtSea:DailyTotalDist + DaysAtSea + DailyTotalDist + DepartAdipose	7	2505.98	3.63	0.05	

Table 4.S5 (continued) Performance of candidate models. Model selection was based on AICc and its weight. Bolded numbers are models with ΔAICc < 2 for which adjusted R^2 were also used for comparison. The model selected for each trip has its ΔAICc shaded.

	PM Trip				
	K	AICc	ΔAICc	AICcWt	Adj. R^2
EnergyGain ~ 1	2	1716.43	22.87	0.00	
+ propOMZdives	3	1709.32	15.76	0.00	
+ propOMZdives + DaysAtSea	4	1709.83	16.26	0.00	
+ propOMZdives + DepartAdipose	4	1698.10	4.54	0.04	
+ propOMZdives + DailyTotalDist	4	1706.50	12.93	0.00	
+ propOMZdives + DaysAtSea + DepartAdipose	5	1696.48	2.92	0.09	
+ propOMZdives + DaysAtSea + DailyTotalDist	5	1706.70	13.14	0.00	
+ propOMZdives + DepartAdipose + DailyTotalDist	5	1695.62	2.06	0.14	
+ propOMZdives + DaysAtSea + DepartAdipose + DailyTotalDist	6	1693.56	**0.00**	0.38	0.234
+ propOMZdives + DaysAtSea:DepartAdipose	4	1709.76	16.20	0.00	
+ propOMZdives + DaysAtSea:DepartAdipose + DailyTotalDist	5	1708.09	14.53	0.00	
+ propOMZdives + DaysAtSea:DepartAdipose + DaysAtSea + DepartAdipose	6	1698.11	4.55	0.04	
+ propOMZdives + DaysAtSea:DepartAdipose + DaysAtSea + DepartAdipose + DailyTotalDist	7	1695.81	2.25	0.12	
+ propOMZdives + DaysAtSea:DailyTotalDist	4	1711.37	17.81	0.00	
+ propOMZdives + DaysAtSea:DailyTotalDist + DepartAdipose	5	1699.33	5.77	0.02	
+ propOMZdives + DaysAtSea:DailyTotalDist + DaysAtSea + DailyTotalDist	6	1708.96	15.40	0.00	
+ propOMZdives + DaysAtSea:DailyTotalDist + DaysAtSea + DailyTotalDist + DepartAdipose	7	1695.28	**1.72**	0.16	0.231

Table 4.S6 Comparisons of the best model (1) against a reduced model (2) dropping the term related to DO levels (*propOMZdives*) and against the null model (3) using *F*-tests.

	PB Trip				
	EnergyGain ~ propOMZdives + DepartAdipose + DailyTotalDist				
	Test	DF	*F*-statistic	*p*-value	AICc
Best model					2502.345
- propOMZdives	1 vs 2	1, 163	7.465	0.007	2507.696
~ 1	1 vs 3	3, 163	17.540	< .0001	2542.766
	PM Trip				
	EnergyGain ~ propOMZdives + DaysAtSea + DepartAdipose + DailyTotalDist				
	Test	DF	*F*-statistic	*p*-value	AICc
Best model					1693.561
- propOMZdives	1 vs 2	1, 98	11.006	0.001	1702.324
~ 1	1 vs 3	4, 98	8.805	< .0001	1716.430

Table 4.S7 Model selection was performed first for the best random structure using the most complete model fitted with REML. Then, candidate models with different combinations of the fixed effects were fitted with ML and compared using AICc, its weight based on AICc, and marginal R^2.

ChangeInDriftRate ~ AvgDOatKami + AvgDOatKami:DOregion + KamiNoSumPerDive + KamiNoSumPerDive:Ecoregion + Ecoregion + DOregion + KamiNoSumPerDive:PctOfTrip + PctOfTrip + I(PctOfTrip^2), random=(~1|TOPPID)

	PB Trip				PM Trip			
	K	AICc	ΔAICc	AICcWt	K	AICc	ΔAICc	AICcWt
varIdent(~1|Ecoregion * DOregion)	18	-1369.30	**0.00**	0.79	18	-1351.33	2.17	0.24
varIdent(~1|Ecoregion)	16	-1366.61	2.70	0.21	16	-1353.50	**0.00**	0.72
varIdent(~1|DOregion)	15	-1344.66	24.65	0.00	15	-1345.11	8.40	0.01
None	14	-1346.22	23.08	0.00	14	-1347.26	6.24	0.03

Table 4.S7 (continued) Model selection was performed first for the best random structure using the most complete model fitted with REML. Then, candidate models with different combinations of the fixed effects were fitted with ML and compared using AICc, its weight based on AICc, and marginal R^2.

ChangeInDriftRate~ AvgDOatKami + AvgDOatKami:DOregion + KamiNoSumPerDive + KamiNoSumPerDive:Ecoregion
+ Ecoregion + DOregion + KamiNoSumPerDive:PctOfTrip + PctOfTrip + I(PctOfTrip^2) , random=(~1|TOPPID)

	PB Trip					PM Trip				
	weights = varIdent(form=1 | Ecoregion * DOregion)					_weights = varIdent(form=1 | Ecoregion)_				
	K	AICc	ΔAICc	AICcWt	R^2	K	AICc	ΔAICc	AICcWt	R^2
Full model	18	-1564.04	4.34	0.03		16	-1545.80	**1.47**	0.17	0.244
- KamiNoSumPerDive:PctOfTrip	17	-1565.94	2.44	0.08		15	-1547.27	**0.00**	0.36	0.245
- KamiNoSumPerDive:Ecoregion	16	-1566.72	**1.66**	0.12	0.308	14	-1540.63	6.64	0.01	
- AvgDOatKami:DOregion	17	-1564.40	3.98	0.04		15	-1545.03	2.24	0.45	
- KamiNoSumPerDive:PctOfTrip, - KamiNoSumPerDive:Ecoregion	15	-1568.38	**0.00**	0.28	0.307	13	-1539.27	8.00	0.01	
- KamiNoSumPerDive:PctOfTrip, - AvgDOatKami:DOregion	16	-1566.25	2.13	0.10		14	-1546.96	**0.31**	0.31	0.248
- KamiNoSumPerDive:Ecoregion, - AvgDOatKami:DOregion	15	-1566.45	**1.93**	0.11	0.306	13	-1539.19	8.08	0.01	
- KamiNoSumPerDive:PctOfTrip, - KamiNoSumPerDive:Ecoregion, - AvgDOatKami:DOregion	14	-1568.07	**0.31**	0.26	0.305	12	-1539.14	8.13	0.01	

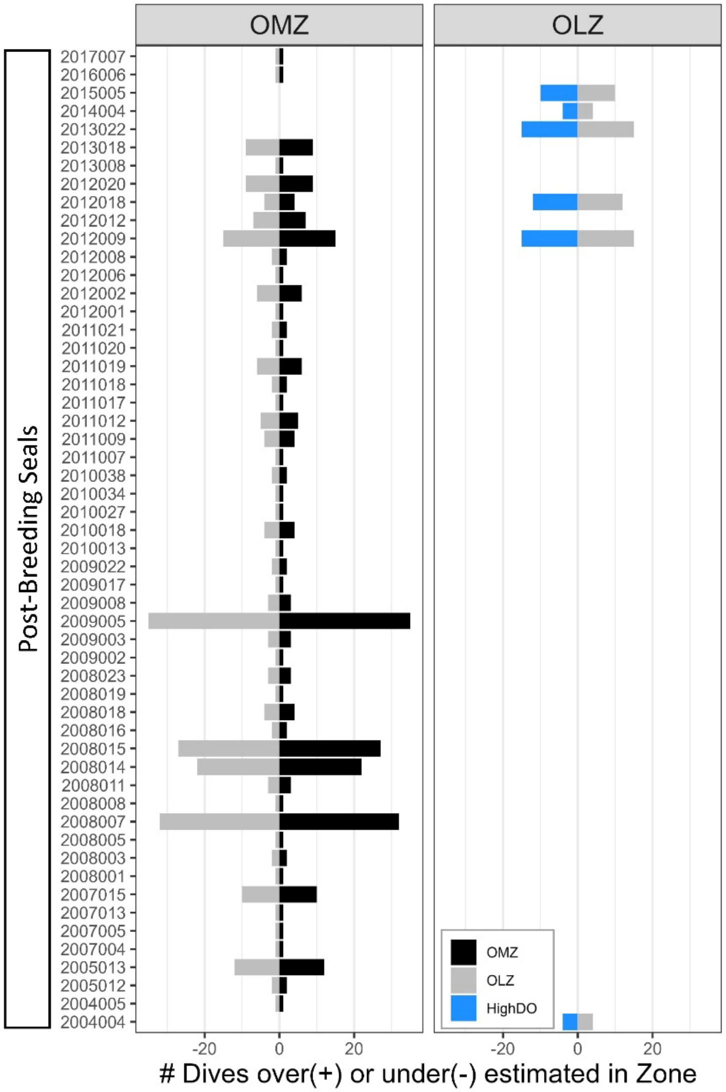
Table 4.S8 Comparisons of the best model (1) against a reduced model (2) dropping the terms related to DO levels (*AvgDOatKami* and its interaction with other variables), a reduced model (3) with only the terms related to the timing of the bouts and (3) the null model using likelihood ratio tests. Conditional R^2 are provided.

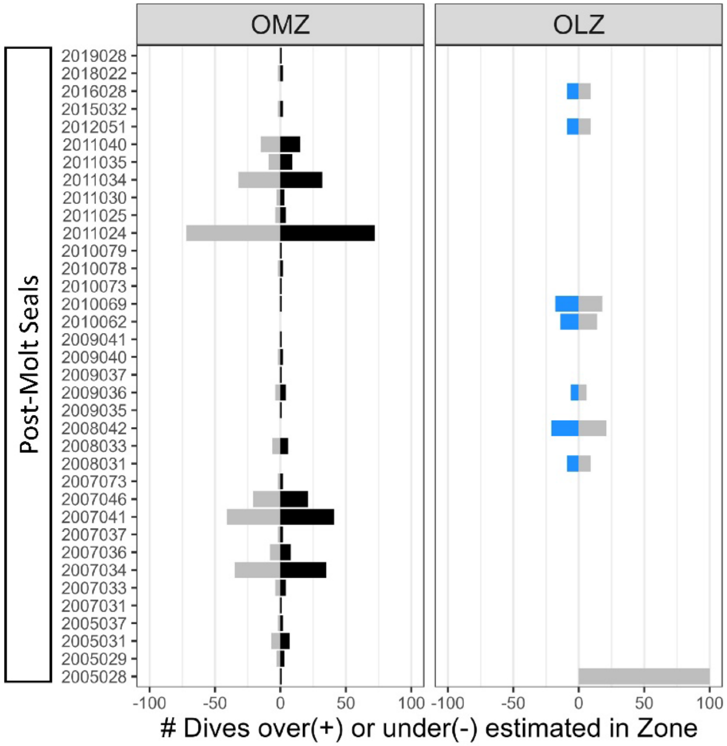
	PB Trip						
	*lme(ChangeInDriftRate ~ AvgDOatKami + AvgDOatKami:DOregion + NoKamiPerDive + Ecoregion + DOregion + PctOfTrip + I(PctOfTrip^2), weights = varIdent(form = ~1|Ecoregion * DOregion), random = (~1|TOPPID))*						
	Test	DF	AIC	LL	L ratio	p	R^2
Best model		15	-1570.425	800.213			0.337
- AvgDOatKami terms	1 vs. 2	13	-1571.426	798.713	2.999	0.2232	0.333
~ PctOfTrip + I(PctOfTrip^2)	1 vs. 3	9	-1570.758	794.388	11.668	0.0698	0.283
~ 1	1 vs. 4	7	-1475.785	744.893	110.640	< .0001	0.022

Table 4.S8 (continued) Comparisons of the best model (1) against a reduced model (2) dropping the terms related to DO levels (*AvgDOatKami* and its interaction with other variables), a reduced model (3) with only the terms related to the timing of the bouts and (3) the null model using likelihood ratio tests. Conditional R^2 are provided.

<table>
<tr><th></th><th colspan="7">PM Trip</th></tr>
<tr><td></td><td colspan="7"><i>lme(ChangeInDriftRate ~ AvgDOatKami + AvgDOatKami:DOregion + NoKamiPerDive + NoKamiPerDive :Ecoregion + Ecoregion + DOregion + PctOfTrip + I(PctOfTrip^2), weights = varIdent(form = ~1|Ecoregion), random = (~1|TOPPID))</i></td></tr>
<tr><td></td><td>Test</td><td>DF</td><td>AIC</td><td>LL</td><td>L ratio</td><td><i>p</i></td><td>R^2</td></tr>
<tr><td>Best model</td><td></td><td>15</td><td>-1549.278</td><td>789.634</td><td></td><td></td><td>0.299</td></tr>
<tr><td>- AvgDOatKami terms</td><td>1 vs. 2</td><td>13</td><td>-1549.286</td><td>787.6431</td><td>3.991</td><td>0.1359</td><td>0.287</td></tr>
<tr><td>~ PctOfTrip + I(PctOfTrip^2)</td><td>1 vs. 3</td><td>7</td><td>-1524.918</td><td>769.459</td><td>40.360</td><td>< .0001</td><td>0.107</td></tr>
<tr><td>~ 1</td><td>1 vs. 4</td><td>5</td><td>-1494.881</td><td>752.441</td><td>74.396</td><td>< .0001</td><td>0.056</td></tr>
</table>

Figure 4.S1 The number of dives per seal for which there was a discrepancy between the low oxygen zone determined by the index versus dissolved oxygen levels at the max dive depth. 54 of 205 PB seals and 36 of 159 PM seals are shown in the figure. The remaining seals had 0 dives with discrepancies. Positive values indicate the index overestimated how many dives reached that zone while negative values indicate underestimation. The index results in a bias towards a greater use of lower oxygen zones.


OMZ
OLZ
Post-Breeding Seals
2017007
2016006
2015005
2014004
2013022
2013018
2013008
2012020
2012018
2012012
2012009
2012008
2012006
2012002
2012001
2011021
2011020
2011019
2011018
2011017
2011012
2011009
2011007
2010038
2010034
2010027
2010018
2010013
2009022
2009017
2009008
2009005
2009003
2009002
2008023
2008019
2008018
2008016
2008015
2008014
2008011
2008008
2008007
2008005
2008003
2008001
2007015
2007013
2007005
2007004
2005013
2005012
2004005
2004004
-20
0
20
-20
0
20
OMZ
OLZ
HighDO
Dives over(+) or under(-) estimated in Zone


OMZ
OLZ
Post-Molt Seals
2019028
2018022
2016028
2015032
2012051
2011040
2011035
2011034
2011030
2011025
2011024
2010079
2010078
2010073
2010069
2010062
2009041
2009040
2009037
2009036
2009035
2008042
2008033
2008031
2007073
2007046
2007041
2007037
2007036
2007034
2007033
2007031
2005037
2005031
2005029
2005028
-100
-50
0
50
100
-100
-50
0
50
100
Dives over(+) or under(-) estimated in Zone

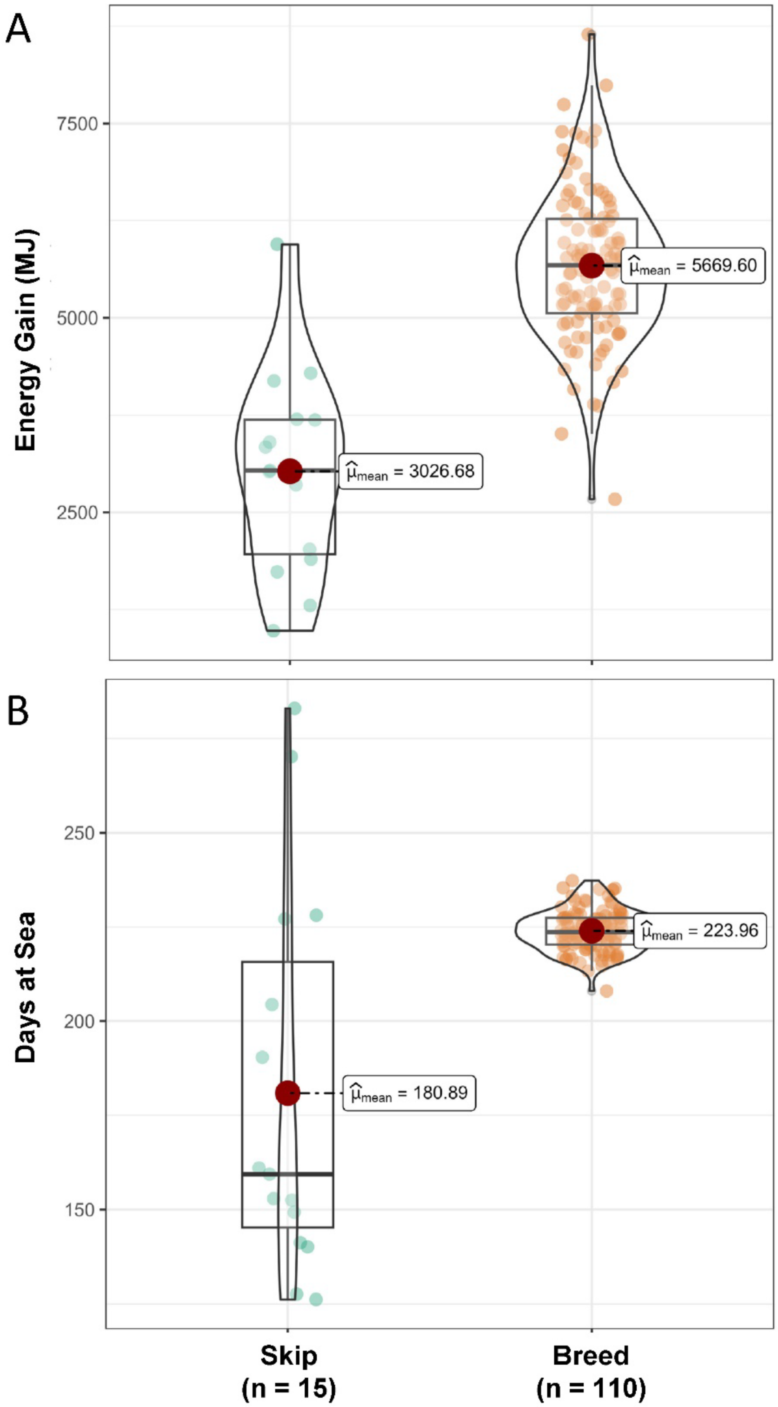


Figure 4.S2 A comparison of energy gain (A) and days at sea (B) between seals that skipped pupping and seals that successfully bred after returning from the post-molt trip. Plot created using R package ggstatsplot (version 0.11.1; Patil, 2021).

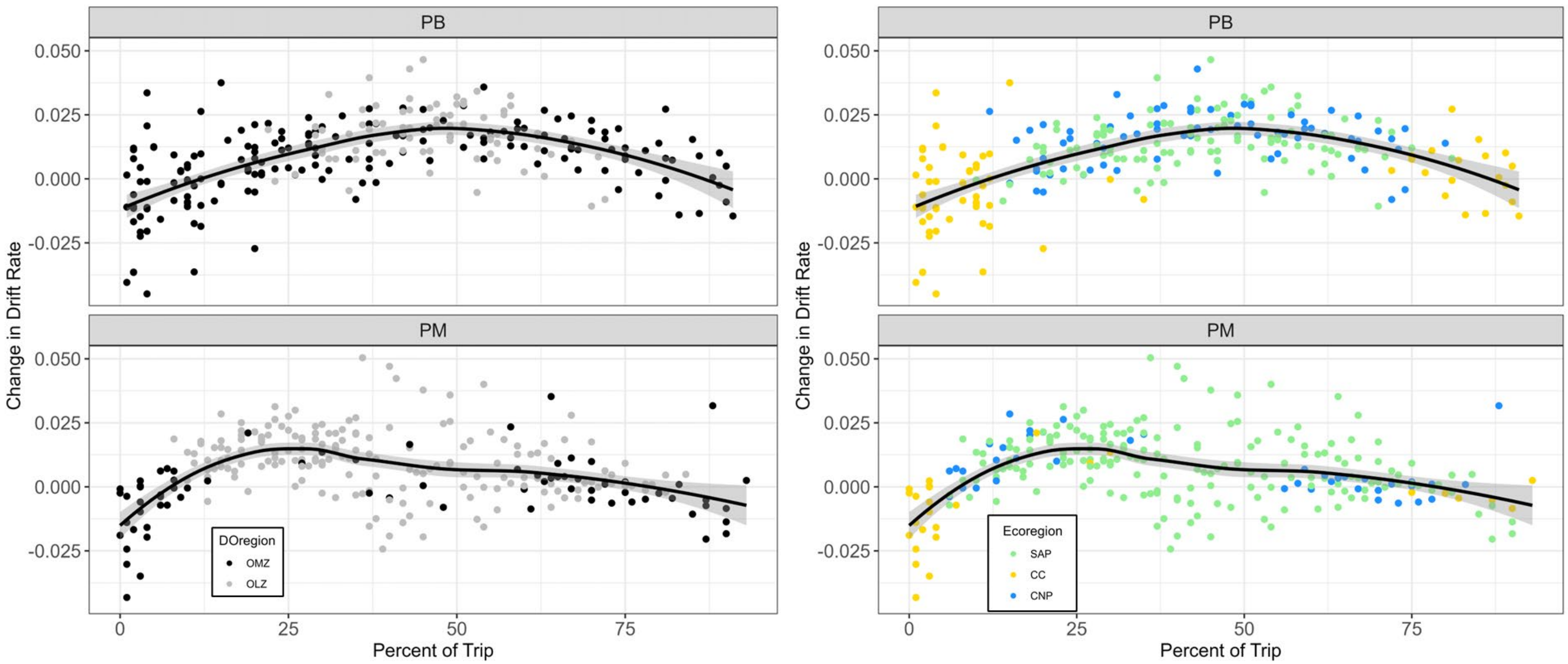


Figure 4.S3 The relationship between change in drift rate over a 6-day period and percent of trip for both trips. Data points are color coded by DO region (left) or ecoregion (right).

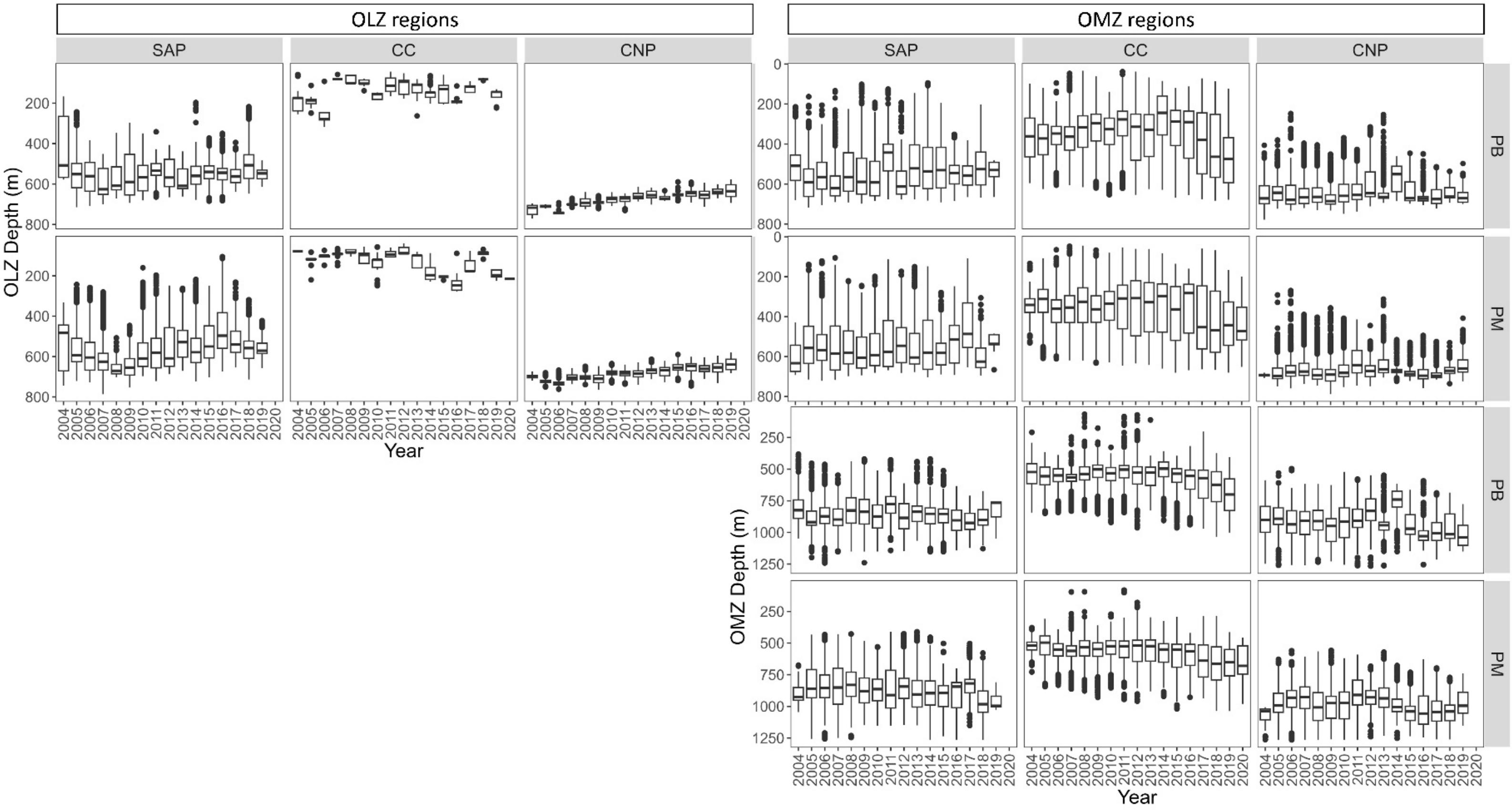


Figure 4.S4 Interannual variability from 2004-2020 in OLZ depth in OLZ regions (top left), OLZ depth in OMZ regions (top right), and OMZ depth (bottom right) encountered by seals in each ecoregion (columns) during each trip (rows).

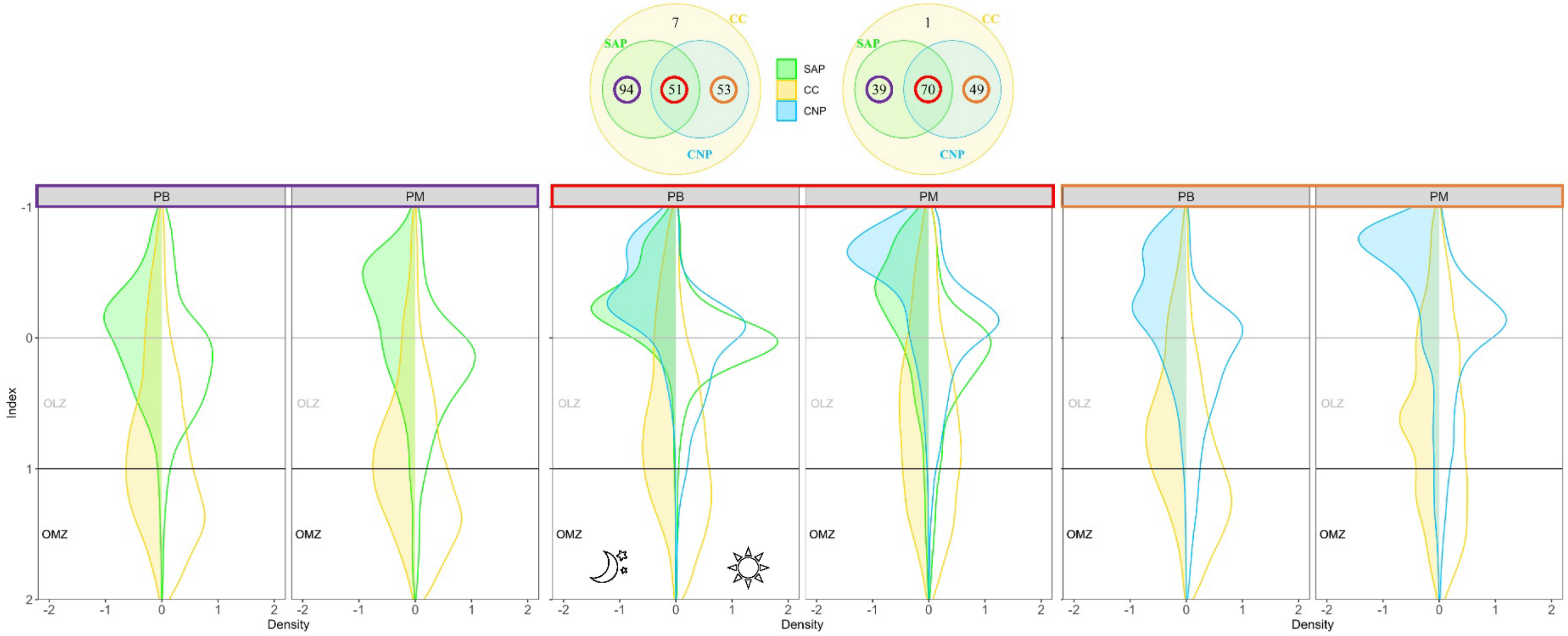


Figure 4.S5 Daytime (positive values) and nighttime (negative values) density distributions of the DO zonation index for each ecoregion calculated for the dives of the seals that belong in the sections of the Venn-diagram indicated by the circle of matching color. Density distributions were weighted by the number of dives for each seal.

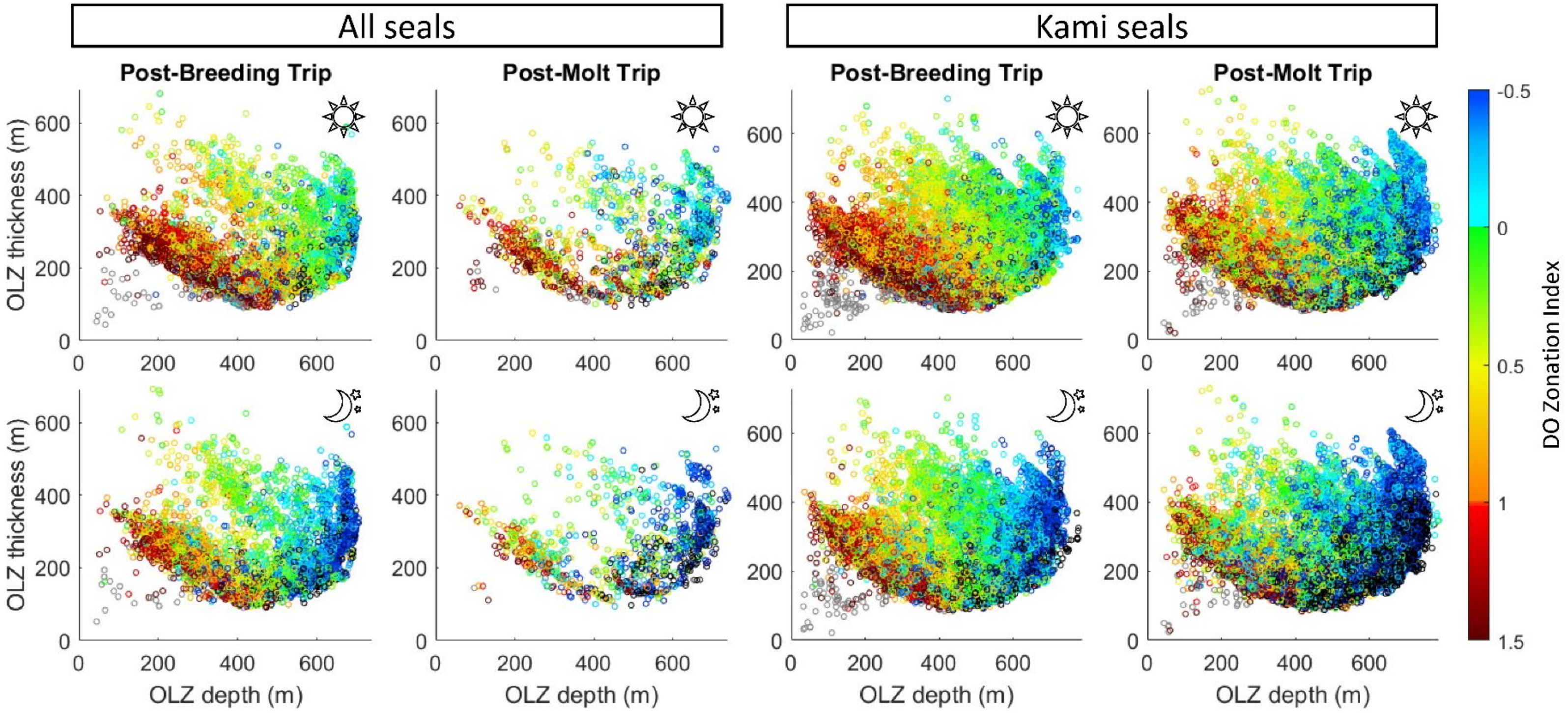


Figure 4.S6 Scatterplots depicting the patterns in the DO zonation index for all seals (left) and Kami Seals (right). In each panel of figures, the left and right columns are dives in the post-breeding and post-molt trips, respectively, while the top and bottom rows are daytime and nighttime dives, respectively.

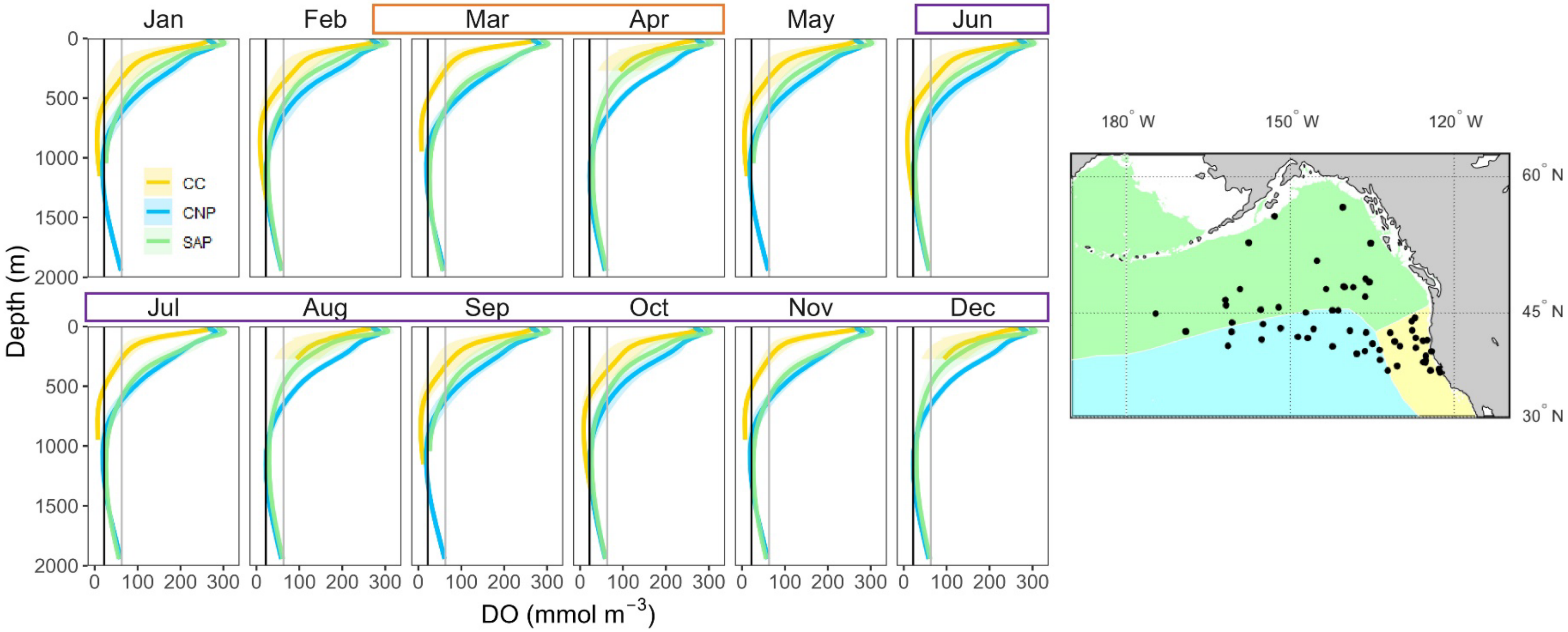


Figure 4.S7 Seasonal variability of dissolved oxygen profiles encountered by seals. Dissolved oxygen profiles were averaged at 20 randomly chosen locations within each ecoregion based on seal tracks. The months of the post-breeding trip are boxed in orange and post-molt trip in purple.

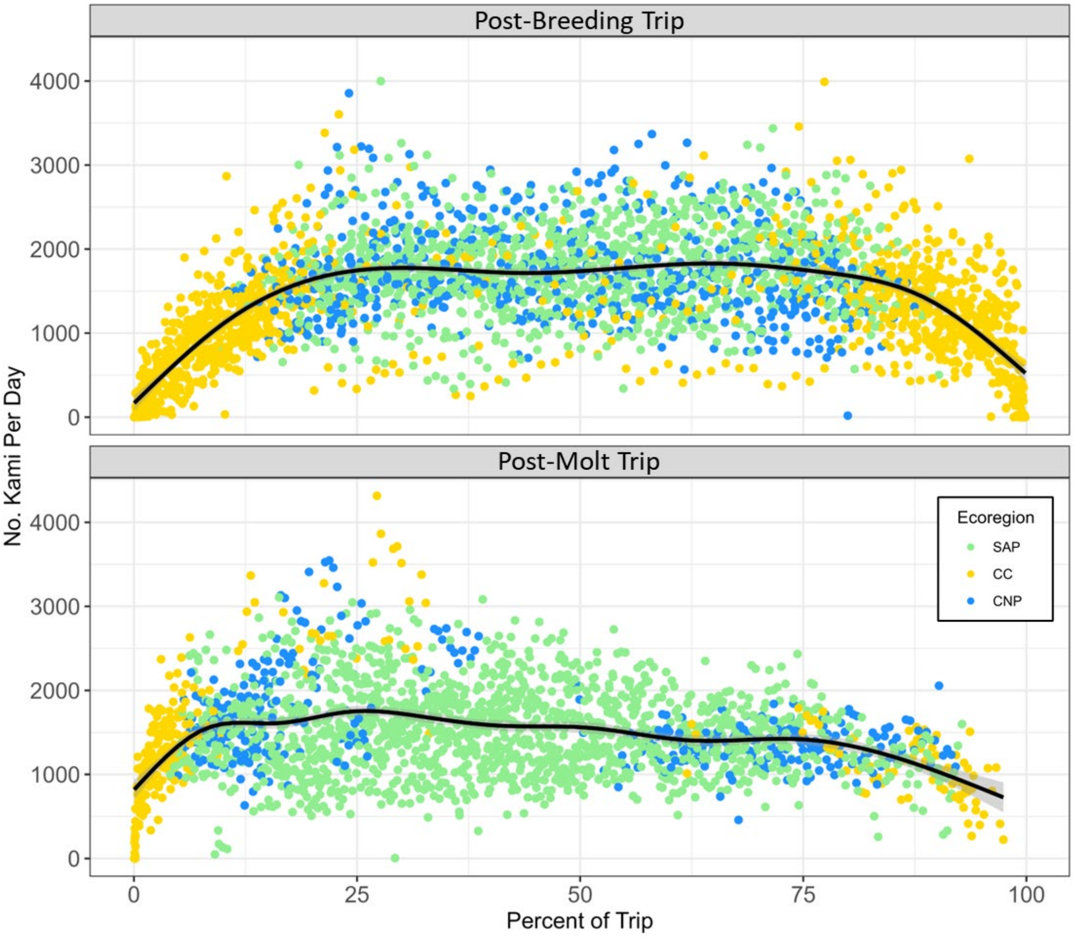


Figure 4.S8 The number of Kami signals per day across each trip with points color coded by ecoregion.

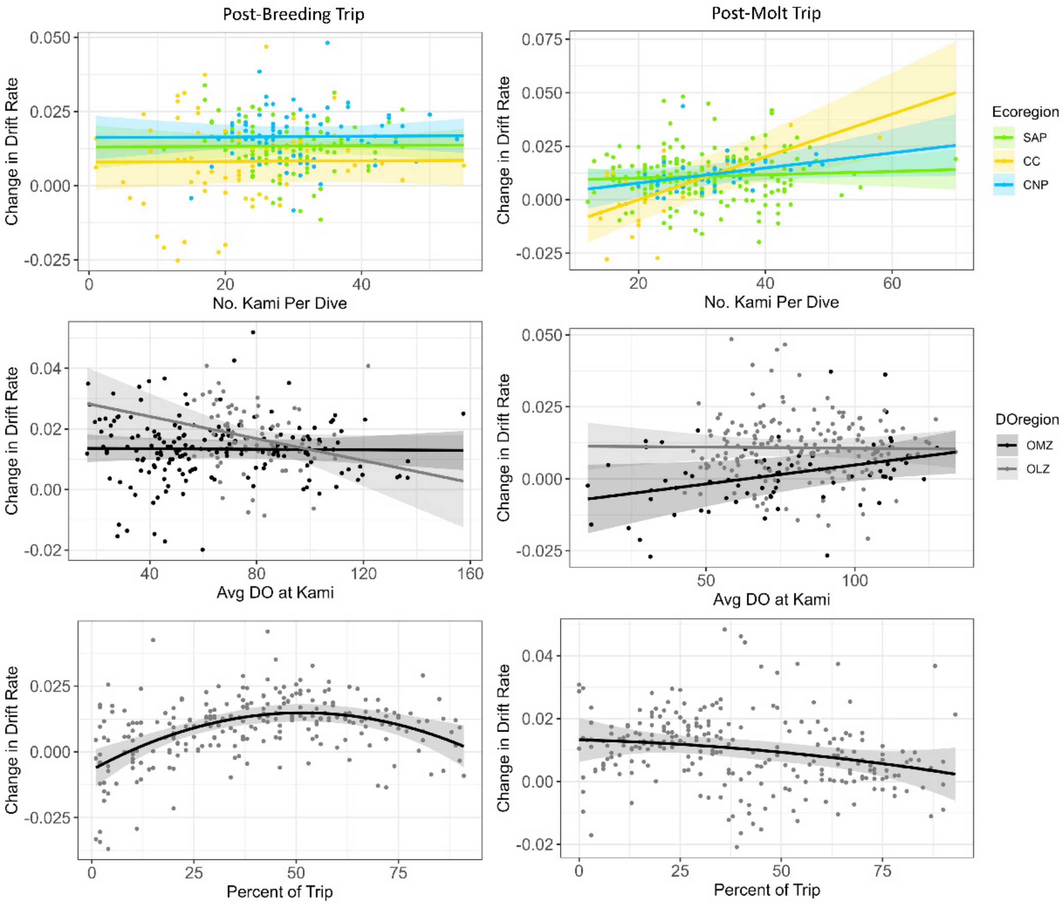


Figure 4.S9 Marginal effects plots for each ecoregion (top row) and DO region (middle row) for each trip. Predicted values of the change in drift rate are plotted against the number of Kami signals per dive (top row), average dissolved oxygen levels at the median depth of the Kami signals (middle row), and the percent of trip (bottom row).

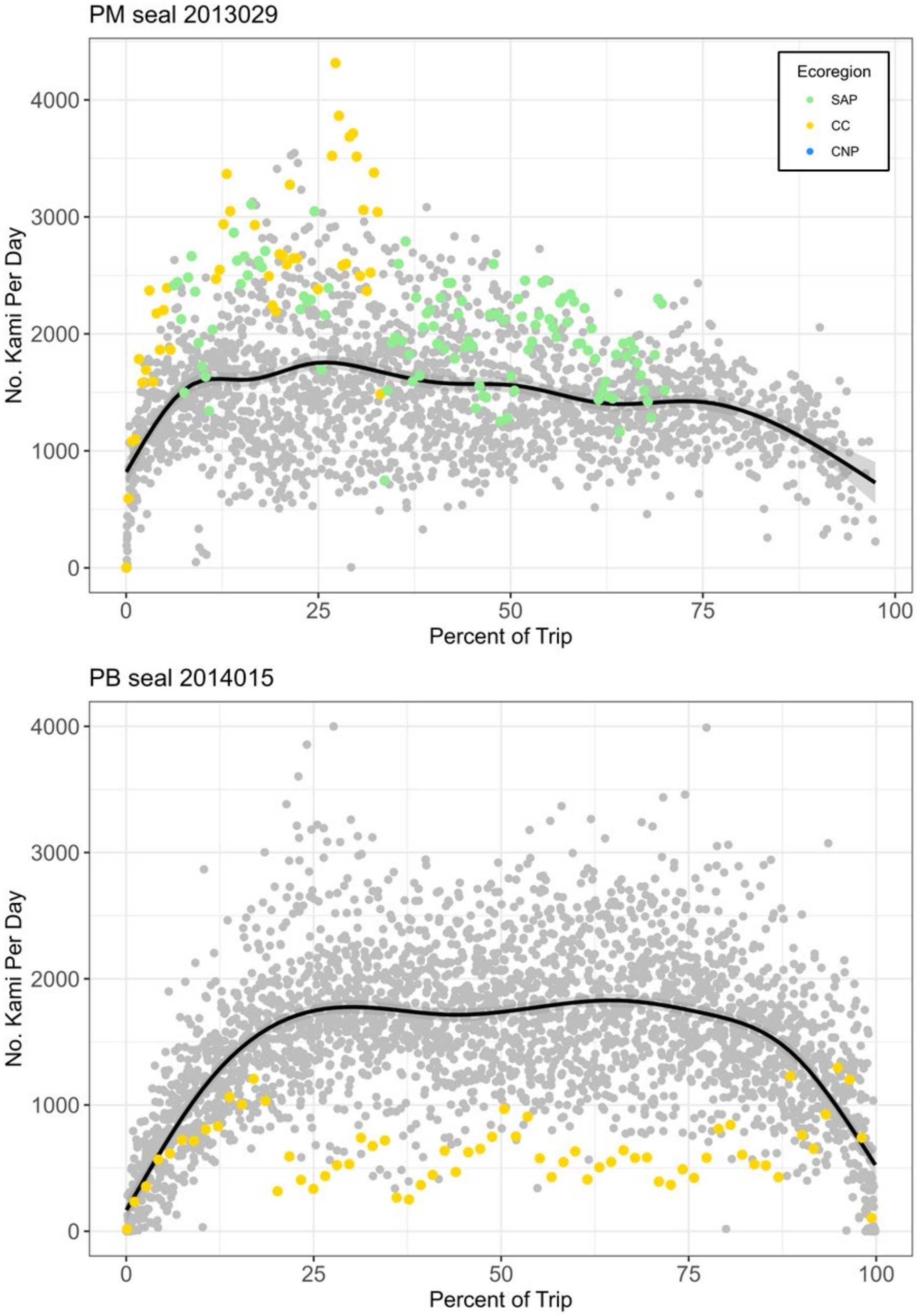


Figure 4.S10 The number of Kami signals per day across the trip for PM seal 2013029 and PB seal 2014015 compared to other seals on the same trip. The points for the individual seals are color coded by ecoregion.

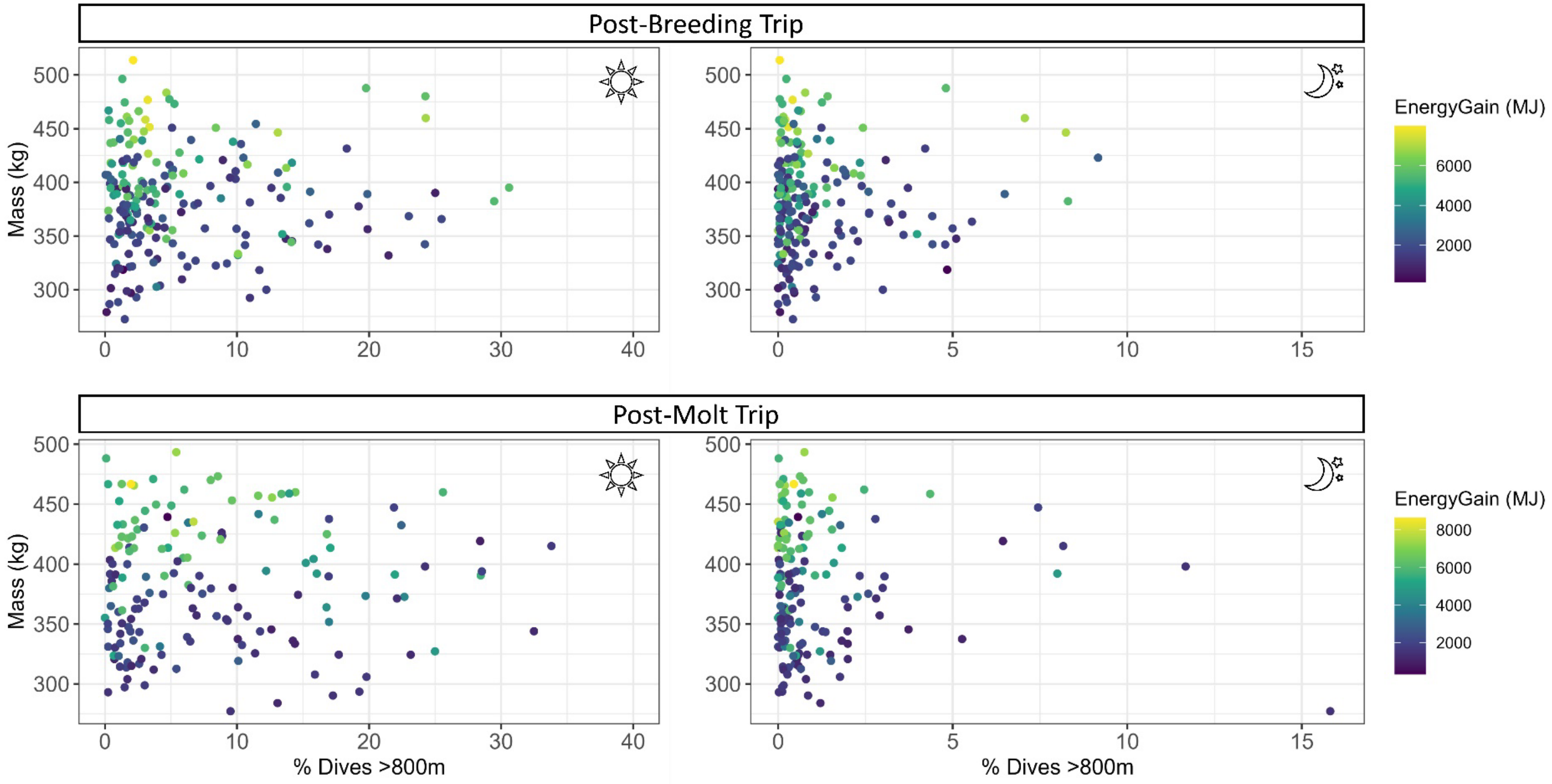


Figure 4.S11 The relationship between the proportion of dives > 800 m and foraging success. Mass was calculated as the average between departure and arrival mass.

Synthesis

Given its three-dimensional structure and dynamic conditions, the marine environment provides a complex, albeit challenging, habitat in which to study the movement ecophysiology of organisms (Hussey et al., 2015; Melo-Merino et al., 2020). Understanding how environmental factors influence both horizontal and vertical movement is important for better predicting the ecological consequences of changing ocean conditions. Vertical movement in particular is physiologically constrained by steep gradients of physical and biogeochemical properties, including pressure, light, temperature, and dissolved oxygen (e.g., Benoit-Bird et al., 2009; Bernal et al., 2017; Braun et al., 2015; Brill, 1994; Burford et al., 2022; Carlisle et al., 2017; Vedor et al., 2021; Worm et al., 2005). This dissertation focused on the effects of temperature and dissolved oxygen, both of which are currently undergoing the greatest and most concerning changes in the ocean at a global scale due to climate change (Bopp et al., 2013).

The changes occurring in temperature and dissolved oxygen can affect marine megafauna either directly through physiological mechanisms or indirectly through the distribution of their prey relative to these variables. The mechanism depends on whether the animals are water-breathing or air-breathing and ectotherms or endotherms. While water-breathing ectotherms can find and follow isotherms, air-breathers must withstand thermal gradients repetitively as they dive to find food and return to the surface for air. Here we reviewed the thermoregulatory strategies of air-breathing marine vertebrates and found that the physiological demands of thermoregulation alongside diving, exercise, and digestion may be synergistic or antagonistic depending on the context. We also synthesized the various strategies described in the literature for balancing these potentially conflicting physiological demands and highlighted questions that remain open (Chapter 1).

Given that earlier studies on thermal physiology were primarily conducted in the laboratory, the coordination of thermal responses with the dive response was not well understood. However, the advancement of biologging tools has allowed us to measure relevant physiological variables in free-ranging animals and assess the ecological relevance of previous findings. We demonstrated the use of physiological biologgers to investigate the dual role of peripheral perfusion for diving and thermoregulation in marine mammals (Chapter 2). Using northern elephant seals as a model species, we explored how deep-diving marine mammals thermoregulate while encountering temperature gradients by analyzing concurrent measurements of water temperature, heat flux, body temperature, and behavior. We found that peripheral cooling allows for prioritization of the dive response, but a thermoregulatory debt accrued during deep diving may require modulating diving behavior to prevent large deviations from normothermia (Chapter 3).

Unlike temperature which affects both marine ectotherms and endotherms, albeit to different extents, dissolved oxygen has no direct effect on air-breathers. Their ability to maintain a relatively constant body temperature (within a relatively large range of ambient temperatures) and breathe air allows their metabolism and activity to be independent of the temperature and dissolved oxygen experienced while diving. Therefore, air-breathing endotherms are expected to be less physiologically vulnerable to ocean warming and deoxygenation but indirectly affected by trophically-mediated consequences of climate change (Albouy et al., 2020; Gulland et al., 2022).

Previous work has shown that the difference in temperature-dependence of metabolism between endotherms and ectotherms explains trophic interactions (i.e., competition and predation) and the resulting global distribution of these marine predators (Cairns et al., 2008; Deutsch et al., 2020; Grady et al., 2019). However, temperature is often only considered in the horizontal dimension (i.e., sea surface temperature), which does not reflect the range of temperatures experienced nor the representative temperature at mean foraging depths of these marine predators. Moreover, temperature influences both the availability of dissolved oxygen in the water as well as the rate of oxygen utilization of water-breathing ectotherms (Pörtner & Gutt, 2016; Vaquer-Sunyer & Duarte, 2011; Verberk et al., 2011). Globally, ocean waters are warming and will therefore have lower dissolved oxygen concentrations (Matear & Hirst, 2003). To meet metabolic requirements, water-breathing ectotherms (e.g., fish) may shift to depths with sufficient oxygen and suitable temperature, if such a sweet spot exists. In reality, both vertical and horizontal displacement are likely to occur to varying extents for different species (Deutsch et al., 2015, 2020). Given that species have different thermal and hypoxia tolerances (Childress & Seibel, 1998; Duskey, 2023; Seibel, 2011), it becomes difficult to predict the ecosystem level impacts of ocean warming and deoxygenation. Studying the indirect effects of temperature and dissolved oxygen on the movement patterns, distribution, and foraging success of top predators can provide insight into changing ecosystem dynamics.

Given their large size, high trophic level, and key role in transporting nutrients and energy, marine megafauna serve as sentinel species for changing ecosystem dynamics (Estes et al., 2016; Hazen et al., 2019). We demonstrated that northern elephant seals can serve as a sentinel species for the mesopelagic ecosystem and examined their movement and foraging behavior relative to low-oxygen zones. We found that at a population level, elephant seals primarily use the oxygen-limited zone across their foraging range rather than the oxygen minimum zone as previously hypothesized and have higher foraging success in regions without oxygen minimum zones. The patterns of low-oxygen zone utilization across the North Pacific suggest that the diving behavior of seals is driven by their physiological capacity for breath-hold diving and the diel migration of their prey rather than the changing oxyscape (Chapter 4). The depths at which the deep scattering layer aggregates during the daytime is not only influenced by dissolved oxygen but also temperature and light levels (Benoit-Bird et al., 2009; Robinson et al., 2010; Vaquer-Sunyer & Duarte, 2011). Although we focused on dissolved oxygen in this chapter, integrating co-varying environmental factors would provide a more holistic understanding of how these vertical gradients influence the distribution of mesopelagic micronekton and thus indirectly affect the behavior of their predators.

Our results support the use of animal-borne dissolved oxygen sensors on elephant seals to track changing oxygen levels. While animal-borne temperature sensors are ubiquitous and already integrated into global ocean-observing systems (McMahon et al., 2021), reliable long-term dissolved oxygen sensors are still being developed (e.g., Bailleul et al., 2015; Coffey et al., 2020; Coffey & Holland, 2015; Logan et al., 2023). In addition to sensing the environmental changes, changes in the three-dimensional movement and foraging behavior of marine top predators should reflect changes to the distribution of their prey (Braun et al., 2022; McMahon et al., 2019), which are more likely to be directly impacted by changes in temperature and dissolved oxygen (Deutsch et al., 2015, 2020; Little et al., 2020). The long-term dataset available for northern elephant seals enables the detection of behavioral shifts at a population level, which could provide an early-warning system for changes in the mesopelagic ecosystem that could eventually trickle up the trophic web and severely impact other marine organisms that depend on the mesopelagic for food (Iglesias et al., 2023; Kordas et al., 2022; Simmonds & Isaac, 2007).

By investigating how temperature and dissolved oxygen affects the ecophysiology of a deep-diving mesopelagic predator, this dissertation demonstrated the importance of analyzing movement in multiple dimensions to better understand how environmental factors interact with physiological demands, impose physiological constraints, and influence behavior. Expanding such studies to other marine megafauna to better understand their ecophysiology will be critical for evaluating how stressors, including global warming and anthropogenic disturbance, will affect individuals and scale up to the population level, which could ultimately affect entire ecosystems.

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Appendices

Appendix A1

Table A1.1 List of species common and scientific names that we considered to be true air-breathing divers and were included in the species counts for Figure 1.1.

The absolute latitudes were determined to the nearest 5° based on species distribution maps accessed from the IUCN Red List (https://www.iucnredlist.org). All species of marine mammals were included, except for river dolphins and those data deficient species for which the distribution map did not exist on the IUCN Red List. Within procellariiformes, albatross, shearwaters, and the 4 species of diving petrels were included. Only species in the family alcidae were included for Charadriiformes. Pelicans, tropicbirds, and frigatebirds were excluded for Pelecaniformes as these seabirds are not pursuit divers nor do they have comparable diving abilities.

To determine the range in body mass within each common group, the smallest and largest species were identified and denoted in the table with † and ‡, respectively. Mass in kg is provided in parentheses after their common name and the reference is included. For the taxonomic groups that have only one species, the range in body mass for that specie is provided.

Common Name	*Scientific Name*	*Latitude*	
		Low	*High*
MARINE MAMMALS			
Baleen whales (n=13)			
Antarctic minke whale	*Balaenoptera bonaerensis*	0	90
Blue whale‡ (122000 kg)[2]	*Balaenoptera musculus*	0	90
Bowhead	*Balaena mysticetus*	55	85
Bryde’s whale	*Balaenoptera edeni*	0	45
Common minke whale	*Balaenoptera acutorostrata*	0	85
Fin whale	*Balaenoptera physalus*	20	85
Gray whale	*Eschrichtius robustus*	20	75
Humpback whale	*Megaptera novaeangliae*	0	85
North Atlantic right whale	*Eubalaena glacialis*	25	70
North Pacific right whale	*Eubalaena japonica*	30	65

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Pygmy right whale† (4000 kg)[3]	*Caperea marginata*	20	60
Sei whale	*Balaenoptera borealis*	0	75
Southern right whale	*Eubalaena australis*	10	65
Toothed whales (n=65)			
Andrew's beaked whale	*Mesoplodon bowdoini*	25	50
Arnoux's beaked whale	*Berardius arnuxii*	20	80
Atlantic humpbacked dolphin	*Sousa teuszii*	0	25
Atlantic spotted dolphin	*Stenella frontalis*	0	50
Atlantic white-sided dolphin	*Lagenorhynchus acutus*	40	80
Australian snubfin dolphin	*Orcaella heinsohni*	0	20
Baird's beaked whale	*Berardius bairdii*	25	65
Beluga whale	*Delphinapterus leucas*	55	90
Blainville's beaked whale	*Mesoplodon densirostris*	0	65
Bottlenose dolphin	*Tursiops truncatus*	0	65
Burmeister's porpoise	*Phocoena spinipinnis*	5	55
Chilean (Black) dolphin	*Cephalorhynchus eutropia*	35	55
Clymene dolphin	*Stenella clymene*	0	40
Commerson’s dolphin	*Cephalorhynchus commersonii*	40	55
Cuvier's beaked whale	*Ziphius cavirostris*	0	65
Dall's porpoise	*Phocoenoides dalli*	35	65
Dusky dolphin	*Lagenorhynchus obscurus*	10	55
Dwarf sperm whale	*Kogia sima*	0	40
False killer whale	*Pseudorca crassidens*	0	65
Fraser’s dolphin	*Lagenodelphis hosei*	0	40
Ginkgo-toothed beaked whale	*Mesoplodon ginkgodens*	0	40
Gray's beaked whale	*Mesoplodon grayi*	10	65
Harbor porpoise	*Phocoena phocoena*	20	85
Heaviside’s dolphin	*Cephalorhynchus heavisidii*	15	30
Hector’s dolphin	*Cephalorhynchus hectori*	35	45
Hector's beaked whale	*Mesoplodon hectori*	30	55
Hourglass dolphin	*Lagenorhynchus cruciger*	35	60
Hubbs’ beaked whale	*Mesoplodon carlhubbsi*	30	50
Indo-Pacific beaked whale	*Indopacetus pacificus*	0	40
Indo-Pacific bottlenose dolphin	*Tursiops aduncus*	0	40
Indo-Pacific finless porpoise	*Neophocaena phocaenoides*	0	30
Indo-Pacific humpbacked dolphin	*Sousa chinensis*	0	30
Irrawaddy dolphin	*Orcaella brevirostis*	0	30
Killer whale	*Orcinus orca*	0	90
Long-beaked common dolphin	*Delphinus capensis*	0	40

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Long-finned pilot whale	*Globicephala melas*	15	75
Melon-headed whale	*Peponocephala electra*	0	40
Narwhal	*Monodon monoceros*	65	90
Northern bottlenose whale	*Hyperoodon ampullatus*	15	75
Northern right whale dolphin	*Lissodelphis borealis*	35	50
Pacific white-sided dolphin	*Lagenorhynchus obliquidens*	25	60
Pantropical spotted dolphin	*Stenella attenuata*	0	40
Peale's dolphin	*Lagenorhynchus australis*	35	60
Perrin's beaked whale	*Mesoplodon perrini*	35	40
Pygmy beaked whale	*Mesoplodon peruvianus*	0	30
Pygmy killer whale	*Feresa attenuata*	0	45
Pygmy sperm whale	*Kogia breviceps*	0	55
Risso’s dolphin	*Grampus griseus*	0	60
Rough-toothed dolphin	*Steno bredanensis*	0	45
Shepherd's beaked whale	*Tasmacetus shepherdi*	35	55
Short-beaked common dolphin	*Delphinus delphis*	0	60
Short-finned pilot whale	*Globicephala macrorhynchus*	0	55
Southern bottlenose whale	*Hyperoodon Planifrons*	20	80
Southern right whale dolphin	*Lissodelphis peronii*	10	65
Sowerby's beaked whale	*Mesoplodon bidens*	30	70
Spade-toothed whale	*Mesoplodon traversii*	25	50
Spectacled porpoise	*Phocoena dioptrica*	30	65
Sperm whale‡ (11000)	*Physeter macrocephalus*	0	75
Spinner dolphin	*Stenella longirostris*	0	40
Stejneger's beaked whale	*Mesoplodon stejnegeri*	35	65
Strap-toothed beaked whale	*Mesoplodon layardii*	25	60
Striped dolphin	*Stenella coeruleoalba*	0	60
True's beaked whale	*Mesoplodon mirus*	25	50
Vaquita† (20 kg)[4]	*Phocoena sinus*	30	35
White-beaked dolphin	*Lagenorhynchus albirostris*	45	85
Manatees/Dugongs (n=4)			
Amazonian manatee	*Trichechus inunguis*	0	10
Dugong† (400 kg)[5]	*Dugong dugon*	0	30
West African manatee	*Trichechus senegalensis*	0	20

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West Indian manatee‡ (900 kg)[6]	*Trichechus manatus*	0	40
Earless seals (n=18)			
Baikal seal† (45 kg)[7]	*Pusa sibirica*	55	60
Bearded seal	*Erignathus barbatus*	55	85
Caspian seal	*Pusa caspica*	40	50
Crabeater seal	*Lobodon carcinophagus*	55	90
Gray seal	*Halichoerus grypus*	40	75
Harbor seal	*Phoca vitulina*	35	85
Harp seal	*Pagophilus groenlandicus*	45	85
Hawaiian monk seal	*Neomonachus schauinslandi*	20	30
Hooded seal	*Cystophora cristata*	45	85
Leopard seal	*Hydrurga leptonyx*	55	90
Mediterranean monk seal	*Monachus monachus*	35	45
Northern elephant seal	*Mirounga angustirostris*	25	60
Ribbon seal	*Histriophoca fasciata*	45	85
Ringed seal	*Pusa hispida*	55	90
Ross seal	*Ommatophoca rossii*	55	90
Southern elephant seal‡ (2200)[8]	*Mirounga leonina*	35	90
Spotted seal	*Phoca largha*	35	75
Weddell seal	*Leptonychotes weddellii*	55	90
Eared seals (n=16)			
Antarctic fur seal	*Arctocephalus gazella*	45	65
Australian fur seal	*Arctocephalus pusillus doriferus*	35	45
Australian sea lion	*Neophoca cinerea*	25	35
California sea lion	*Zalophus californianus*	10	60
Cape fur seal	*Arctocephalus pusillus pusillus*	15	35
Galápagos fur seal† (30 kg)[9]	*Arctocephalus galapagoensis*	0	5
Galápagos sea lion	*Zalophus wollebaeki*	0	5
Guadalupe fur seal	*Arctocephalus townsendi*	20	35
Juan Fernández fur seal	*Arctocephalus philippii*	15	45
New Zealand fur seal	*Arctocephalus forsteri*	25	55

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New Zealand sea lion	*Phocarctos hookeri*	45	55
Northern fur seal	*Callorhinus ursinus*	35	65
South American fur seal	*Arctocephalus australis*	10	55
South American sea lion	*Otaria byronia*	5	55
Steller sea lion‡ (1000 kg)[10]	*Eumetopias jubatus*	35	65
Subantarctic fur seal	*Arctocephalus tropicalis*	30	60
Odobenids (n=1)			
Walrus (600-1500 kg)[11]	*Odobenus rosmarus*	55	85
Mustelids (n=2)			
Marine otter† (5 kg)[12]	*Lontra felina*	10	55
Sea otter‡ (30 kg)[13]	*Enhydra lutris*	30	60
Ursids (n=1)			
Polar bear (200-600 kg)[14]	*Ursus maritimus*	50	80
DIVING SEABIRDS			
Sphenisciformes (n=18)			
Adélie penguin	*Pygoscelis adeliae*	55	80
African (Jackass) penguin	*Spheniscus demersus*	15	35
Chinstrap penguin	*Pygoscelis antarcticus*	50	70
Emperor penguin‡ (45 kg)[15]	*Aptenodytes forsteri*	60	80
Erect-crested penguin	*Eudyptes sclateri*	45	55
Fjordland penguin	*Eudyptes pachyrhynchus*	35	45
Galápagos penguin	*Spheniscus mendiculus*	0	5
Gentoo penguin	*Pygoscelis papua*	50	65
Humboldt penguin	*Spheniscus humboldti*	5	40
King penguin	*Aptenodytes patagonicus*	45	65
Little penguin† (1 kg)[16]	*Eudyptula minor*	30	45
Macaroni penguin	*Eudyptes chrysolophus*	40	65
Magellanic penguin	*Spheniscuc magellanicus*	25	55
Northern Rockhopper penguin	*Eudyptes moseleyi*	30	55

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Royal penguin	*Eudyptes schlegeli*	50	55
Snares penguin	*Eudyptes robustus*	40	55
Southern Rockhopper penguin	*Eudyptes chrysocome*	40	65
Yellow-eyed penguin	*Megadyptes antipodes*	40	50
Procellariiformes (n=52)			
Amsterdam albatross	*Diomedea amsterdamensis*	25	45
Antipodean albatross	*Diomedea antipodensis*	30	65
Atlantic yellow-nosed albatross	*Thalassarche chlororhynchos*	5	50
Balearic shearwater	*Puffinus mauretanicus*	30	65
Bannerman's shearwater	*Puffinus bannermani*	25	35
Black-browed albatross	*Thalassarche melanophris*	10	65
Black-footed albatross	*Phoebastria nigripes*	0	90
Black-vented shearwater	*Puffinus opisthomelas*	15	35
Bryan's shearwater	*Puffinus bryani*	25	35
Buller's albatross	*Thalassarche bulleri*	5	60
Buller's shearwater	*Ardenna bulleri*	0	60
Campbell albatross	*Thalassarche impavida*	20	65
Cape Verde shearwater	*Calonectris edwardsii*	0	40
Chatham albatross	*Thalassarche eremita*	50	55
Christmas shearwater	*Puffinus nativitatis*	0	40
Common diving petrel† (0.2 kg)[17]	*Pelecanoides urinatrix*	20	65
Cory's shearwater	*Calonectris borealis*	0	60
Flesh-footed shearwater	*Ardenna carneipes*	0	60
Fluttering shearwater	*Puffinus gavia*	20	50
Galapagos shearwater	*Puffinus subalaris*	0	20
Great shearwater	*Ardenna gravis*	0	65
Grey-headed albatross	*Thalassarche chrysostoma*	30	70
Heinroth's shearwater	*Puffinus Heinrothi*	0	5
Hutton's shearwater	*Puffinus huttoni*	10	40
Indian Yellow-nosed albatross	*Thalassarche carteri*	20	50
Laysan albatross	*Phoebastria immutabilis*	15	65
Light-mantled albatross	*Phoebetria palpebrata*	40	80
Little shearwater	*Puffinus assimilis*	10	50
Magellanic diving petrel	*Pelecanoides magellani*	40	55
Manx shearwater	*Puffinus Puffinus*	0	75
Newell's shearwater	*Puffinus newelli*	0	25

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Northern Royal albatross	*Diomedea sanfordi*	15	65
Persian shearwater	*Puffinus persicus*	0	30
Peruvian Diving petrel	*Pelecanoides garnotii*	0	40
Pink-footed shearwater	*Ardenna creatopus*	0	60
Rapa shearwater	*Puffinus myrtae*	25	30
Salvin's albatross	*Thalassarche salvani*	20	60
Scopoli's shearwater	*Calonectris diomedea*	0	50
Short-tailed albatross	*Phoebastria albatrus*	15	65
Short-tailed shearwater	*Ardenna tenuirostris*	0	75
Shy albatross	*Thalassarche cauta*	20	45
Sooty albatross	*Phoebetria fusca*	20	70
Sooty shearwater	*Ardenna grisea*	0	70
South Georgia diving petrel	*Pelecanoides georgicus*	40	60
Southern royal albatross	*Diomedea epomophora*	20	65
Streaked shearwater	*Calonectris leucomelas*	0	50
Townsend's shearwater	*Puffinus auricularis*	10	25
Tropical shearwater	*Puffinus bailoni*	0	40
Wandering albatross‡ (12 kg)[18]	*Diomedea exulans*	25	65
Waved albatross	*Phoesbastria irrorata*	0	15
Wedge-tailed shearwater	*Ardenna pacifica*	0	40
Yelkouan shearwater	*Puffinus yelkouan*	35	45
Pelecaniformes (n=42)			
Abbott's booby	*Papasula abbotti*	5	15
Auckland shag	*Leucocarbo colensoi*	45	50
Australasian gannet	*Morus serrator*	15	45
Bank cormorant	*Phalacrocorax neglectus*	20	35
Black-faced cormorant	*Phalacrocorax fuscescens*	30	40
Blue-footed booby	*Sula nebouxii*	0	35
Bounty shag	*Leucocarbo ranfurlyi*	45	50
Brandt's cormorant	*Phalacrocorax penicillatus*	20	60
Bronze shag	*Leucocarbo chalconotus*	40	45
Brown booby	*Sula leucogaster*	0	40
Campbell shag	*Leucocarbo campbelli*	50	55
Cape cormorant	*Phalacrocorax capensis*	5	35
Cape gannet	*Morus capensis*	0	35
Chatham shag	*Leucocarbo onslowi*	45	50

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Crowned cormorant	*Microcarbo coronatus*	20	35
Double-crested cormorant	*Phalacrocorax auritus*	20	60
European shag	*Phalacrocorax aristotelis*	30	70
Flightless cormorant‡ (5 kg)[19]	*Phalacrocorax harrisi*	0	5
Great cormorant	*Phalacrocorax carbo*	0	75
Great Pied cormorant	*Phalacrocorax varius*	5	40
Guanay cormorant	*Leucocarbo bougainvillii*	0	45
Indian cormorant	*Phalacrocorax fuscicollis*	10	35
Japanese cormorant	*Phalacrocorax capillatus*	25	50
Kerguelen shag	*Leucocabo verrucosus*	45	50
Little black cormorant	*Phalacrocorax sulcirostris*	0	40
Little cormorant	*Microcarbo niger*	0	35
Little pied cormorant	*Microcarbo melanoleucos*	0	45
Masked booby	*Sula dactylatra*	0	35
New Zealand shag	*Leucocarbo carunculatus*	35	40
Northern gannet	*Morus bassanus*	20	75
Pelagic cormorant	*Phalacrocorax pelagicus*	30	70
Peruvian booby	*Sula variegata*	0	40
Pitt shag	*Phalacrocorax featherstoni*	40	45
Pygmy cormorant	*Microcarbo pygmeus*	30	45
Red-faced cormorant	*Phalacrocorax urile*	45	60
Red-footed booby† (1 kg)[20]	*Sula sula*	0	30
Red-legged cormorant	*Phalacrocorax gaimardi*	10	50
Rock shag	*Leucocarbo magellanicus*	35	55
Socotra cormorant	*Phalacrocorax nigrogularis*	10	30
South Georgian shag	*Phalacrocorax georgianus/atriceps*	40	65
Spotted shag	*Phalacrocorax punctatus*	35	45
White-breasted cormorant	*Phalacrocorax lucidus*	0	75
Charadriiformes (n=24)			
Ancient murrelet	*Synthliboramphus antiquus*	30	60
Atlantic puffin	*Fratercula arctica*	30	85
Black guillemot	*Cepphus grylle*	45	90
Cassin's auklet	*Ptychoramphus aleuticus*	25	55
Common murre	*Uria aalge*	35	80
Craveri's murrelet	*Synthliboramphus Craveri*	25	40

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Crested auklet	*Aethia cristatella*	40	65
Guadalupe murrelet	*Synthliboramphus hypoleucus*	25	50
Horned puffin	*Fratercula corniculata*	35	70
Japanese murrelet	*Synthliboramphus wumizusume*	30	50
Kittlitz's murrelet	*Brachyramphus Brevirostris*	50	70
Least auklet† (0.08 kg)[21]	*Aethia pusilla*	40	65
Little auk	*Alle alle*	35	90
Long-billed murrelet	*Brachyramphus perdix*	45	65
Marbled murrelet	*Brachyramphus marmoratus*	35	60
Parakeet auklet	*Aethia psittacula*	35	65
Pigeon guillemot	*Cepphus columba*	35	65
Razorbill	*Alca torda*	30	85
Rhinoceros auklet	*Cerorhinca monocerata*	30	60
Scripps's murrelet	*Syntlhboramphus scrippsi*	25	50
Spectacled guillemot	*Cepphus carbo*	35	65
Thick-billed murre‡ (1.5 kg)[22]	*Uria lomvia*	45	85
Tufted puffin	*Fratercula cirrhata*	35	65
Whiskered auklet	*Aethia pygmaea*	45	65
MARINE REPTILES			
Chelonidae (n=6)			
Flatback turtle	*Natator depressus*	0	30
Green turtle‡ (200 kg)[23]	*Chelonia mydas*	0	55
Hawksbill turtle	*Eretmochelys imbricata*	0	50
Kemp's ridley turtle† (30 kg)[24]	*Lepidochelys kempii*	20	55
Loggerhead turtle	*Caretta caretta*	0	60
Olive ridley turtle	*Lepidochelys olivacea*	0	60
Dermochelyidae (n=1)			
Leatherback turtle (300-700 kg)[25]	*Dermachelys coriacea*	0	60
Iguanidae (n=1)			

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Marine iguana (0.9-12 kg)[26]	*Amblyrhynchus cristatus*	0	5
Elapidae (n=1)			
Sea snakes (0.07-0.56 kg)[27]	*70 species – not included in Figure 1*		

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Table A1.2 Latitudinal distribution of marine air-breathing groups. Presence/Absence of species within each group was determined based on species distribution maps accessed from the IUCN Red List (https://www.iucnredlist.org) for each 5° bins of absolute latitude. The number of species (n) is provided for each taxonomic group.

Latitude	*n*	*0-5*	*5-10*	*10-15*	*15-20*	*20-25*	*25-30*	*30-35*	*35-40*	*40-45*	*45-50*	*50-55*	*55-60*	*60-65*	*65-70*	*70-75*	*75-80*	*80-85*	*85-90*
									MARINE MAMMALS										
Baleen whales	13	6	6	7	7	10	11	12	12	12	12	11	12	12	11	9	8	6	6
Toothed whales	65	30	31	34	37	40	45	49	53	54	44	41	36	28	22	12	11	8	5
Manatees/Dugong	4	4	4	4	3	3	2	2	1	1	0	0	0	0	0	0	0	0	0
Earless seals	18	0	0	0	0	1	2	2	5	7	10	9	15	15	13	13	13	11	11
Eared seals	16	2	3	3	5	6	8	9	12	9	11	9	9	5	3	0	0	0	0
Walrus	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
Marine/Sea otters	2	0	0	1	1	1	1	2	2	2	2	2	2	1	0	0	0	0	0
Polar bear	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0
Total	120	42	44	49	53	61	69	76	85	85	79	73	76	63	51	36	34	27	23
									DIVING SEABIRDS										
Sphenisciformes	18	1	2	1	2	2	3	5	6	9	10	11	11	7	7	3	2	2	0
Procellariiformes	52	21	23	26	30	37	41	42	41	41	35	33	27	25	18	7	4	2	1
Pelecaniformes	42	13	16	18	19	23	24	28	29	24	23	17	11	9	6	5	3	0	0
Charadriiformes	24	0	0	0	0	0	4	9	17	19	22	23	20	19	16	8	6	6	5
Total	136	35	41	45	51	62	72	84	93	93	90	84	69	60	47	23	15	10	6
									MARINE REPTILES										
Hard-shelled turtles	6	5	5	5	5	6	6	6	5	5	5	5	4	2	0	0	0	0	0
Leatherback turtle	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
Marine iguana	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	8	7	7	6	6	7	7	7	6	6	6	6	5	3	0	0	0	0	0
Total species	*264*	*84*	*92*	*100*	*110*	*130*	*148*	*167*	*184*	*184*	*175*	*163*	*150*	*126*	*98*	*59*	*49*	*37*	*29*

Table A1.3 Summary of published data on the diving behavior and insulation of marine air-breathing vertebrates that were used to create the figures. Values are means reported in the studies unless denoted by an asterick*, in which case a range was reported in the study and the median value that is displayed in the table was used in the figure(s). These values are meant to be representative of the species, although we recognize that certain species with broad distributions or subpopulations may differ in diving behavior and insulation characteristics. Moreover, these values will vary based on sex, age-class, or season. While we did not attempt to compare values across these different conditions for all the species in the table, we indicate if a particular value is sex-specific (♀ female, ♂ male), or for a particular age-class or season (PB = post-breeding, PM = post-molt). We use these as examples in the figures to highlight the variation between sexes and across seasons.

Aerobic dive limit (ADL) is provided in minutes along with the method used in the study to estimate it. Lactate refers to lactate measurements in post-dive blood samples. All other ADLs were estimated behaviorally from TDR data (bADL) or calculated from total body oxygen stores and metabolic rate (RMR = resting metabolic rate, BMR = basal metabolic rate; FMR = field metabolic rate, DMR = diving metabolic rate, AMR = active metabolic rate, i.e. swimming but not necessarily diving). The subscripts further indicate how metabolic rate was determined (_MR$_{K}$ = estimated according to Kleiber's allometric relationship (Kleiber, 1961), _MR$_{COT}$ = incorporated costs of transport, _MR$_{VO}$ = determined from oxygen consumption rates, _MR$_{HR}$ = heart rate used as a proxy for metabolic rate, _MR$_{DLW}$ = determined from doubly labeled water method, _MR$_{VAR}$ = modeled a variable metabolic rate, e.g. depth-dependent).

Fur/Feather density and blubber thickness are provided as a single value that is meant to be representative of the mean value across the body based on what the study reported, but insulation properties may vary drastically with body location.

Blubber conductivity was determined for the entire integument, unless a superscript ^{B} indicates that the value is only for blubber. Methods used to measure blubber conductivity are indicated along with the value and include the standard (Std) material method, heat flux (HF) disc or plate method, and the hot plate method and are indicated along with the conductivity value.

Common name	Mass	Routine / Max Dive Depth	Routine / Max Dive Duration	Mass-specific Total O_2 stores (mL O_2 kg^{-1})	Aerobic Dive Limit (min)	Fur or Feather Density	Blubber thickness	Blubber Conductivity (W m^{-1} K^{-1})	Figures

Scientific name	(kg)	(m)	(min)	(Lung/Muscle/Blood) %	*Method*	(#/mm^{-2})	(mm)	*Method*	[Sources]
MARINE MAMMALS									
Baleen whales									
Blue whale *Balaenoptera musculus*	122000	113/200	6.6/18	54 (13/33/54)	31.2 *4xBMR*$_K$		135*		Fig. 3, 4, 5, 8 [1–5]
Bowhead whale *Balaena mysticetus*	48250	58*/487	10.5*/63				200		Fig. 3, 8 [4–6]
Common minke whale *Balaenoptera acutorostrata*	6000	<50/105	<5/9				42	0.24* *Std material*	Fig. 3, 6, 8 [4,7,8]
Fin whale *Balaenoptera physalus*	70000	78/474	5.5/20	57 (13/36/51)	28.6 *4xBMR*$_K$		103*♀	0.21 *Hot plate*	Fig. 3, 4, 5, 6, 8 [1–5]
Gray whale *Eschrichtius robustus*	29000	45*/79	3*/28				180		Fig. 3, 8 [4,5,9]
Humpback whale *Megaptera novaeangliae*	29900 ♀	90*/160	6*/10.6						Fig. 3 [4,5,9]
North Atlantic right whale *Eubalaena glacialis*	72960 ♀	120/-	12/-				205*		Fig. 8 [4,10,11]
Toothed whales									
Beluga whale *Delphinapterus leucas*	936	550*/872	6/23	51 (17/32/51)	10* *Lactate*		67*	0.102^B *HF plate*	Fig. 3, 4, 5, 6, 8 [4,5,12–14]
Blainville's beaked whale *Mesoplodon densirostris*	1000	967*/1599	47/84	86.9 (4/54/42)	33.3 *DMR*$_{COT}$				Fig. 3, 4, 5 [4,15]
Bottlenose dolphin *Tursiops truncatus*	194	20/>500	4.1/16	34 (27/40/33)	3.3 *Lactate*		21.3 13.1 (summer) 18.2 (winter)	0.18 *Std material* 0.127 (summer) 0.235 (winter) *HF disc*	Fig. 3, 4, 5, 6, 8 [4,5,16,17]
Cuvier's beaked whale *Ziphius cavirostris*	1000	1202*/2992	58/138		33 *DMR*$_K$				Fig. 3, 5 [4,18]
Harbor porpoise *Phocoena phocoena*	50	20/226	1.2/7	52.5 (18/22/60)	6.91 *2xBMR*$_K$		27.5*	0.1 *HF disc*	Fig. 3, 4, 5, 6, 8 [4,5,19–22]
Killer whale *Orcinus orca*	2650	12/265	3.5*/-	36 (23/41/36)			40*		Fig. 4, 8 [4,5,23,24]
Narwhal *Monodon monoceros*	853	325*/>1000	8*/26	75 (12/50/38)			37.5*		Fig. 3, 4, 8 [4,13]

Northern bottlenose whale *Hyperoodon ampullatus*	3500	800/1483	40/70						Fig. 3 [4,25]
Pacific white-sided dolphin *Lagenorhynchus obliquidens*	80	-/215	3*/6	40 (23/28/49)					Fig. 4 [4,26]
Pantropical spotted dolphin *Stenella attenuata*	75	75*/213	3*/5				7.7	0.2 *HF disc*	Fig. 3, 6, 8 [4,5,20]
Pygmy sperm whale *Kogia breviceps*	368						28	0.14 *Std material*	Fig. 6, 8 [27,28]
Short-finned pilot whale *Globicephala macrorhynchus*	1000	450*/1019	15/21	68.3 (21/42/37)	14.2 DMR_{COT}		19.61	0.19 *Std material*	Fig. 3, 4, 5, 6, 8 [4,27,29]
Sperm whale *Physeter macrocephalus*	35000	650*/2250	45/138	81 (5/64/30)	48.5* DMR_{K}		100		Fig. 3, 4, 5, 8 [4,5,18,30]
Manatees/Dugongs									
Dugong *Dugong dugon*	475*	4/20.5	3/12.3				11.5*	0.37 *Std material*	Fig. 3, 6, 8 [31,32]
West Indian Manatee *Trichechus manatus*	900	6*/12	2.5*/20	21 (33/7/60)			72*		Fig. 3, 4, 8 [4,5,33,34]
Earless seals									
Baikal seal *Pusa sibirica*	47.5	28*/324	4*/>40	79 (5/29/66)	15 *Lactate*		55*		Fig. 3, 4, 5 [4,35,36]
Bearded seal *Erignathus barbatus*	301.2	20/480	3*/19			28.0	48.5*		Fig. 3, 8 [4,5,37–40]
Crabeater seal *Lobodon carcinophagus*	253	90/713	5/24	43 (12/21/67)	8.84 $2xBMR_{K}$	28.2	42		Fig. 3, 4, 5, 8 [37,40–42]
Gray seal *Halichoerus grypus*	172.5	65*/436	4.5*/32	61 (6/26/68)	11.19 $2xBMR_{K}$	22.2	39 (subadult)	0.18 *HF disc*	Fig. 3, 4, 5, 6, 8 [4,37,38,43–46]
Harbor seal *Phoca vitulina*	69.6	53*/481	4.8/35	62 (7/35/57)	10.2 *RMR*	42.77	29.8♀	0.18 *HF disc*	Fig. 3, 4, 5, 6, 8 [4,46–50]
Harp seal *Pagophilus groenlandicus*	138.2 ♀	175*/568	8.5*/>15	73 (7/44/49)	12.1 $1.7xBMR_{K}$	16.9	48.5♀	0.19^{B} *Std material*	Fig. 3, 4, 5, 6, 8 [4,43,51–54]
Hawaiian monk seal *Neomonachus schauinslandi*	140	25*/>500	4.5*/>20			4.5	43.5*		Fig. 3, 8 [4,5,55]
Hooded seal *Cystophora cristata*	145.6 ♀	350*/>1016	15*/>52	90 (7/42/51)	17.2 $1.7xBMR_{K}$	13.8	51.42♀		Fig. 3, 4, 5, 8 [4,47,54]
Leopard seal *Hydrurga leptonyx*	389	28/428	3.8/15	51 (7/47/46)		19.8	46		Fig. 3, 4, 5, 8 [4,37,42,56]

Northern elephant seal *Mirounga angustirostris*	446♀	400*/1735	23*/119	94 (3/26/71)	31.5* *2xBMR$_K$*	14.81	52.01♀	0.18 *Std material*	Fig. 3, 4, 5, 6, 7, 8 [57–59]
Ribbon seal *Histriophoca fasciata*	80.2	400*/>600	-/-	72 (8/43/49)		14.5	44♂		Fig. 6 [4,38,39]
Ringed seal *Pusa hispida*	80♀	60*/500	2.7/>50	52 (12/44/44)	8.9 *2xBMR$_K$*	44.19	32.22♀	0.2 *Hot plate*	Fig. 3, 4, 5, 6, 8 [4,5,37,47,53,60–63]
Ross seal *Ommatophoca rossii*	164	110/792	6.44/>20			20.6	56		Fig. 3, 8 [4,5,64]
Southern elephant seal *Mirounga leonina*	394♀ 2272♂	500*/2388	31.6$^{\mathrm{PB}}$♀, 38.4$^{\mathrm{PM}}$♀, 48♂ /120		29.5$^{\mathrm{PB}}$♀, 28.3$^{\mathrm{PM}}$♀, 44.5♂ RMR		50♀	0.07 *Unknown*	Fig. 3, 5, 6 [4,5,65–67]
Weddell seal *Leptonychotes weddellii*	355	275*/904	13*/96	89 (4/30/66)	20* *Lactate*	13.6	47*♀		Fig. 3, 4, 5, 8 [37,68,69]
Eared seals									
Antarctic fur seal *Arctocephalus gazella*	41.9	23/240	1.2/11	44.7 (25/20/55)	1.6 *FMR$_{DLW}$*	421.94	24.38♀	0.34 *Std material*	Fig. 3, 4, 5, 6, 8 [4,47,70,71]
Australian fur seal *Arctocephalus p. doriferus*	77.7	64/164	3.2/9		1.7 *FMR$_{DLW}$*				Fig. 3, 5 [4,72]
Australian sea lion *Neophoca cinerea*	79.2	60/200	3.1/9	56 (10/20/70)	2.34 *FMR$_{DLW}$*				Fig. 3, 4, 5 [4,72–74]
California sea lion *Zalophus californianus*	66♀	62/536	1.9/16	55 (13/48/39)	2.3 *Lactate* (juvenile)	24.32	15♀	0.24 *Std material*	Fig. 3, 4, 5, 6, 8 [4,5,47,58,75–77]
Cape fur (South African) seal *Arctocephalus p. pusillus*	49.4♀	45/454	2/9.8		3.85 *bADL*	359.06	11.2♀	0.39 *Std material*	Fig. 3, 5, 6, 8 [4,47,78,79]
Galápagos fur seal *Arctocephalus galapagoensis*	27	26/115	3/5		3.2 *bADL*				Fig. 3, 5 [4,5,80,81]
Galápagos seal lion *Zalophus wollebaeki*	75.3* ♀	100*/387	8.6/11	74 (8/25/67)	4.33 *FMR$_{DLW}$*				Fig. 3, 4 [4,82,83]
New Zealand fur seal *Arctocephalus forsteri*	39♀	53*/274	2.5*/11			335.8			Fig. 3 [4,37,84]
New Zealand sea lion *Phocarctos hookeri*	112.4	123/597	3.4/20	48 (12/25/63)	2.3 *FMR$_{DLW}$*	21.6	28		Fig. 3, 4, 5, 8 [4,37,85,86]
Northern fur seal *Callorhinus ursinus*	39♀	65/256	2.2/10	42 (24/33/43)	2.6 *1.7xRMR*	525.79	9.3	0.77 *Std material*	Fig. 3, 4, 5, 6, 8 [4,58,84,87]

Steller sea lion *Eumetopias jubatus*	173.7 ♀	17*/452	2/8	40 (20/35/45)	7.5♀ *2xRMR*	48.16	18.65♀		Fig. 3, 4, 5, 8 [4,47,88–92]
South American sea lion *Otaria flavescens/byronia*	114.2 ♀	30*/325	1.8/12.1	41.6 (15/53/31)	2.22 AMR_{VO}	10.6			Fig. 3, 4, 5 [4,37,93]
Subantarctic fur seal *Arctocephalus tropicalis*	35♀	30*/208	1.5/6.5			417.60	6.4	0.25 *Std material*	Fig. 3, 6, 8 [4,5,47,64]
Odobenids									
Walrus *Odobenus rosmarus*	830♀	50*/133	6.8/25	38 (24/26/50)	10.46 $2xBMR_{K}$	1.8	61.75♀		Fig. 3, 4, 5, 8 [4,5,37,43,62,94]
Mustelids									
Sea otter *Enhydra lutris*	17.3	15*/30‡	1/3‡	69 (45/21/33)	1.6‡ *Lactate*	1189	2.74		Fig. 3, 4, 5, 8 [4,95–98]
Ursids									
Polar bear *Ursus maritimus*	400	4/13.9	0.5/3.2			12.25	55*		Fig. 3, 8 [56,99–101]
DIVING SEABIRDS									
Sphenisciformes									
Adélie penguin *Pygoscelis adeliae*	3.8	25*/180	1.4/5.9	63 (48/26/26)	1.8 DMR_{COT}	0.12	15*		Fig. 3, 4, 5, 8 [4,102,103]
Chinstrap penguin *Pygoscelis antarcticus*	4.1	25*/179	1.3/3.6		2.2 DMR_{COT}				Fig. 3 [4,103]
Emperor penguin *Aptenodytes forsteri*	25	250*/564	5/27.6	68 (33/36/31)	5.6 *Lactate*	0.09 (contours) 0.36 (plumules)	23		Fig. 3, 4, 5, 8 [4,102,104–107]
Galápagos penguin *Spheniscus mendiculus*	2.2	<6/52	<1/3.2						Fig. 3 [4,102]
Gentoo penguin *Pygoscelis papua*	6	<60/225	1.4/9		1.6 DMR_{COT}	0.35	<20		Fig. 3, 5, 8 [102,103,108,109]
King penguin *Aptenodytes patagonicus*	12	<175*/343	3/9.2	55 (34/34/32)	3.4 FMR_{HR}				Fig. 3, 4, 5 [4,106,110]
Little penguin *Eudyptula minor*	1.2	<10/69	0.35/1.5	47 (43/24/33)	0.73* AMR_{VO}				Fig. 3, 4, 5 [111,112]
Magellanic penguin *Spheniscus magellanicus*	3.4	30*/97	1.5*/4.6						Fig. 3 [4]

Macaroni penguin *Eudyptes chrysolophus*	4.5	28*/113	1.8/4		1.5 *AMR_{VO}*				Fig. 5 [4,109]
Royal penguin *Eudyptes schlegeli*	5.3	<35*/226	2.3/7.5		3.5 *$2xBMR_{K}$*				Fig. 3, 5 [4,43]
Procellariiformes									
Black-browed albatross *Thalassarche melanophris*		<4/4.5	<0.1/0.2						Fig 3. [4]
Common diving petrel *Pelecanoides garnotii*	0.132	<50/64	<1						Fig. 3 [4,113]
Pelecaniformes									
Blue-footed booby *Sula nebouxii*		<8/22	<0.3/0.6						Fig. 3 [4]
Crozet shag *Phalacrocorax/L. melanogenis*	2.33	<40/145	1/6.2		4 *bADL*				Fig. 3, 5 [4,114]
Flightless cormorant *Phalacrocorax harrisi*		<15/73	<2/3.3						Fig. 3 [4]
Kerguelen shag *Phalacrocorax/L. verrucosus*	2.45	-/108.5	4.7/5.4		4 *bADL*				Fig. 5 [114]
Northern gannet *Morus bassanus*	2.8	<15/34	<0.3/0.7						Fig. 3 [111,113]
South Georgian shag *Phalacrocorax georgianus*	2.6	45*/125	3.3/6.3		1.7 *2.5xRMR*				Fig 3, 5 [4,115,116]
Charadriiformes									
Ancient murrelet *Synthliboramphus antiquus*	0.197	9.4/24.4	0.43/1	60 (50/6/44)	0.66 *3xBMR*				Fig. 3, 4, 5 [117]
Cassin's auklet *Ptychoramphus aleuticus*	0.171	15*/43	0.6/1.2	61 (50/6/44)	0.66 *3xBMR*				Fig. 3, 4, 5 [4,117]
Rhinoceros auklet *Cerorhinca monocerata*	0.560	20*/60	0.9/2.5	54.4 (49/11/40)	0.9 *AMR*				Fig. 3, 4, 5 [4,118]
Thick-billed murre *Uria lomvia*	1.029	35/210	1.1/4.1	44.8 (48/7/45)	0.78 *$3xRMR_{VO}$*				Fig. 3, 4, 5 [4,119,120]
SEA TURTLES									
Cheloniidae									
Green turtle *Chelonia mydas*	135*	9/138	43/307		78 *$bADL_{VAR}$*				Fig. 3, 5 [121–124]
Hawksbill turtle *Eretmochelys imbricata*	84	18/91	48/138						Fig. 3 [121,125,126]

Loggerhead turtle *Caretta caretta*	72*	32/233	30/614.4	22.2 (70/26/4)	63 $FMR_{VO@26^{\circ}C}$ 127 $FMR_{VO@15^{\circ}C}$				Fig. 3, 4, 5 [121,122,127–130]
Olive ridley turtle *Lepidochelys olivacea*	39	33/408	36/200						Fig. 3 [121,131]
Dermochelyidae									
Leatherback turtle *Dermochelys coriacea*	475	53/1250	22/86.1	27.4 (45/50/5)	37.6 *bADL* *(~3xRMR)*		41*	0.25* *HF disc* (plastron)	Fig. 3, 4, 5, 6, 8 [121,130,132–135]

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Appendix A2

Table A2.1 Publications organized by year since 1940 relevant to the thermal physiology of marine mammals. Refer to the caption of Figure 2.1 for an explanation of what types of publications were included, how they were classified, and how the different categories are defined. The following are indicated in the 'Notes' column: (1) studies that are relevant but traditionally considered a study on diving physiology; (2) whether field studies were performed on land or in the water; (3) the type of biotelemetry technology used for studies that used biotelemetry to study physiology and/or behavior in the lab or field. Biotelemetry methods for (1) physiology: STP = stomach temperature pill (a temperature-sensitive radio transmitter that is ingested), IRT = infrared thermography (used for skin temperature unless otherwise stated), ECG = electrocardiogram (heart rate), HF = heat flux sensor, TR = thermistor (temperature location specified), TC = thermocouple (temperature location specified); (2) behavior: TDR = time-depth recorder (diving behavior), SAT = satellite tag (location/movement data), GPS = global positioning satellite tag (location/movement data), VHF = very high frequency transmitter (location/movement data), CTD = conductivity-temperature-depth tag (*in situ* water temperature).

Publication					**Study Setting**			**Animal State**							**Bio-telemetry**		**Notes**
	Publication	Title		Year	Field	Lab	Modeling	Free-ranging	Trained	Captive	Restrained	Peri-mortem	Carcass	*Ex vivo*	Physiology	Behavior	
1940-1949																	
1	Scholander, PF; Irving, Laurence; Grinnell, SW	On the Temperature and Metabolism of the seal during diving	Journal of Cellular and Comparative Physiology	1942		X					X						diving physiology study
2	Parry, DA;	The structure of whale blubber, and a discussion of its thermal properties	Journal of Cell Science	1949		X								X			

1950-1959																	
3	Scholander, PF; Schevill, WE	Counter-Current Vascular Heat Exchange in the Fins of Whales	Journal of Applied Physiology	1955		X								X			
4	Bartholomew, GA; Wilke, F	Body temperature in the northern fur seal, *Callorhinus ursinus*	Journal of Mammalogy	1956	X						X	X					on land
5	Irving, L; Hart, JS	The metabolism and insulation of seals as bare-skinned mammals in cold water	Canadian Journal of Zoology	1957		X					X						
6	Hart, JS; Irving, L	The energetics of harbor seals in air and in water with special consideration of seasonal changes	Canadian Journal of Zoology	1959		X					X						
1960-1969																	
7	Irving, L; Peyton, LJ; Bahn, CH; Peterson, RS	Regulation of temperature in fur seals	Physiological Zoology	1962	X	X					X	X					
8	Bryden, MM	Insulating capacity of the subcutaneous fat of the southern elephant seal	Nature	1964		X								X			
9	Ling, JK	Functional significance of sweat glands and sebaceous glands in seals	Nature	1965		X								X			
10	Ling, JK	The skin and hair of the Southern Elephant Seal *Mirounga leonina* (L.)	Australian Journal of Zoology	1968		X								X			

		III. morphology of the adult integument															
1970-1979																	
11	Tarasoff, FJ; Fisher, HD	Anatomy of the hind flippers of two species of seals with reference to thermoregulation	Canadian Journal of Zoology	1970		X								X			
12	Hampton, IFG; Whittow, GC; Szekerczes, J; Rutherford, S	Heat transfer and body temperature in the Atlantic bottlenosed dolphin, *Tursiops truncatus*	The International Journal of Biometerology	1971		X			X						X		STP
13	McGinnis, SM; Southworth, TP	Thermoregulation in the northern elephant seal, *Mirounga angustirostris*	Comparative Biochemistry and Physiology	1971	X	X		X		X					X		STP, implanted radio telemeters ($T_{subcutaneous}$), field component on land
14	White, FN; Odell, DK	Thermoregulatory behavior of the northern elephant seal, *Mirounga angustirostris*	Journal of Mammalogy	1971	X			X							X		STP, on land
15	McGinnis, SM; Whittow, GC; Ohata, CA; Huber, H	Body heat dissipation and conservation in two species of dolphins	Comparative Biochemistry and Physiology Part A: Physiology	1972		X				X					X		STP, implanted radio telemeters ($T_{subcutaneous}$)

16	Ohata, CA; Matsuura, DT; Whittow, GC; Tinker, SW	Diurnal Rhythm of Body Temperature in the Hawaiian Monk Seal (*Monachus schauinslandi*)	Pacific Science	1972		X				X					X		STP
17	Whittow, GC; Matsuura, DT; Lin, YC	Temperature regulation in the California sea lion (*Zalophus californianus*)	Physiological Zoology	1972		X								X			
18	Gentry, RL	Thermoregulatory behavior of eared seals	Behaviour	1973	X			X									on land
19	Matsuura, DT; Whittow, GC	Evaporative heat loss in the California sea lion and harbor seal	Comparative Biochemistry and Physiology Part A: Physiology	1974		X				X	X				X		rectal telemetry capsule
20	Morrison, P; Rosenmann, M; Estes, JA	Metabolism and thermoregulation in the sea otter	Physiological Zoology	1974		X				X	X						
21	Odell, DK	Behavioral thermoregulation in the California sea lion	Behavioral Biology	1974	X			X									on land
22	Ohata, CA; Whittow, GC	Conductive heat loss to sand in California sea lions and a harbor seal	Comparative Biochemistry and Physiology	1974		X				X							
23	Whittow, GC; Hampton, IFG; Matsuura, DT; Ohata, CA; Smith,	Body Temperature of Three Species of Whales	Journal of Mammalogy	1974		X				X					X		STP, IRT

	RM; Allen, JF																
24	Luecke, RH; Natarajan, V; South, RE	A mathematical biothermal model of the California sea lion	Journal of Thermal Biology	1975			X										
25	McGinnis, SM	Peripheral Heat Exchange in Phocids	Rapp. P.-v. Reun. Cons. int. Explor. Mer.	1975	X	X		X		X					X		STP, field component performed on land
26	Miller, K; Irving, L	Metabolism and temperature regulation in young harbor seals *Phoca vitulina richardi*	American Journal of Physiology-Legacy Content	1975		X				X							
27	Molyneux, GS; Bryden, MM	Arteriovenous anastomoses in the skin of the Weddell seal, *Leptonychotes weddelli*	Science	1975		X								X			
28	Whittow, GC; Szekerczes, J; Kridler, E; Olsen, DL	Skin structure of the Hawaiian monk seal (*Monachus schauinslandi*)	Pacific Science	1975		X								X			
29	Hampton, IFG; Whittow, GC	Body temperature and heat exchange in the Hawaiian spinner dolphin, *Stenella longirostris*	Comparative Biochemistry and Physiology Part A: Physiology	1976		X			X	X					X		IRT

30	Miller, K; Rosenmann, M; Morrison, P	Oxygen uptake and temperature regulation of young harbor seals (*Phoca vitulina richardi*) in water	Comparative Biochemistry and Physiology Part A: Physiology	1976		X				X							
31	Hammel, HT; Elsner, RW; Heller, HC; Maggert, JA; Bainton, CR	Thermoregulatory responses to altering hypothalamic temperature in the harbor seal	American Journal of Physiology. Regulatory, Integrative and Comparative Physiology	1977		X					X						
32	Ohata, CA; Miller, LK	Northern fur seal thermoregulation: Thermal responses to forced activity on land	Journal of Thermal Biology	1977	X							X					on land
33	Ohata, CA; Miller, LK	Some temperature responses of northern fur seal (Callorhinus ursinus) pups	Journal of Mammalogy	1977	X						X						on land
34	Ohata, CA; Miller, LK; Kajimura, H	Northern fur seal thermoregulation: Thermal responses to pelagic conditions	Journal of Thermal Biology	1977	X							X					in water
35	Bryden, MM; Molyneux, GS	Arteriovenous anastomoses in the skin of seals. II. The California sea lion *Zalophus californianus* and the northern fur seal *Callorhinus ursinus* (Pinnipedia: Otariidae)	The Anatomical Record	1978		X								X			

36	Molyneux, GS; Bryden, MM	Arteriovenous anastomoses in the skin of seals. I. The Weddell Seal *Leptonychotes weddelli* and the Elephant Seal *Mirounga leonina* (Pinnipedia: Phocidae)	The Anatomical Record	1978		X								X			
37	Øritsland, NA; Ronald, K	Aspects of temperature regulation in harp seal pups evaluated by in vivo experiments and computer simulations	Acta Physiologica Scandinavica	1978		X	X				X						
38	Blix, AS; Grav, H; Ronald, K	Some aspects of temperature regulation in newborn harp seal pups	American Journal of Physiology-Regulatory, Integrative and Comparative Physiology	1979		X								X			
39	Blix, AS; Miller, LK; Keyes, MC; Grav, HJ; Elsner, R	Newborn northern fur seals (*Callorhinus ursinus*)--do they suffer from cold?	American Journal of Physiology-Regulatory, Integrative and Comparative Physiology	1979		X				X	X		X	X			
40	Gallivan, GJ; Ronald, K	Temperature regulation in freely diving harp seals (*Phoca groenlandica*)	Canadian journal of Zoology	1979		X				X					X		STP, diving physiology study

41	Zapol, WM; Liggins, GC; Schneider, RC; Qvist, J; Snider, MT; Creasy, RK; Hochachka, PW	Regional blood flow during simulated diving in the conscious Weddell seal	Journal of Applied Physiology	1979		X					X						diving physiology study
1980-1989																	
42	Kooyman, GL; Wahrenbrock, EA; Castellini, MA; Davis, RW; Sinnett, EE	Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: Evidence of preferred pathways from blood chemsitry and behavior	Journal of Comparative Physiology B	1980	X			X			X					X	TDR, diving physiology study, in water
43	Costa, DP; Kooyman, GL	Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, *Enhydra lutris*	Canadian Journal of Zoology	1982		X				X				X	X		STP, implanted radio telemeters ($T_{subcutaneous}$)
44	Blix, AA; Fay, FH; Ronald, K	On testicular cooling in phocid seals	Polar Research	1983	X	X						X	X				field component on land
45	Gallivan, GJ; Best, RC; Kanwisher, JW	Temperature regulation in the Amazonian manatee *Trichechus inunguis*	Physiological Zoology	1983		X				X					X		STP
46	Irvine, AB	Manatee metabolism and its influence on distribution in Florida	Biological Conservation	1983		X				X					X		STP

47	Costa, DP; Kooyman, GL	Contribution of specific dynamic action to heat balance and thermoregulation in the sea otter *Enhydra lutris*	Physiological Zoology	1984		X				X							
48	Brodie, P; Paasche, A	Thermoregulation and energetics of fin and sei whales based on postmortem, stratified temperature measurements	Canadian Journal of Zoology	1985	X							X					in water
49	Limberger, D; Trillmich, F; Biebach, H; Stevenson, RD	Temperature regulation and microhabitat choice by free-ranging Galapagos fur seal pups (*Arctocephalus galapagoensis*)	Oecologia	1986	X			X							X		STP, IRT, on land
50	Yasui, WY; Gaskin, DE	Energy budget of a small cetacean, the harbour porpoise, *Phocoena phocoena* (L.)	Ophelia	1986		X	X							X			
51	Folkow, LP; Blix, AS	Nasal heat and water exchange in gray seals	American Journal of Physiology-Regulatory, Integrative and Comparative Physiology	1987		X			X								
52	Hill, RD; Schneider, RC; Liggins, GC; Schuette, AH; Elliott,	Heart rate and body temperature during free diving of Weddell seals	The American Physiological Society	1987	X			X							X	X	ECG, blood samples, thermistor-tipped catheter (T_{blood}), TDR, VHF, diving

	RL; Guppy, M; Hochachka, PW; Qvist, J; Falke, KJ; Zapol, WM; Lig-Gins, GC																	physiology study, in water
53	Thompson, SD; Ono, KA; Oftedal, OT; Boness, DJ	Thermoregulation and resting metabolic rate of California sea lion (*Zalophus californianus*) pups	Physiological Zoology	1987	X						X							on land
54	Campagna, C; Le Boeuf, BJ	Thermoregulatory behaviour of southern sea lions and its effect on mating strategies	Behaviour	1988	X			X										on land
55	Ryg, M; Smith, TG; Øritsland, NA	Thermal significance of the topographical distribution of blubber in ringed seals (*Phoca hispida*)	Canadian Journal of Fisheries and Aquatic Sciences	1988		X						X	X	X				
56	Folkow, LP; Blix, AS	Thermoregulatory control of expired air temperature in diving harp seals	American Journal of Physiology-Regulatory, Integrative and Comparative Physiology	1989		X			X		X							diving physiology study
57	Kasting, NW; Adderley, SAL; Safford, T; Hewlett, KG	Thermoregulation in beluga (*Delphinapterus leucas*) and killer (*Orcinus orca*) whales	Physiological Zoology	1989		X			X									

1990-1999																	
58	Doidge, DW	Integumentary heat loss and blubber distribution in the beluga, *Delphinapterus leucas*, with comparisons to the narwhal, *Monodon monoceros*	Canadian Bulletin of Fisheries and Aquatic Science	1990		X							X	X			
59	Hokkanen, JEI	Temperature regulation of marine mammals	Journal of Theoretical Biology	1990			X										
60	Innes, S; Worthy, GAJ.; Lavigne, DM; Ronald, K	Surface area of phocid seals	Canadian Journal of Zoology	1990		X								X			
61	Lavigne, DM; Innes, S; Worthy, GAJ; Edwards, EF	Lower critical temperatures of blue whales, *Balaenoptera musculus*	Journal of Theoretical Biology	1990			X										
62	Øristland, NA; Markussen, NH	Outline of a physiologically based model for population energetics	Ecological Modelling	1990			X										
63	Ryg, M; Lydersen, C; Markussen, NH; Smith, TG; Oritsland, NA	Estimating the blubber content of phocid seals	Canadian Journal of Fisheries and Aquatic Sciences	1990		X							X	X			

64	Trites, AW	Thermal budgets and climate spaces: the impact of weather on the survival of Galapagos (*Arctocephalus galapagoensis Heller*) and northern fur seal pups (*Callorhinus ursinus L.*)	Functional Ecology	1990			X										
65	Worthy, GAJ; Edwards, EF	Morphometric and biochemical factors affecting heat loss in a small temperate cetacean (*Phocoena phocoena*) and a small tropical cetacean (*Stenella attenuata*)	Physiological Zoology	1990		X							X	X			
66	Francis, JM; Boness, DJ	The effect of thermoregulatory behaviour on the mating system of the Juan Fernandez fur seal, *Arctocephalus philippii*	Behaviour	1991	X			X									on land
67	Little, GJ	Thyroid morphology and function and its role in thermoregulation in the newborn southern elephant seal (*Mirounga leonina*) at Macquarie Island	Journal of Anatomy	1991	X	X					X			X			field component on land
68	Smith, TG; Hammill, MO; Taugbøl, G	A review of the developmental, behavioural and physiological adaptations of the	Arctic	1991		X					X		X	X			

		ringed seal, *Phoca hispida*, to life in the Arctic winter															
69	Worthy, GAJ	Insulation and thermal balance of fasting harp and grey seal pups	Comparative Biochemistry and Physiology Part A: Physiology	1991		X				X		X		X	X		STP
70	Cuyler, LC; Wiulsrød, R; Øritsland, NA	Thermal infrared radiation from free living whales	Marine Mammal Science	1992	X			X							X		IRT, in water
71	Folkow, LP; Blix, AS	Metabolic rates of minke whales (*Balaenoptera acutorostrata*) in cold water	Acta Physiologica Scandinavica	1992	X	X		X				X					field component in water
72	Rommel, SA; Pabst, DA; McLellan, WA; Mead, JG; Potter, CW	Anatomical evidence for a countercurrent heat exchanger associated with dolphin testes	The Anatomical Record	1992		X							X	X			
73	Ponganis, PJ; Kooyman, GL; Castellini, MA; Ponganis, EP; Ponganis, KV	Muscle temperature and swim velocity profiles during diving in a Weddell seal, *Leptonychotes weddellii*	Journal of Experimental Biology	1993	X			X							X	X	percutaneous TR_{muscle}, TDR, swim velocity, diving physiology study, in water

74	Rommel, SA; Pabst, DA; McLellan, WA	Functional morphology of the vascular plexuses associated with the cetacean uterus	The Anatomical Record	1993		X							X	X			
75	Ryg, M; Lydersen, C; Knutsen, LØ; Bjørge, A; Smith, TG; Øritsland, NA	Scaling of insulation in seals and whales	Journal of Zoology	1993		X							X	X			
76	Watts, P; Hansen, S; Lavigne, DM	Models of heat loss by marine mammals: thermoregulation below the zone of irrelevance	Journal of Theoretical Biology	1993			X										
77	Kvadsheim, PH; Folkow, LP; Blix, AS	A new device for measurement of the thermal conductivity of fur and blubber	Journal of Thermal Biology	1994		X								X			
78	Rommel, SA; Pabst, DA; Mclellan, WA; Williams, TM; Friedl, WA	Temperature regulation of the testes of the bottlenose dolphin (*Tursiops truncatus*): evidence from colonic temperatures	Journal of Comparative Physiology B	1994		X			X								
79	Beck, GG; Smith, TG	Distribution of blubber in the northwest Atlantic harp seal, *Phoca groenlandica*	Canadian Journal of Zoology	1995		X							X	X	X		
80	Boily, P	Theoretical heat flux in water and habitat selection of phocid seals and beluga	Journal of Theoretical Biology	1995			X										

		whales during the annual molt															
81	Hansen, S; Lavigne, DM; Innes, S	Energy metabolism and thermoregulation in juvenile harbor seals (*Phoca vitulina*) in air	Physiological Zoology	1995		X				X					X		STP
82	Kastelein, RA; Van der Sijs, SJ; Staal, C; Nieuwstraten, SH	Blubber thickness in harbour porpoises (*Phocoena phocoena*)	Food Consumption and Growth of Marine Mammals	1995		X				X					X		IRT
83	Little, GJ	Body temperature in the newborn southern elephant seal, *Mirounga leonina*, at Macquarie Island	Marine Mammal Science	1995	X						X						on land
84	Pabst, DA; Rommel, SA; Mclellan, WA; Williams, TM; Rowles, TK	Thermoregulation of the intra-abdominal testes of the bottlenose dolphin (*Tursiops truncatus*) during exercise	The Journal of Experimental Biology	1995		X			X						X		TC_{rectal}
85	Rommel, SA; Early, GA; Matassa, KA; Pabst, DA; McLellan, WA	Venous structures associated with thermoregulation of phocid seal reproductive organs	The Anatomical Record	1995		X							X	X			
86	Boily, P; Lavigne, DM	Thermoregulation of juvenile grey seals,	Canadian Journal of Zoology	1996		X				X					X		STP

		Halichoerus grypus, in air															
87	Kvadsheim, PH; Folkow, LP; Blix, AS	Thermal conductivity of minke whale blubber	Journal of Thermal Biology	1996		X								X			
88	Hansen, S; Lavigne, DM	Ontogeny of the thermal limits in the harbor seal (*Phoca vitulina*)	Physiological Zoology	1997		X				X					X		STP
89	Heyning, JE; Mead, JG	Thermoregulation in the mouths of feeding gray whales	Science	1997		X								X			
90	Hind, AT; Gurney, WS	The metabolic cost of swimming in marine homeotherms	The Journal of Experimental Biology	1997			X										
91	Kastelein, RA; Koene, P; Nieuwstraten, SH; Labberté, S	Skin surface temperature changes in a harbour porpoise (*Phocoena phocoena*) while on land	The Biology of the Harbour Porpoise	1997		X				X					X		IRT
92	Kvadsheim, PH; Folkow, LP	Blubber and flipper heat transfer in harp seals	Acta Physiologica Scandinavica	1997		X	X		X					X			
93	Kvadsheim, PH; Gotaas, ARL; Folkow, LP; Blix, AS	An experimental validation of heat loss models for marine mammals	Journal of Theoretical Biology	1997		X	X		X			X		X			
94	Rosen, DAS; Renouf, D	Seasonal changes in blubber distribution in Atlantic harbor seals: indications of thermodynamic considerations	Marine Mammal Science	1997		X				X							

95	Hind, AT; Gurney, WSC	Are there thermoregulatory constraints on the timing of pupping for harbour seals?	Canadian Journal of Zoology	1998			X										
96	Koopman, HN	Topographical distribution of the blubber of harbor porpoises (*Phocoena phocoena*)	Journal of Mammalogy	1998		X							X				
97	Heath, ME; Ridgway, SH	How dolphins use their blubber to avoid heat stress during encounters with warm water	American Journal of Physiology-Regulatory, Integrative and Comparative Physiology	1999		X			X						X		HF, TC_{rectal}
98	Noren, DP; Williams, TM; Berry, P; Butler, E	Thermoregulation during swimming and diving in bottlenose dolphins, *Tursiops truncatus*	Journal of Comparative Physiology B	1999	X				X								diving physiology study, in water
99	Williams, TM; Noren, D; Berry, P; Estes, JA; Allison, C; Kirtland, J	The diving physiology of bottlenose dolphins (*Tursiops truncatus*). III. Thermoregulation at depth	Journal of Experimental Biology	1999	X				X						X	X	ECG, TDR, diving physiology study, in water
2000-2009																	
100	Boily, P; Kvadsheim, PH; Folkow, LP	Cutaneous heat flux models do not reliably predict metabolic rates of marine mammals	Journal of Theoretical Biology	2000		X	X				X		X	X			
101	Boyd, IL	Skin temperatures during free-ranging swimming and diving in Antarctic fur seals	Journal of Experimental Biology	2000	X		X	X							X	X	$\Delta TR_{skin-water}$, TDR, field component in water

102	Donohue, MJ; Costa, DP; Goebel, ME; Baker, JD	The ontogeny of metabolic rate and thermoregulatory capabilities of northern fur seal, *Callorhinus ursinus*, pups in air and water	Journal of Experimental Biology	2000	X						X						on land and in water
103	Mauck, B; Eysel, U; Dehnhardt, G	Selective heating of vibrissal follicles	Journal of Experimental Biology	2000		X			X						X		IRT (vibrissal pad)
104	Heyning, JE	Thermoregulation in feeding baleen whales: Morphological and physiological evidence	Aquatic Mammals	2001		X				X					X		IRT (tongue)
105	Jobsis, PD; Ponganis, PJ; Kooyman, GL	Effects of training on forced submersion responses in harbor seals	Journal of Experimental Biology	2001		X			X		X				X		ECG, muscle blood flow (via laser Doppler), diving physiology study
106	Rommel, SA; Pabst, DA; McLellan, WA	Functional morphology of venous structures associated with the male and female reproductive systems in Florida manatees (*Trichechus manatus latirostris*)	The Anatomical Record: An Official Publication of the American Association of Anatomists	2001		X								X			

107	Koopman, HN; Pabst, DA; Mclellan, WA; Dillaman, RM; Read, AJ	Changes in blubber distribution and morphology associated with starvation in the harbor porpoise (*Phocoena phocoena*): evidence for regional differences in blubber structure and function	Physiological and Biochemical Zoology	2002		X							X	X			
108	Kvadsheim, PH; Aarseth, JJ	Thermal function of phocid seal fur	Marine Mammal Science	2002		X								X			
109	Meagher, EM; McLellan, WA; Westgate, AJ; Wells, RS; Frierson Jr, D; Pabst, DA	The relationship between heat flow and vasculature in the dorsal fin of wild bottlenose dolphins *Tursiops truncatus*	Journal of Experimental Biology	2002	X						X				X		ECG, HF with integrated TC_{skin}, in water
110	Noren, DP	Thermoregulation of weaned northern elephant seal (*Mirounga angustirostris*) pups in air and water	Physiological and Biochemical Zoology	2002		X				X							
111	Twiss, SD; Wright, NC; Dunstone, N; Redman, P; Moss, S; Pomeroy, PP	Behavioral evidence of thermal stress from overheating in UK breeding gray seals	Marine Mammal Science	2002	X			X									in water

112	Mauck, B; Bilgmann, K; Jones, DD; Eysel, U; Dehnhardt, G	Thermal windows on the trunk of hauled-out seals: hot spots for thermoregulatory evaporation?	Journal of Experimental Biology	2003		X			X	X					X		IRT
113	Rommel, SA; Caplan, H	Vascular adaptations for heat conservation in the tail of Florida manatees (*Trichechus manatus latirostris*)	Journal of Anatomy	2003		X							X	X			
114	Rosen, DAS; Trites, AW	No evidence for bioenergetic interaction between digestion and thermoregulation in Steller sea lions *Eumetopias jubatus*	Physiological and Biochemical Zoology	2003		X			X								
115	Elsner, R; George, JC; O'hara, T	Vasomotor responses of isolated peripheral blood vessels from bowhead whales: thermoregulatory implications	Marine Mammal Science	2004		X								X			
116	Elsner, R; Meiselman, HJ; Baskurt, OK	Temperature-viscosity relations of bowhead whale blood: A possible mechanism for maintaining cold blood flow	Marine Mammal Science	2004		X								X			
117	Ortiz, RM; Worthy, GAJ	Could lower body fat mass contribute to cold-water susceptibility in calves of the West Indian manatee	Marine Mammal Science	2004		X				X							

		(*Trichechus manatus*)?															
118	Rutishauser, MR; Costa, DP; Goebel, ME; Williams, TM	Ecological implications of body composition and thermal capabilities in young Antarctic fur seals (*Arctocephalus gazella*)	Physiological and Biochemical Zoology	2004	X		X				X						field component on land and in water
119	Samuel, AM; Worthy GAJ	Variability in fatty acid composition of bottlenose dolphin (*Tursiops truncatus*) blubber as a function of body site, season, and reproductive state	Canadian Journal of Zoology	2004		X								X			
120	Silva, RG	Assessment of body surface temperature in cetaceans: an iterative approach	Brazilian Journal of Biology	2004			X										
121	Struntz, DJ; McLellan, WA; Dillaman, RM; Blum, JE; Kucklick, JR; Pabst, DA	Blubber development in bottlenose dolphins (*Tursiops truncatus*)	Journal of Morphology	2004		X							X	X			
122	Bossart, GD; Meisner, RA; Rommel, SA; Ghim,	Pathological features of the Florida manatee cold stress syndrome	Aquatic Mammals	2005		X							X				

	S-J; Jenson, AB																
123	Dunkin, RC; McLellan, WA; Blum, JE; Pabst, DA	The ontogenetic changes in the thermal properties of blubber from Atlantic bottlenose dolphin *Tursiops truncatus*	Journal of Experimental Biology	2005		X							X	X			
124	Harding, KC; Fujiwara, M; Axberg, Y; Härkönen, T	Mass-dependent energetics and survival in harbour seal pups	Functional Ecology	2005	X		X				X						field component on land
125	Kvadsheim, PH; Folkow, LP; Blix, AS	Inhibition of shivering in hypothermic seals during diving	American Journal of Physiology-Regulatory, Integrative and Comparative Physiology	2005		X			X		X				X		EMG, TC_{brain}, TC_{rectal}, diving physiology study
126	McCafferty, DJ; Moss, S; Bennett, K; Pomeroy, PP	Factors influencing the radiative surface temperature of grey seal (*Halichoerus grypus*) pups during early and late lactation	Journal of Comparative Physiology B	2005	X						X				X		IRT (rectal), on land
127	Rotherham, LS; van Der Merwe, M; Bester, MN; Oosthuizen, WH	Morphology and distribution of sweat glands in the Cape fur seal, *Arctocephalus pusillus pusillus* (Carnivora: Otariidae)	Australian Journal of Zoology	2005		X								X			

128	Thornton, SJ; Hochachka, PW; Crocker, DE; Costa, DP; LeBoeuf, BJ; Spielman, DM; Pelc, NJ	Stroke volume and cardiac output in juvenile elephant seals during forced dives	Journal of Experimental Biology	2005		X					X						diving physiology
129	Willis, K; Horning, M	A novel approach to measuring heat flux in swimming animals	Journal of Experimental Marine Biology and Ecology	2005	X	X		X	X						X		HF with integrated TC_{skin}, field component in water
130	Willis, K; Horning, M; Rosen, DAS; Trites, AW	Spatial variation of heat flux in Steller sea lions: evidence for consistent avenues of heat exchange along the body trunk	Journal of Experimental Marine Biology and Ecology	2005		X	X		X						X	X	HF with integrated TR_{skin}, swim speed
131	Beentjes, MP	Behavioral thermoregulation of the New Zealand sea lion (*Phocarctos hookeri*)	Marine Mammal Science	2006	X			X					X				
132	Ponganis, PJ; Stockard, T Knower; Levenson, DH; Berg, L; Baranov, EA	Cardiac output and muscle blood flow during rest-associated apneas of elephant seals	Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology	2006		X				X					X		muscle blood flow (via laser Doppler), ECG, thermistor-tipped catheter (T_{blood})

133	Koopman, HN	Phylogenetic, ecological, and ontogenetic factors influencing the biochemical structure of the blubber of odontocetes	Marine Biology	2007		X								X			
134	Mellish, JE; Horning, M; York, AE	Seasonal and spatial blubber depth changes in captive harbor seals (*Phoca vitulina*) and Steller's sea lions (*Eumetopias jubatus*)	Journal of Mammalogy	2007		X			X								
135	Werth, AJ	Adaptations of the cetacean hyolingual apparatus for aquatic feeding and thermoregulation	The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology	2007		X								X			
136	Westgate, AJ; McLellan, WA; Wells, RS; Scott, MD; Meagher, EM; Pabst, DA	A new device to remotely measure heat flux and skin temperature from free-swimming dolphins	Journal of Experimental Marine Biology and Ecology	2007	X			X							X	X	HF with integrated TR_{skin}, swim velocity, TDR, VHF, in water
137	Hasselberg, BA; Thomas, JA	Using an infrared temperature sensor to study microhabitat selection in captive California Sea Lions (*Zalophus californianus*)	Aquatic Mammals	2008		X				X					X		IRT

138	Meagher, EM; McLellan, WA; Westgate, AJ; Wells, RS; Blum, JE; Pabst, DA	Seasonal patterns of heat loss in wild bottlenose dolphins (*Tursiops truncatus*)	Journal of Comparative Physiology B	2008	X						X				X		HF with integrated TC_{skin}, TC_{rectal}, in water
139	Montie, EW; Garvin, SR; Fair, PA; Bossart, GD; Mitchum, GB; McFee, WE; Speakman, T; Starczak, VR; Hahn, ME	Blubber morphology in wild bottlenose dolphins (*Tursiops truncatus*) from the Southeastern United States: influence of geographic location, age class, and reproductive state	Journal of Morphology	2008		X								X			
140	Noren, SR; Pearson, LE; Davis, J; Trumble, SJ; Kanatous, SB	Different thermoregulatory strategies in nearly weaned pup, yearling, and adult Weddell seals (*Leptonychotes weddelli*)	Physiological and Biochemical Zoology	2008	X						X						on land
141	Ponganis, PJ; Kreutzer, U; Stockard, TK; Lin, P-C; Sailasuta,	Blood flow and metabolic regulation in seal muscle during apnea	Journal of Experimental Biology	2008		X			X						X		muscle blood flow (via laser Doppler)

	N; Tran, T-K; Hurd, R; Jue, T																
142	Yeates, LC; Houser, DS	Thermal tolerance in bottlenose dolphins (*Tursiops truncatus*)	Journal of Experimental Biology	2008		X			X								
143	Castellini, MA; Trumble, SJ; Mau, TL; Yochem, PK; Stewart, BS; Koski, MA	Body and blubber relationships in Antarctic pack ice seals: implications for blubber depth patterns	Physiological and Biochemical Zoology	2009	X						X						on land
144	Hammill, MO; Ryg, M; Chabot, D	Seasonal changes in energy requirements of harp seals	Journal of Northwest Atlantic Fishery Science	2009			X										
145	Liwanag, HEM; Williams, TM; Costa, DP; Kanatous, SB; Davis, RW; Boyd, IL	The effects of water temperature on the energetic costs of juvenile and adult California sea lions (Zalophus californianus): the importance of skeletal muscle thermogenesis for thermal balance	Journal of Experimental Biology	2009		X			X						X		STP
146	Noren, SR; Wells, RS	Blubber deposition during ontogeny in free-ranging bottlenose dolphins: balancing disparate	Journal of Mammalogy	2009	X						X						in water

		roles of insulation and locomotion															
2010-2019																	
147	Barbieri, MM; McLellan, WA; Wells, RS; Blum, JE; Hofmann, S; Gannon, J; Pabst, DA	Using infrared thermography to assess seasonal trends in dorsal fin surface temperatures of free-swimming bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida	Marine Mammal Science	2010	X			X							X		IRT (dorsal fin), in water
148	Blix, AS; Walløe, L; Messelt, EB; Folkow, LP	Selective brain cooling and its vascular basis in diving seals	Journal of Experimental Biology	2010		X					X			X	X		TC$_{brain}$, TC$_{blood}$, TC$_{muscle}$, TC$_{rectal}$, diving physiology study
149	Liwanag, HEM	Energetic costs and thermoregulation in northern fur seal (*Callorhinus ursinus*) pups: the importance of behavioral strategies for thermal balance in furred marine mammals	Physiological and Biochemical Zoology	2010		X			X	X							
150	Meir, JU; Ponganis, PJ	Blood temperature profiles of diving elephant seals	Physiological and Biochemical Zoology	2010	X			X							X	X	P$_{O2}$ electrode, TR$_{blood}$, TDR, SAT, VHF, diving physiology study, in water

151	Nienaber, J; Thomton, H; Horning, M; Polasek, L; Mellish, J-A	Surface temperature patterns in seals and sea lions: a validation of temporal and spatial consistency	Journal of Thermal Biology	2010		X			X						X		IRT
152	Norris, AL; Houser, DS; Crocker, DE	Environment and activity affect skin temperature in breeding adult male elephant seals (*Mirounga angustirostris*)	Journal of Experimental Biology	2010	X			X							X		IRT, on land
153	Houser, DS; Yeates, LC; Crocker, DE	Cold stress induces an adrenocortical response in bottlenose dolphins (*Tursiops truncatus*)	Journal of Zoo and Wildlife Medicine	2011		X			X	X							
154	Bagge, LE; Koopman, HN; Rommel, SA; McLellan, WA; Pabst, DA	Lipid class and depth-specific thermal properties in the blubber of the short-finned pilot whale and the pygmy sperm whale	Journal of Experimental Biology	2012		X								X			
155	Durban, JW; Pitman, RL	Antarctic killer whales make rapid, round-trip movements to subtropical waters: evidence for physiological maintenance migrations?	Biology Letters	2012	X			X								X	SAT, in water
156	Erdsack, N; Hanke, FD; Dehnhardt, G; Hanke, W	Control and amount of heat dissipation through thermal windows in harbor seals (*Phoca vitulina*)	Journal of Thermal Biology	2012		X	X	X	X						X		IRT

157	Khamas, WA; Smodlaka, H; Leach-Robinson, J; Palmer, L	Skin histology and its role in heat dissipation in three pinniped species	Acta Veterinaria Scandinavica	2012		X								X			
158	Liwanag, HEM; Berta, A; Costa, DP; Abney, M; Williams, TM	Morphological and thermal properties of mammalian insulation: the evolution of fur for aquatic living	Biological Journal of the Linnean Society	2012		X								X			
159	Liwanag, HEM; Berta, A; Costa, DP; Budge, SM; Williams, TM	Morphological and thermal properties of mammalian insulation: the evolutionary transition to blubber in pinnipeds	Biological Journal of the Linnean Society	2012		X								X			
160	McClelland, SJ; Gay, M; Pabst, DA; Dillaman, R; Westgate, AJ; Koopman, HN	Microvascular patterns in the blubber of shallow and deep diving odontocetes	Journal of Morphology	2012		X								X			
161	Mellish, J; Nienaber, J; Polasek, L; Horning, M	Beneath the surface: Profiling blubber depth in pinnipeds with infrared imaging	Journal of Thermal Biology	2012		X			X						X		IRT
162	Paterson, W; Sparling, CE;	Seals like it hot: Changes in surface temperature of harbour seals (*Phoca*	Journal of Thermal Biology	2012		X				X					X		IRT

	Thompson, D; Pomeroy, PP; Currie, JI; McCafferty, DJ	*vitulina*) from late pregnancy to moult															
163	Erdsack, N; Dehnhardt, G; Hanke, W	Coping with heat: function of the natal coat of Cape fur seal (*Arctocephalus pusillus pusillus*) pups in maintaining core body temperature	PLoS ONE	2013		X				X	X				X		IRT
164	Ford Jr, TJ; Werth, AJ; George, JC	An intraoral thermoregulatory organ in the bowhead whale (*Balaena mysticetus*), the corpus cavernosum maxillaris	The Anatomical Record	2013		X								X	X		IRT (oral cavity)
165	Rodríguez-Prieto, V; Rubio-García, A; Melero, M; García, D; Sánchez-Vizcaíno, JM	Identification of the pattern of appearance and development of thermal windows in the skin of juvenile Pacific walruses (*Odobenus rosmarus divergens*) in a controlled environment	Marine Mammal Science	2013		X			X						X		IRT
166	Dalton, AJM; Rosen, DAS; Trites, AW	Broad thermal capacity facilitates the primarily pelagic existence of northern fur seals (*Callorhinus ursinus*)	Marine Mammal Science	2014		X			X								

167	Erdsack, N; Dehnhardt, G; Hanke, W	Thermoregulation of the vibrissal system in harbor seals (*Phoca vitulina*) and Cape fur seals (*Arctocephalus pusillus pusillus*)	Journal of Experimental Marine Biology and Ecology	2014	X				X						X		IRT (vibrissal pad), on land
168	Garlepp, L; Logan, M; Kirkwood, R	Behavioral responses of Australian fur seals (*Arctocephalus pusillus doriferus*) to environmental variations	Marine Mammal Science	2014	X			X									on land
169	Horgan, P; Booth, D; Nichols, C; Lanyon, JM	Insulative capacity of the integument of the dugong (*Dugong dugon*): thermal conductivity, conductance and resistance measured by in vitro heat flux	Marine biology	2014		X								X			
170	Liwanag, HEM; Oraze, J; Costa, DP; Williams, TM	Thermal benefits of aggregation in a large marine endotherm: huddling in California sea lions	Journal of Zoology	2014	X			X							X		IRT, on land
171	Pearson, LE; Liwanag, HEM; Hammill, MO; Burns, JM	Shifts in thermoregulatory strategy during ontogeny in harp seals (*Pagophilus groenlandicus*)	Journal of Thermal Biology	2014		X							X	X			
172	Pearson, LE; Liwanag, HEM; Hammill,	To each its own: Thermoregulatory strategy varies among neonatal polar phocids	Comparative Biochemistry and Physiology Part A: Molecular &	2014		X							X	X			

	MO; Burns, JM		Integrative Physiology														
173	Rosen, DAS; Trites, AW	Thermal limits in young northern fur seals, *Callorhinus ursinus*	Marine Mammal Science	2014		X			X								
174	Ball, HC; Stavarz, M; Oldaker, J; Usip, S; Londraville, RL; George, JC; Thewissen, JGM; Duff, RJ	Seasonal and ontogenetic variation in subcutaneous adipose of the bowhead whale (*Balaena mysticetus*)	The Anatomical Record	2015		X								X			
175	Ekdale, EG; Kienle, SS	Passive Restriction of Blood Flow and Counter-Current Heat Exchange Via Lingual Retia in the Tongue of a Neonatal Gray Whale E schrichtius robustus (Cetacea, Mysticeti)	The Anatomical Record	2015		X							X				
176	Erdsack, N; Dehnhardt, G; Witt, M; Wree, A; Siebert, U; Hanke, W	Unique fur and skin structure in harbour seals (*Phoca vitulina*)—thermal insulation, drag reduction, or both?	Journal of the Royal Society Interface	2015		X								X			
177	Gmuca, NV; Pearson,	The fat and the furriest: morphological	Physiological and	2015		X								X			

	LE; Burns, JM; Liwanag, HEM	changes in harp seal fur with ontogeny	Biochemical Zoology														
178	Gómez-Campos, E; Borrell, A; Correas, J; Aguilar, A	Topographical variation in lipid content and morphological structure of the blubber in the striped dolphin	Scientia Marina	2015		X								X			
179	Hashimoto, O; Ohtsuki, H; Kakizaki, T; Amou, K; Sato, R; Doi, S; Kobayashi, S; Matsuda, A; Sugiyama, M; Funaba, M	Brown adipose tissue in cetacean blubber	PLoS ONE	2015		X								X			
180	Hindle, AG; Horning, M; Mellish, JAE	Estimating total body heat dissipation in air and water from skin surface heat flux telemetry in Weddell seals	Animal Biotelemetry	2015	X		X	X							X	X	STP, HF sensor with integrated thermistor (T_{skin}), IRT, TDR, accelerometer, SAT, VHF, field component on land and in water

181	Melero, M; Rodríguez-Prieto, V; Rubio-García, A; García-Párraga, D; Sánchez-Vizcaíno, JM	Thermal reference points as an index for monitoring body temperature in marine mammals	BMC Research Notes	2015		X			X						X		IRT
182	Mellish, J-A; Hindle, A; Skinner, J; Horning, M	Heat loss in air of an Antarctic marine mammal, the Weddell seal	Journal of Comparative Physiology B	2015	X		X	X			X				X		IRT, field component on land
183	Noren, SR; Udevitz, MS; Triggs, L; Paschke, J; Oland, L; Jay, CV	Identifying a reliable blubber measurement site to assess body condition in a marine mammal with topographically variable blubber, the Pacific walrus	Marine Mammal Science	2015		X			X								
184	Sakurai, Y; Okamatsu-Ogura, Y; Saito, M; Kimura, K; Nakao, R; Ohnuma, A; Kobayashi, M	Brown adipose tissue expresses uncoupling protein 1 in newborn harbor seals (*Phoca vitulina*)	Marine Mammal Science	2015		X								X			
185	Zeng, X; Ji, J; Hao, Y; Wang, D	Topographical distribution of blubber in finless porpoises (*Neophocaena asiaeorientalis sunameri*): a result	Zoological Studies	2015		X							X	X			

		from adapting to living in coastal waters															
186	Codde, SA; Allen, SG; Houser, DS; Crocker, DE	Effects of environmental variables on surface temperature of breeding adult female northern elephant seals, *Mirounga angustirostris*, and pups	Journal of Thermal Biology	2016	X			X							X		IRT, on land
187	Cornick, LA; Quakenbush, LT; Norman, SA; Pasi, C; Maslyk, P; Burek, DA; Goertz, CEC; Hobbs, RC	Seasonal and developmental differences in blubber stores of beluga whales in Bristol Bay, Alaska using high-resolution ultrasound	Journal of Mammalogy	2016	X						X		X				in water
188	Beltran, RS; Testa, JW; Burns, JM	An agent-based bioenergetics model for predicting impacts of environmental change on a top marine predator, the Weddell seal	Ecological Modelling	2017			X										
189	Ladds, MA; Slip, DJ; Harcourt, RG	Intrinsic and extrinsic influences on standard metabolic rates of three species of Australian otariid	Conservation physiology	2017		X			X								
190	Sharma, N; Liwanag, HEM	The effects of submergence on the	Marine Mammal Science	2017		X								X			

		thermal function of pinniped fur															
191	Singleton, EM; McLellan, WA; Koopman, HN; Pokorny, A; Scharf, FS; Pabst, DA	Lipid composition and thermal properties of the blubber of Gervais' beaked whale (*Mesoplodon europaeus*) across ontogeny	Marine Mammal Science	2017		X								X			
192	Chaise, LL; Prinet, I; Toscani, C; Gallon, SL; Paterson, W; McCafferty, DJ; Théry, M; Ancel, A; Gilbert, C	Local weather and body condition influence habitat use and movements on land of molting female southern elephant seals (*Mirounga leonina*)	Ecology and Evolution	2018	X			X								X	GPS, VHF, on land
193	Erdsack, N; Phillips, SRM; Rommel, SA; Pabst, DA; McLellan, WA; Reynolds, JE	Heat flux in manatees: an individual matter and a novel approach to assess and monitor the thermal state of Florida manatees (*Trichechus manatus latirostris*)	Journal of Comparative Physiology B	2018		X			X								
194	García-Aguilar, AC; Turrent, C; Elorriaga-Verplancken, FR;	Climate change and the northern elephant seal (*Mirounga angustirostris*) population in Baja California, Mexico	PLoS ONE	2018	X			X									on land

	Arias-Del-Razo, A; Schramm, Y																
195	Krmpotic, CM; Loza, CM; Negrete, J; Scarano, AC; Carlini, AA; Guerrero, A; Barbeito, CG	Integument in Antarctic seals: a comparative study and its relation to extreme environments	Acta Zoologica	2018		X								X			
196	Rojano-Doñate, L; McDonald, BI; Wisniewska, DM; Johnson, M; Teilmann, J; Wahlberg, M; Højer-Kristensen, J; Madsen, PT	High field metabolic rates of wild harbour porpoises	Journal of Experimental Biology	2018	X	X		X	X		X					X	TDR, accelerometer, SAT, VHF, field component in water
197	Zeh, DR; Heupel, MR; Hamann, M; Jones, R; Limpus, CJ; Marsh, H	Evidence of behavioural thermoregulation by dugongs at the high latitude limit to their range in eastern Australia	Journal of Experimental Marine Biology and Ecology	2018	X			X								X	SAT, GPS, acoustic transmitter (depth & T_{water}), in water

198	Adamczak, SK; Pabst, DA; McLellan, WA; Thorne, LH	Using 3D Models to Improve Estimates of Marine Mammal Size and External Morphology	Frontiers in Marine Science	2019			X						X				
199	Chaise, LL; McCafferty, DJ; Krellenstein, A; Gallon, SL; Paterson, WD; Théry, M; Ancel, A; Gilbert, C	Environmental and physiological determinants of huddling behavior of molting female southern elephant seals (*Mirounga leonina*)	Physiology & Behavior	2019	X			X							X	X	STP, IRT, VHF, TDR, on land
200	Guerrero, AI; Rogers, TL	From low to high latitudes: changes in fatty acid desaturation in mammalian fat tissue suggest a thermoregulatory role	BMC Evolutionary Biology	2019		X								X			
201	Ji, J; Nabi, G; Zeng, X; Hao, Y; Wang, D	Histological variation in blubber morphology of the endangered east asian finless porpoise (*Neophocaena asiaeorientalis sunameri*) with ontogeny and reproductive states	Zoological Studies	2019		X							X	X			
202	Kastelein, RA; Helder-Hoek, L; Jennings, N; van	Reduction in Body Mass and Blubber Thickness of Harbor Porpoises (*Phocoena phocoena*) Due to Near-Fasting for 24	Aquatic Mammals	2019		X			X								

	Kester, R; Huisman, R	Hours in Four Seasons															
203	Lonati, GL; Singleton, EM; Phelps, CE; Koopman, HN; Pabst, DA	The density of odontocete integument depends on blubber lipid composition and temperature	Marine Mammal Science	2019		X								X			
204	Pearson, LE; Weitzner, EL; Burns, JM; Hammill, MO; Liwanag, HEM	From ice to ocean: changes in the thermal function of harp seal pelt with ontogeny	Journal of Comparative Physiology B	2019		X	X							X			
205	Pitman, RL; Durban, JW; Joyce, T; Fearnbach, H; Panigada, S; Lauriano, G	Skin in the game: Epidermal molt as a driver of long-distance migration in whales	Marine Mammal Science	2019	X			X								X	SAT, TDR, in water
206	Plön, S; Frainer, G; Wedderburn-Maxwell, A; Cliff, G; Huggenberger, S	Dorsal fin and hump vascular anatomy in the Indo-Pacific humpback dolphin (*Sousa plumbea*) and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*)	Marine Mammal Science	2019		X								X			

207	Tuneu-Corral, C; Szteren, D; Cassini, MH	Living on the edge: thermoregulatory behaviour of South American sea lions, *Otaria flavescens*, at the northern limit of their Atlantic distribution	Acta Ethologica	2019	X			X									on land
2020-2021																	
208	Adamczak, SK; Pabst, DA; McLellan, WA; Thorne, LH	Do bigger bodies require bigger radiators? Insights into thermal ecology from closely related marine mammal species and implications for ecogeographic rules	Journal of Biogeography	2020			X						X				not included in figure
209	Adamczak, SK; McLellan, WA; Read, AJ; Wolfe, CLP; Thorne, LH	The impact of temperature at depth on estimates of thermal habitat for short-finned pilot whales	Marine Mammal Science	2020	X			X								X	not included in figure, TDR
210	Chambault, P; Tervo, OM; Garde, E; Hansen, RG; Blackwell, SB; Williams, TM; Dietz, R; Albertsen, CM; Laidre, KL;	The impact of rising sea temperatures on an Arctic top predator, the narwhal	Scientific Reports	2020	X			X								X	not included in figure, SAT, GPS, in water

	Nielsen, NH																
211	da Silva, AP; Machado, ASD; Le Bas, AE; Silva, RG; dos Anjos Silva, E; Hernandez-Blazquez, FJ	The skin structures and their role in the thermoregulation of the South American fur seal (*Arctocephalus australis*)	The Anatomical Record	2020		X								X			not included in figure
212	Haase, CG; Fletcher Jr, RJ; Slone, DH; Reid, JP; Butler, SM	Traveling to thermal refuges during stressful temperatures leads to foraging constraints in a central-place forager	Journal of Mammalogy	2020	X			X								X	not included in figure, SAT, GPS, in water
213	Heide-Jørgensen, MP; Blackwell, SB; Williams, TM; Sinding, MHS; Skovrind, M; Tervo, OM; Garde, E; Hansen, RG;	Some like it cold: Temperature-dependent habitat selection by narwhals	Ecology and evolution	2020	X			X								X	not included in figure, TDR, CTD, SAT, GPS, in water

	Nielsen, NH; Ngô, MC																
214	Walcott, SM; Kirkham, AL; Burns, JM	Thermoregulatory costs in molting Antarctic Weddell seals: impacts of physiological and environmental conditions	Conservation physiology	2020	X						X				X		not included in figure, IRT, on land
215	Guerrero, AI; Rogers, TL; Sepúlveda, M	Conditions influencing the appearance of thermal windows and the distribution of surface temperature in hauled-out southern elephant seals	Conservation Physiology	2021	X			X							X		not included in figure, IRT, in water
216	John, JS; Thometz, NM; Boerner, K; Denum, L; Kendall, TL; Richter, BP; Gaspard, JC; Williams, TM	Metabolic tradeoffs in tropical and subtropical marine mammals-Unique maintenance and locomotion costs in West Indian manatees and Hawaiian monk seals	Journal of Experimental Biology	2021		X			X							X	not included in figure, accelerometry, on land
217	Sumich, JL	Why Baja? A bioenergetic model for comparing metabolic rates and thermoregulatory	Marine Mammal Science	2021			X										not included in figure

		costs of gray whale calves (*Eschrichtius robustus*)															
218	Wright, T; Davis, RW; Pearson, HC; Murray, M; Sheffield-Moore, M	Skeletal muscle thermogenesis enables aquatic life in the smallest marine mammal	Science	2021		X								X			not included in figure