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REVIEW

CENTENARY ARTICLE

Field physiology in the aquatic realm: ecological energetics and diving behavior provide context for elucidating patterns and deviations

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ABSTRACT

Comparative physiology has developed a rich understanding of the physiological adaptations of organisms, from microbes to megafauna. Despite extreme differences in size and a diversity of habitats, general patterns are observed in their physiological adaptations. Yet, many organisms deviate from the general patterns, providing an opportunity to understand the importance of ecology in determining the evolution of unusual adaptations. Aquatic air-breathing vertebrates provide unique study systems in which the interplay between ecology, physiology and behavior is most evident. They must perform breath-hold dives to obtain food underwater, which imposes a physiological constraint on their foraging time as they must resurface to breathe. This separation of two critical resources has led researchers to investigate these organisms' physiological adaptations and trade-offs. Addressing such questions on large marine animals is best done in the field, given the difficulty of replicating the environment of these animals in the lab. This Review examines the long history of research on diving physiology and behavior. We show how innovative technology and the careful selection of research animals have provided a holistic understanding of diving mammals' physiology, behavior and ecology. We explore the role of the aerobic diving limit, body size, oxygen stores, prey distribution and metabolism. We then identify gaps in our knowledge and suggest areas for future research, pointing out how this research will help conserve these unique animals.

KEY WORDS: Aerobic dive limit, Body size, Diving physiology, Ecophysiology, Metabolism, Oxygen stores

Introduction

Over the last century, comparative physiology has developed a rich understanding of the physiological adaptations of organisms across various environments and scales, from microbes to megafauna. We often start by looking for organisms in extreme environments where the physiological adaptation will be most profound and thus readily studied. Using this guiding framework, known as the Krogh Principle (Krogh, 1929), and performing studies in the laboratory, where experimental protocols are most readily developed and conditions are controlled, we have gained an understanding of the general patterns of organisms' physiological adaptive landscapes (Green et al., 2018). Given that physics underlies chemistry which underlies biology and physiology, these general patterns, such as the relationship between body size and metabolic rate, should be expected (Brown et al., 2004). However, many organisms deviate from these broad or general adaptive patterns. Though the deviations were initially considered 'noise', we now recognize that this 'noise' provides tremendous opportunities to expand our understanding of the range of animals' physiological responses to different and challenging environments (Costa and Shaffer, 2012).

In this Review, we use research on diving marine mammals to demonstrate how studying physiology in the field deepens our understanding of animals in nature by combining physiology, behavior and ecology. Diving animals offer a unique opportunity to study the interface between behavior and physiology because their ability to dive and find food is directly limited by their physiology. The diving ability of animals is a function of their oxygen stores (held in the lung, blood and muscle) and the rate of oxygen consumption as determined by their diving metabolic rate. Novel instrumentation and approaches have made it possible to study these animals as they carry out their everyday lives in nature. Insights from field research studies have clarified that physiology cannot be studied in isolation in a lab as this also requires knowledge of the animal's behavior and ecological context, which can only be studied in the field.

During the past century, Journal of Experimental Biology (JEB) has played an important role in reporting research in this area, as nearly 25% of the publications cited in this Review were published in JEB. The range of studies is quite broad but, for example, varies from metabolic rate measurements in the lab and field (e.g. Castellini et al., 1992; Costa and Gales, 2000; Ponganis et al., 2009, 2007; Quick et al., 2020; Reed et al., 1994; Rojano-Doñate et al., 2018; Sparling and Fedak, 2004; Williams et al., 2004; Yeates et al., 2007), to measurements of oxygen stores and estimates of aerobic dive limits (e.g. Hassrick et al., 2010; Ponganis et al., 2015, 2007; Tift et al., 2017; Velten et al., 2013; Weise and Costa, 2007; Williams et al., 1993). By taking advantage of technological innovations, many of the above studies have expanded our understanding to the ecologically relevant setting – in the field. We highlight existing gaps in diving physiology and suggest future directions that would illuminate some unresolved mysteries. As ecophysiologists, we aim to understand how animals make a living and why certain species or populations are more vulnerable to changing conditions. Such holistic knowledge is needed to tackle present-day conservation challenges (Cooke et al., 2021; Hays et al., 2019).

The progression from the lab to the field: diving physiology as a hallmark example

The study of marine mammals' diving physiology and foraging behavior highlights the progression of research from the lab to the field. Aquatic air-breathing vertebrates obtain their food underwater but need to surface to breathe. Whether a marine iguana, a penguin, a seal or a dolphin, the fundamental constraints are the same.

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Glossary

Aerobic dive limit
The point during a dive when lactic acid begins to increase above resting levels, i.e. the threshold where the animal goes from exclusively oxidative metabolism to including anaerobic metabolism.

Benthic foraging
Animals that forage on or near the ocean floor.

Bradycardia
Reduction in heart rate.

Capital breeding strategy
A reproductive pattern where the female acquires all of the energy required for lactation prior to giving birth. Once the female gives birth, she relies on stored energy reserves to complete lactation.

Demersal prey
Prey that are found on or near the ocean floor.

Field metabolic rate
Measurement of the oxidative energy expended by an animal while it is freely living in nature.

Hypoperfusion
Reduction in blood flow to the tissue.

Hypoxemic tolerance
The ability of a tissue to tolerate a lack of oxygen.

Lung collapse
The physical collapse of the lungs associated with increased pressure as the animal descends.

Maternal condition
A measure of a female's energy and protein stores. A female in good condition will have large protein and energy stores. In contrast, a female in poor condition will have low energy and protein stores. Also used as an index of the animal's health.

Mesopelagic foraging
Organisms that forage in the water column in depths between 200 and 1000 m.

Nitrogen washout
The process of dissolved nitrogen being transported out of the animal through the cardio-respiratory system.

Otariids
Members of the Family Otariidae, also known as the 'eared seals', including sea lions and fur seals.

Phocids
Members of Family Phocidae, also known as the 'earless or true seals', which consists of the seals.

Post-dive surface interval
The time between the end of a dive when the animal reaches the surface and the beginning of the next dive.

Time–activity budget
An approach where the total energy an animal expends is determined by summing the cost of each activity and the amount of time spent in each activity.

Foundational lab-based research by Per Scholander (1940) showed that gray seals (*Halichoerus grypus*) exhibited a dive response that included reductions in heart rate, peripheral circulation and metabolism. Immediately after the dive, lactic acid concentrations in the blood increased significantly and then decreased as this byproduct of anaerobic metabolism was cleared. This early work demonstrated the extreme physiological capabilities of marine mammals, highlighted their utility as 'Krogh organisms' and stimulated many lab-based research efforts (reviewed by Kooyman, 2015). A few examples include experiments investigating the cardiovascular response of a forcibly submerged elephant seal (*Mirounga angustirostris*) (Elsner et al., 1966a), the diving bradycardia (see Glossary) of a trained bottlenose dolphin (*Tursiops truncatus*) (Elsner et al., 1966b), California sea lions (*Zalophus californianus*) being trained to induce bradycardia in air (Ridgway et al., 1975), and lung collapse (see Glossary) and nitrogen washout (see Glossary) in an open ocean-trained bottlenose dolphin (Ridgway and Howard, 1979).

The importance of these physiological mechanisms to animals in nature became clear when field studies were carried out (Kooyman and Campbell, 1972; Kooyman et al., 1973, 1980). Finding an animal conducive to study in the field is equally as important as finding an animal in an extreme environment. Weddell seals (*Leptonychotes weddelli*) are an excellent example of an animal with a life history conducive to study. They live in 'fast ice' (ice attached to the shore) where they use cracks in the ice to access the water to dive for food and return for air in between dives. Because they have no land predators, Weddell seals are tame, allowing researchers to approach them. Similarly, many endemic species of the Galapagos Islands are not afraid of humans, again because of the absence of land predators. For example, the ability to approach and closely observe Galapagos sea lions (*Zalophus wollebaki*) and fur seals (*Arctocephalus galapagoensis*) has facilitated long-term studies that have yet to be replicated with temperate otariids (Schwarz et al., 2022; see Glossary).

Taking advantage of Weddell seals' natural behavior of returning to an ice hole to breathe after long, deep dives, investigators created a 'field laboratory' by transporting the seal to a region with only one accessible ice hole, allowing the researchers to sample the seal and attach and recover data loggers in between dives (Kooyman and Campbell, 1972). Early studies measured the heart rate of freely diving seals and their blood chemistry, blood nitrogen levels, diving metabolic rate and most importantly, their post-dive lactate levels (Castellini et al., 1992; Guppy et al., 1986; Hill, 1986; Kooyman et al., 1980; Ponganis et al., 1993).

The development of the time–depth recorder – arguably the most important contribution to the field of diving physiology – was made possible by a key technological innovation, the microprocessor computer. The earliest deployments of time–depth recorders were on lactating fur seals and sea lions because, like Weddell seals, they are predictably accessible. Mothers reliably return to the colony to suckle their pups, thus facilitating the recovery of instrumented animals (Gentry and Kooyman, 1986). They are also in more accessible regions of the world than Antarctica. Since these early developments, increased storage capacity and novel sensors have expanded the physiological parameters that could be measured on a diving animal (e.g. Favilla et al., 2022; Horning and Hill, 2005; Kuhn and Costa, 2006; Kuhn et al., 2009; McDonald et al., 2021).

Nowadays, field-based physiological research is possible on even some of the most cryptic species, such as beaked whales (*Ziphius cavirostris*, *Mesoplodon densirostris* and *Mesoplodon bidens*) and the largest, the blue whale (*Balenoptera musculus*) (Alcazar-Trevino et al., 2021; Goldbogen and Madsen, 2021; Tyack et al., 2006; Visser et al., 2022). Sensors that measure behavior (swim velocity, 3-axis acceleration), underwater orientation (using magnetometers and gyroscopes), horizontal movement via geolocation, foraging events (via cameras or accelerometers) and environmental parameters (light, sound, temperature, salinity, chlorophyll, dissolved oxygen, environmental DNA) have provided more context to the concurrent physiological measurements (e.g. Johnson et al., 2009; Williams and Hindle, 2021; Visser et al., 2021). We continue to expand our ability to study unique animals, their ecology with physiology, and provide significant insight into the biology of animals in nature (Williams and Ponganis, 2021).

The aerobic dive limit, linking behavior and physiology

The initial diving studies conducted in the lab documented the 'dive response' as a profound bradycardia with reduced metabolism during a dive followed by a significant post-dive increase in lactate acid (Scholander, 1940). Even though Scholander (1940) cautioned that this needed to be verified in the field, the ‘textbook’ explanation became that anaerobic metabolism was a standard component of an animal’s dive response. It wasn’t until Kooyman and colleagues (1980) measured post-dive blood lactate levels in freely diving Weddell seals that we understood that aerobic diving was the norm. They found that Weddell seals could dive up to 20 min before post-dive blood lactate levels increased. The dive duration at which lactate levels first increased above pre-dive levels was defined as the aerobic dive limit (ADL; see Glossary) (Kooyman et al., 1980) but has also been called the diving lactate threshold (DLT) (see Butler, 2006, for idiosyncratic definitions; see Kooyman et al., 2021, for a review of its history and misuse). Beyond this ‘threshold,’ a substantial increase in the post-dive surface interval (see Glossary) is required to clear the lactate acid to restore it to pre-dive levels. Unfortunately, the ADL has only been directly measured in a few species because of logistical challenges: Weddell seals (Kooyman et al., 1980), Baikal seals (*Pusa sibirica*) (Ponganis et al., 1997a), California sea lions (Ponganis et al., 1997c), emperor penguins (*Aptenodytes forsteri*) (Ponganis et al., 1997b), beluga whales (*Delphinapterus leucas*) (Shaffer et al., 1996) and bottlenose dolphins (Williams et al., 1999).

These relationships between dive duration and subsequent surface time have ecological significance for diving species. When animals dive aerobically (below the ADL), the post-dive surface interval is short relative to the dive duration. However, when they exceed the ADL, the post-dive surface interval (or recovery time) becomes a more significant proportion of the dive cycle. Thus, an animal spends more time at the surface recovering from a dive than underwater in a dive, reducing its overall efficiency (Fig. 1A). This led to the concept that animals should dive aerobically for routine sustained diving, reserving anaerobic dives for rare or extreme events (Kooyman et al., 1980).

With the commercialization and reduced cost of electronic tags, researchers have been able to deploy instruments on a wide array of animals in the field, revealing their routine behavior and extreme diving capabilities (reviewed by Andrews and Enstipp, 2016). To put the diving behavior of animals in context, a few studies have measured diving behavior while simultaneously measuring the animals’ oxygen stores (muscle, blood and respiratory system) and estimating their diving metabolic rate (e.g. Costa et al., 2001, 2004; Fowler et al., 2007; Hassrick et al., 2010; Kuhn et al., 2006; Lydersen et al., 1992; Ponganis et al., 1997a,b,c, 1993; Shero et al., 2012, 2015; Weise and Costa, 2007; Weise et al., 2010; Yeates et al., 2007). For other species, such as beaked and baleen whales, studies calculate the ADL by extrapolation from the few species where oxygen stores and metabolism have been measured (Croll et al., 2001; Quick et al., 2020; Tyack et al., 2006).

Field studies have shown that most animals dive within their estimated ADL (Butler, 2004; Ponganis et al., 2015); however, animals occasionally dive well beyond their ADL to avoid predators or disturbances. Usually, these long dives are followed by a prolonged post-dive surface interval (Horning, 2012). However, elephant seals have been observed to make a series of prolonged dives with no change in their post-dive surface interval (Hassrick et al., 2010). A female elephant seal’s typical dive duration is 21–35 min (calculated ADL range: 28–35 min; Hassrick et al., 2010; Robinson et al., 2012), but these seals frequently perform consecutive dives longer than 40 min in duration with short post-dive surface intervals (~2 min) in between (Fig. 1B). These dives are pushing the limits of our understanding of diving physiology (Kooyman et al., 2021).

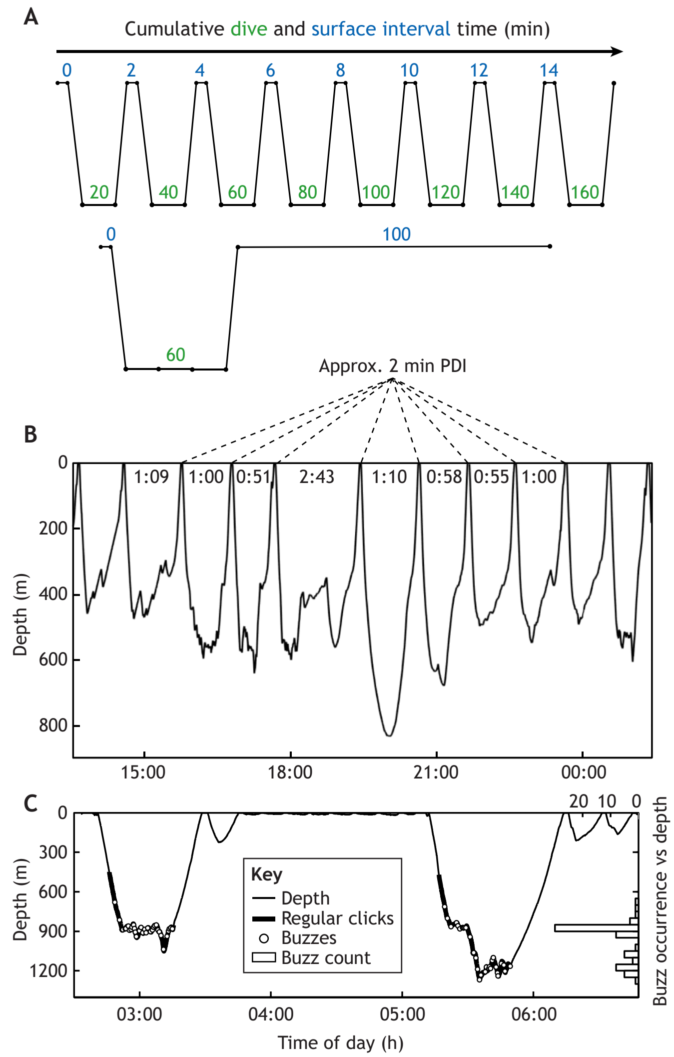

Fig. 1. Our theoretical understanding of aerobic versus anaerobic diving and example dive profiles from two deep-diving species that challenge our understanding of their diving physiology. (A) A simplistic depiction of the theoretical implications of aerobic (top) versus anerobic (bottom) diving. More time is spent diving rather than at the surface when diving aerobically. (B) Dive depth and duration (top values, h:min) of a female northern elephant seal (*Mirounga angustirostris*) that consistently dived longer than the calculated aerobic dive limit (ADL) and spent negligible time at the surface (dashed lines indicate the post-dive interval, PDI). (C) Deep dives of beaked whales (*Ziphius cavirostris*) have high buzz counts (histogram on the right) indicative of foraging and occur between bouts of shallow diving (modified from Tyack et al., 2006).

Similarly, it has been suggested that beaked whales (*Z. cavirostris* and *M. densirostris*) consistently exceed their estimated aerobic dive limit when foraging normally, typically making 58 min dives (Tyack et al., 2006). They routinely forage below 1000 m and, when disturbed, have achieved a record depth of 2992 m, the deepest dive of any mammal (Schorr et al., 2014). Nevertheless, these long foraging dives are followed by shallow dives that are cumulatively longer than the deeper foraging dives (Fig. 1C) (Tyack et al., 2006). As these shallow dives require less active swimming, the oxygen stores could be used to process the accumulated lactic acid instead of supporting the swimming muscles. However, recent work suggests that the extreme diving ability of beaked whales may be enabled by a low diving metabolic rate, coupled with the largest mass-specific oxygen stores of any cetacean (Pabst et al., 2016; Quick et al., 2020; Velten et al., 2013). Near-complete depletion of oxygen stores, exceptional hypoxemic tolerance (see Glossary), reduced diving metabolic rate and an increased buffering capacity to withstand acidosis in the muscle enable deep-diving species such as beaked whales (2992 m, 138 min), elephant seals (2388 m, 120 min), Weddell seals (904 m, 96 min) and emperor penguins (564 m, 27.6 min) to carry out their long and deep dives (Fig. 1) (Castellini et al., 1992; Castellini and Somero, 1981; Elsner et al., 1970; Folkow et al., 2008; Kerem and Elsner, 1973; Meir et al., 2009; Ponganis et al., 2009, 2007, 2010; Tift and Ponganis, 2019).

Although less extreme in their diving capabilities, some marine mammals, such as Australian (*Neophoca cinerea*) (Costa and Gales, 2003) and New Zealand (*Phocarctos hookeri*) sea lions (Chilvers et al., 2006), routinely dive beyond their estimated ADL (based on measurements of their oxygen stores and estimates of diving metabolic rate) (Costa and Gales, 2000). However, like elephant seals, their post-dive interval is shorter than the duration of their dive. While a definitive explanation is still lacking, we hypothesize that they exceed their ADL but tolerate the increased lactic acid, perhaps through an increased buffering capacity (Castellini et al., 1992). Such discrepancies between behavioral and physiological data provide opportunities to delve further into the mechanisms behind deviations from the norm.

Combining knowledge of behavior, physiology and ecology can enhance our understanding, as for the diving patterns of beaked whales, or perhaps reveal instances where knowledge gaps still exist. In the case of Australian and New Zealand sea lions, biochemical and/or molecular analyses of muscle tissue could offer insights into how they dive beyond their theoretical ADL (Berenbrink, 2021). Although measuring blood lactate concentrations using serial post-dive blood samples is the gold standard for determining an individual's ADL, measuring blood lactate levels at intervals throughout the dive may provide valuable insight into how these sea lions are able to perform such feats. Measurements of venous lactate concentrations throughout the dive have only been accomplished a few times (Guppy et al., 1986; Ponganis et al., 2009). In these instances, lower-than-expected lactate concentrations led the authors to suggest that lactate could accumulate in the locomotory muscle or that a depressed metabolic rate could explain the low blood lactate levels. A lactate sensor that could measure lactate levels during a dive in the blood and muscle would provide insight into the production, accumulation, transport and processing of lactate in the blood and muscle, the primary oxygen stores for most diving mammals. Continuous lactate measurements in the blood would also reveal when animals dive past their ADL and transition from aerobic to anaerobic metabolism.

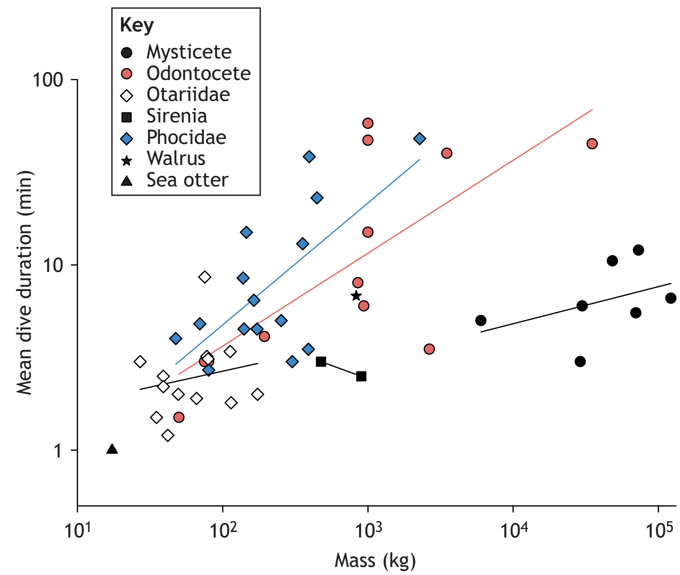

Fig. 2. Variation in dive duration with body mass of marine mammals. While mean dive duration increases with mean body mass, the relationship is specific to each taxonomic group. Data were obtained from the review by Favilla and Costa (2020). The following species are represented. Mysticete: blue whale *Balaenoptera musculus*, bowhead whale *Balaena mysticetus*, minke whale *Balaenoptera acutorostrata*, fin whale *Balaenoptera physalus*, gray whale *Eschrichtius robustus*, humpback whale *Megaptera novaeangliae*, North Atlantic right whale *Eubalaena glacialis*. Odontocete: beluga whale *Delphinapterus leucas*, Blainville's beaked whale *Mesoplodon densirostris*, bottlenose dolphin *Tursiops truncatus*, Cuvier's beaked whale *Ziphius cavirostris*, harbor porpoise *Phocoena phocoena*, killer whale *Orcinus orca*, narwhal *Monodon monoceros*, northern bottlenose whale *Hyperoodon ampullatus*, Pacific white-sided dolphin *Lagenorhynchus obliquidens*, pantropical spotted dolphin *Stenella attenuata*, short-finned pilot whale *Globicephala macrorhynchus*, sperm whale *Physeter macrocephalus*. Phocidae: Baikal seal *Pusa sibirica*, bearded seal *Erignathus barbatus*, crabeater seal *Lobodon carcinophagus*, gray seal *Halichoerus grypus*, harbor seal *Phoca vitulina*, harp seal *Pagophilus groenlandicus*, Hawaiian monk seal *Neomonachus schauinslandi*, hooded seal *Cystophora cristata*, leopard seal *Hydrurga leptonyx*, northern elephant seal *Mirounga angustirostris*, ringed seal *Pusa hispida*, Ross seal *Ommatophoca rossii*, southern elephant seal *Mirounga leonina*, Weddell seal *Leptonychotes weddellii.* Otariidae: Antarctic fur seal *Arctocephalus gazella*, Australian fur seal *Arctocephalus p. doriferus*, Australian sea lion *Neophoca cinerea*, California sea lion *Zalophus californianus*, Cape fur (South African) seal *Arctocephalus p. pusillus*, Galápagos fur seal *Arctocephalus galapagoensis*, Galápagos seal lion *Zalophus wollebaeki*, New Zealand fur seal *Arctocephalus forsteri*, New Zealand sea lion *Phocarctos hookeri*, northern fur seal *Callorhinus ursinus*, Steller sea lion *Eumetopias jubatus*, South American sea lion *Otaria flavescens/byronia*, Subantarctic fur seal *Arctocephalus tropicalis.* Sirenia: dugong *Dugong dugon*, West Indian manatee *Trichechus manatus*. Walrus *Odobenus rosmarus*. Sea otter *Enhydra lutris*.

Insights from the unexpected

As diving capabilities were measured in more species, it became evident that body size was a significant predictor of diving capacity (Fig. 2). This is because metabolic rate (i.e. oxygen demand) typically scales to body mass$^{0.75}$ while oxygen stores (i.e. supply) appear to scale with body mass$^{1.0}$ (Ponganis, 2016; Verberk et al., 2020). Thus, larger animals can dive longer and deeper (Halsey, 2011; Halsey et al., 2006; Ponganis et al., 2015). While this general pattern applies across an extensive array of taxa, including ectotherms and endotherms, from insects to air-breathing marine vertebrates, there are deviations associated with the organism's phylogeny and ecology (Verberk et al., 2020). For example, the largest species of sea lions perform the shortest and shallowest dives. In contrast, the smallest species make the longest and the second deepest dives (Fig. 3) (Costa and Valenzuela-Toro, 2021). The higher mass-specific metabolic rate of otariids partially offsets the advantages of large body size (Fig. 3). In contrast, a similar increase in body size in phocids (see Glossary) significantly increases their diving capacity. Phocids as a group are larger than otariids, which would increase their ADL but also provides a greater fasting ability, enabling their capital breeding system (Costa and Maresh, 2022; see Glossary).

In a diving animal, the optimal body size is a tradeoff between diving capacity and food requirements/prey availability. The exceptional diving ability of the smallest sea lion (Galapagos sea lion) is made possible by its possessing significantly higher mass-

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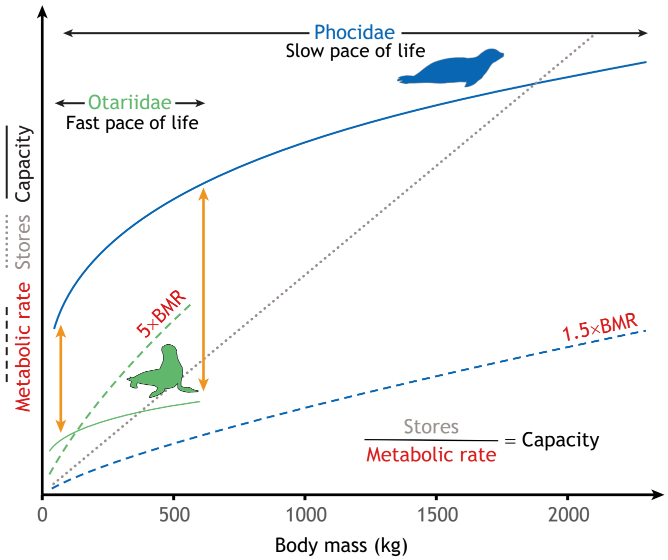

Fig. 3. Allometric scaling relationships of oxygen or fat stores, field metabolic rate, and diving or fasting capacity in marine mammals. Otariidae (green) and Phocidae (blue) were chosen to represent the differences between the metabolic rates of marine mammals with a fast (e.g. 5× predicted basal metabolic rate, BMR) versus slow (e.g. 1.5× predicted BMR) pace of life, respectively (field metabolic rate∝mass$^{0.75}$; dashed lines), and the resulting differences (emphasized by orange arrows) in their physiological capacities (diving or fasting capacity∝mass$^{0.25}$; solid lines), calculated from oxygen or fat stores (∝mass$^{1.0}$; gray dotted line) divided by metabolic rate. Mass ranges used for otariids (30–600 kg) and phocids (50–2300 kg) encompass representative averages (sex specific, if the species is sexually dimorphic) for the smallest and largest species in each group (otariids: Galapagos fur seal and male Steller sea lion; phocids: Baikal seal and male southern elephant seal). Mass data were obtained from the review by Favilla and Costa (2020) and Loughlin and Gelatt (2018).

specific oxygen stores (i.e. greater blood volume and muscle myoglobin) than other members of this family (Otariidae), which are equivalent to the levels seen in the 'true seals' (Phocidae; Fig. 3; Villegas-Amtmann et al., 2012; Villegas-Amtmann and Costa, 2010). Similarly, elevated mass-specific oxygen stores have been reported in the smallest marine mammal, the sea otter (*Enhydra lutris*) (Thometz et al., 2015). While not a particularly long or deep diver, the sea otter's large oxygen stores are necessary, given its high mass-specific metabolic rate, to routinely achieve 1–2 min dives.

In the case of the Galapagos sea lion, the ecological context provides insight into these deviations between body size and diving ability. Although the Galapagos Islands experience significant upwelling, the productivity of this region is still less than that of other upwelling systems that support air-breathing endotherms such as penguins, fur seals and sea lions (Villegas-Amtmann et al., 2011). The Galapagos sea lion's small size keeps its food requirements low, allowing it to subsist in an environment where prey is generally available but of lower overall abundance (Fig. 4). Given the warmer, less-productive surface waters, Galapagos sea lions need long dives to feed in the deeper, cooler, nutrient-rich waters. The resulting tradeoff between optimal body size for diving versus energy requirements and prey availability is resolved by having higher mass-specific oxygen stores and a lower mass-specific metabolism than larger sea lions in temperate regions (Costa and Valenzuela-Toro, 2021; Villegas-Amtmann and Costa, 2010; Villegas-Amtmann et al., 2017). However, it is unclear how this increase in oxygen stores and reduction in metabolism is achieved. Did it result from selection for genes that code for greater mass-specific blood volume and myoglobin stores, or could this be associated with hypoxic preconditioning induced by chronic exposure to hypoxia associated with prolonged diving (Kodama et al., 1977; Lu et al., 2005; Sharp et al., 2004)?

In another instance of divergence from this allometric pattern, the largest species of sea lions perform the shortest, shallowest dives (Fig. 5). This implies that, at least for these sea lions, the evolution of large body size was not related to diving ability, but rather was associated with some aspect of the animals' ecology (Hückstädt et al., 2016). From an ecological perspective, large body size confers greater fasting ability (Fig. 3), providing a buffer against variations in prey availability and allowing longer intervals and/or transits between prey patches. However, the disadvantage of large body size is that the animal requires more prey. Large body size may be favored when prey are patchy, but the prey in the patch are abundant (Fig. 4). This relationship has been documented in large whales (Goldbogen et al., 2019; Goldbogen and Madsen, 2018). Still, it has yet to be examined for smaller marine mammals, where it is more challenging to measure prey availability. As with the large whales, merging multiple data streams with prey field measurements will extend these observations to additional species (Hooker et al., 2002; Naito et al., 2017; Tournier et al., 2021).

This tradeoff between body size, diving ability and prey availability has also been described for elephant seals and beaked whales. The large size of female elephant seals allows them to make dives that are of sufficient duration to effectively reach the depth of mesopelagic prey (i.e. mesopelagic foraging; see Glossary). However, given their large body size, they need to consume 1000–2000 of these abundant but small mesopelagic prey per day, spending at least 80% of their day foraging (Adachi et al., 2021). While subadult male elephant seals are of similar size to adult females, they also forage in the mesopelagic zone (LeBoeuf et al., 1996) until they mature. As males become larger than females (up to 5–6 times) as a result of extreme sexual dimorphism, they can no longer meet their energy requirements foraging in the mesopelagic regions and transition to feeding on or near the continental shelf on larger prey (Kienle et al., 2022). While beaked whales are bigger than elephant seals, they are able to forage on fewer large mesopelagic prey, because they have biosonar, which allows them to search a much larger sensory volume and find prey more effectively (Naito et al., 2017).

The basis of unresolved questions: metabolism

How marine mammals regulate their metabolism and thus manage their oxygen stores is key to understanding their diving capabilities. While it is well established that metabolic rate varies non-linearly with body mass, the slope of this relationship continues to be debated (Brown et al., 2005; Heusner, 1987; White and Seymour, 2005). This question remains unresolved despite the fundamental role of metabolism in terms of understanding behavior, energetics and adaptive scope. There has been debate whether marine mammals have elevated basal metabolic rate (BMR) to offset the aquatic environment's greater thermal demands (Costa and Maresh, 2017; Davis, 2019; Williams et al., 2001). Still, some authors argue that there is no difference in the metabolism between terrestrial and marine mammals (Lavigne et al., 1986; Leaper and Lavigne, 2007). However, various factors determine resting metabolic rate (RMR) or BMR, including body mass, body composition, diet, reproductive status, age, sex and phylogeny (McNab, 1986, 2001; White, 2011), and extant marine mammals have transitioned into the ocean at least 5 times from different terrestrial lineages (Uhen, 2007). We should

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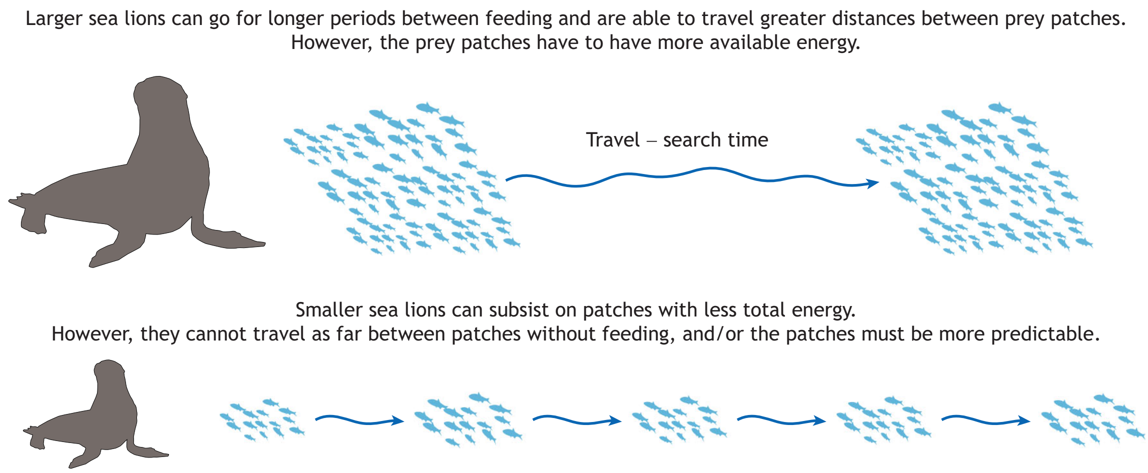

Fig. 4. Relationship between body size and daily energy (prey) requirements. Larger animals (top) can fast or go without food for longer than small animals. This allows them to spend more time traveling between food patches or between foraging bouts. Smaller animals (bottom) require less energy (prey) per day, but have to feed more frequently and require prey to be more evenly distributed or have prey patches that require shorter transit times.

not be surprised if they exhibit distinctly different metabolic adaptations associated with their different phylogeny and ecologies.

While providing insight into an animal's basal homeostatic state, measurements of BMR/RMR do not assess the energetic costs of animals free-ranging in nature. A more ecologically relevant measure is the field metabolic rate (FMR; see Glossary), which quantifies the animal's total energy expenditure after all metabolic costs are covered. Such measurements can provide insight into the energetic strategies employed by marine mammals (Butler et al., 2004; Costa, 2008). Previous FMR measurements have found that otariids have a high-energy lifestyle and expend energy ~5 times the predicted BMR (Costa and Valenzuela-Toro, 2021) (Fig. 3). High FMRs are associated with a fast pace of life, which enables elevated rates of prey-energy acquisition, which in turn allows greater energy investment in reproduction (Schmitz and Lavigne, 1984; Wright et al., 2018). Harbor porpoises (*Phocoena phocoena*) and pilot whales (*Globicephala macrorhynchus*) are predicted to have a similarly fast-paced life enabled by a high metabolism (Aguilar Soto et al., 2008; Aoki et al., 2017; Rojano-Doñate et al., 2018), whereas the lower FMR (1.5–3 times) predicted for elephant seals (Maresh et al., 2015), Weddell seals (Williams et al., 2004) and beaked whales (Pabst et al., 2016; Quick et al., 2020; Velten et al., 2013) is consistent with a slower pace of life and extended diving ability.

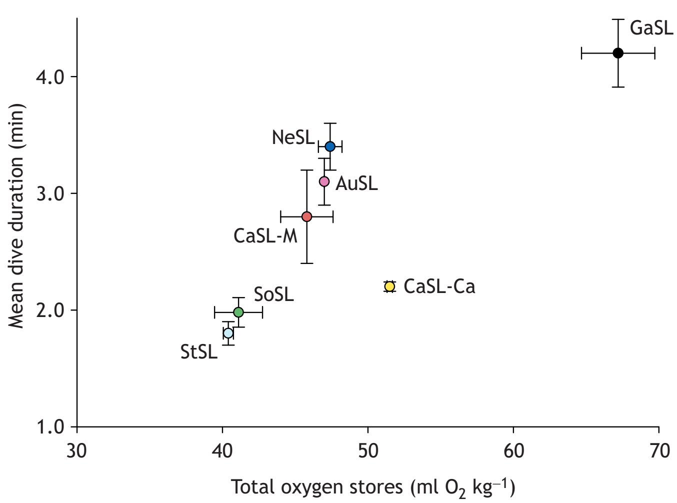

Fig. 5. Relationship between mean dive duration and total oxygen stores for seven species of sea lions, highlighting the exceptions to the trend that large body size confers longer diving ability. The smallest sea lion, the Galapagos sea lion (GaSL) at 77 kg, has the largest oxygen stores and dives the longest (Villegas-Amtmann and Costa, 2010), whereas the southern sea lion (SoSL) and Steller sea lions (StSL) are the largest sea lions (131 and 275 kg, respectively) but have the smallest oxygen stores and perform short dives (Hückstädt et al., 2016; Richmond et al., 2006). Data are means and error bars are s.e.m. (which are too small to be seen for the Australian sea lion's total oxygen stores). Average adult female data and masses are reported. AuSL, Australian sea lion (88 kg) (Fowler et al., 2007); CaSL-M, California sea lion in Mexico (93 kg) (Villegas-Amtmann et al., 2012); CaSL-CA, California sea lion in California (87 kg) (Weise and Costa, 2007); NeSL, New Zealand sea lion (112 kg) (Costa et al., 1998).

Measurements using doubly labeled water on sea lions and fur seals have revealed the importance of the thermal environment on FMR (Costa and Valenzuela-Toro, 2021). Galapagos fur seals and sea lions live in the warm and less productive environment of the Galapagos Islands and thus have lower FMRs than other sea lions and fur seals (Costa and Trillmich, 1988; Trillmich and Kooyman, 2001; Villegas-Amtmann et al., 2017). Ironically, there are no measurements of their RMR or standard metabolic rate (SMR), which would indicate whether they have reductions in their overall metabolism or have modified their time–activity budget (see Glossary) to allow for a lower FMR. While challenging, respirometry measurements of RMR have been carried out in the field with northern fur seals, Antarctic fur seals (*Arctocephalus gazella*) and Weddell seals (Donohue et al., 2000; Rutishauser et al., 2004; Williams et al., 2004). Unlike for pinnipeds, there is relatively little information on SMR or FMR of cetaceans and even less for ocean 'giants' (i.e. baleen whales; see fig. 1 in Watanabe and Goldbogen, 2021); therefore, there is a need for more metabolic rate data to continue advancing our understanding of marine mammal bioenergetics (McHuron et al., 2022).

However, measuring FMR at the scale of days does not provide information on how metabolic regulation plays a role in the diving capabilities of extreme divers (Costa and Gales, 2003). When the ADL has not been directly measured (via blood lactate), calculating the ADL requires a measure or estimate of the diving metabolic rate (DMR) in addition to the animal's oxygen stores (Ponganis et al., 1993). The question remains about which metabolic rate estimate most accurately represents their DMR, particularly when a

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species-specific value is unavailable (as is often the case for large cetaceans). A few studies have attempted to measure DMR directly via respirometry in the lab (Webb et al., 1998) or with trained animals (Fahlman et al., 2008; Gerlinsky et al., 2013; Hurley and Costa, 2001; Sparling and Fedak, 2004). However, the ecological significance of these measurements is limited, given the constraints of the pools and the psychological effects of conditioned diving. The isolated ice-hole field lab has provided the best measures of DMR in freely diving Weddell seals (Castellini et al., 1992; Ponganis et al., 1993; Williams et al., 2004), but this method is challenging to apply to other free-ranging divers.

A workaround to measuring whole-body oxygen consumption directly via respirometry (the gold standard for calculating metabolic rate) is to measure the rate of oxygen utilization in the primary oxygen stores of the body (i.e. lung, blood and muscle), which – along with the magnitude of oxygen stores – is what determines the ADL (Ponganis et al., 2011). This method has been most successful during voluntary diving in emperor penguins (Ponganis et al., 2009, 2007; Williams et al., 2012) and in Weddell seals, where studies have measured oxygen depletion in the blood (Qvist et al., 1986) and locomotory muscle (Guyton et al., 1995). A few other systems make this research feasible with the current methods for measuring oxygen *in vivo*. For example, the paradigms of translocating juvenile elephant seals and the short foraging trips during lactation of California sea lions have made similar work possible in these species and age classes (McDonald and Ponganis, 2013; Meir et al., 2009, 2013; Tift et al., 2017), albeit only for blood–oxygen stores.

Hypometabolism (metabolism that is lower than the standard resting, post-absorptive state; Kooyman, 1989) has been proposed by many as a mechanism that allows extreme divers to extend their dives and stay within their ADL (Butler, 2004; Hastie et al., 2007; Maresh et al., 2014; Sparling and Fedak, 2004; Thompson and Fedak, 1993). Studies on blood–oxygen stores have concluded that neither elephant seals nor emperor penguins become hypometabolic during routine dives. Further investigation across species of different diving capacities is warranted to determine the generality of this pattern and identify the exceptional cases. Determining how hypometabolism is achieved mechanistically would require concurrent body temperature and blood flow measurements. This would elucidate whether hypothermia-induced metabolic depression and selective hypoperfusion (especially to metabolically demanding organs; see Glossary) are associated with diving hypometabolism. Developing a suite of sensors to concurrently measure oxygen depletion in the blood and muscle would help to refine our understanding of oxygen management and our interpretation of ADL across species and during natural diving behavior.

Caution is required when using the calculated ADL, as it assumes that all the oxygen is depleted when the ADL is reached (Fig. 6). However, true ADL (as initially defined by Kooyman et al., 1980) may be primarily associated with the depletion of one rather than uniform depletion of all three oxygen stores (i.e. muscle for emperor penguins and California sea lions; McDonald and Ponganis, 2013; Williams et al., 2011a,b). Moreover, studies on voluntary diving in animals have shown that animals often begin their next dive before completely restoring their oxygen debt and lactate levels, which may lead to increasing DMR across a dive bout (Castellini et al., 1992; Fahlman et al., 2008). Additionally, a change in behavior during deep dives (e.g. more gliding, less stroking) can help conserve energy and reduce oxygen consumption, thereby extending the ADL (Fig. 6; Martin Lopez et al., 2015; Williams et al., 2000). Thus, activity level and duration will result in variation in DMR from dive to dive and even within a dive. ADL is not a single value; it is a graded response appropriate to highly plastic diving behavior (see Rosen et al., 2017, for a case study example on Steller sea lions). Nonetheless, researchers attempt to find an average value or range of values that provide essential context for their ecology and behavior.

Physiological limits and behavioral plasticity affect population demographics

Is an understanding of the ADL useful to conservation? By understanding a species' ADL, we can identify when animals are pushing their physiological limits and whether the scope of their behavioral plasticity may be sufficient to survive in the face of their changing environment (Costa and Valenzuela-Toro, 2021). For example, animals that forage at or near the benthos or in the mesopelagic realm operate closer to their physiological limits (Arnould and Costa, 2006; Costa et al., 2001, 2004) These animals often exceed their ADL. Given that these deep-diving species routinely forage close to or at their physiological capacity, they are limited in their capacity to increase their diving ability as their habitat changes as a result of climate change or interactions with fisheries (both of which cause the larger fish that they depend upon for food to be less available; Chilvers and Wilkinson, 2009). For example, the Australian and New Zealand sea lions specialize in benthic foraging (see Glossary) or demersal prey (see Glossary) and seem to be pushing their diving limits (based on their oxygen stores). Their populations are endangered and declining.

In contrast, the California sea lion – a generalist that feeds on prey throughout the water column – has recovered from previous exploitation and is thriving (Chilvers and Meyer, 2017; Costa et al., 2006; Goldsworthy et al., 2022; Hamer et al., 2013; Laake et al., 2018). Regardless, resource limitation would affect all juvenile

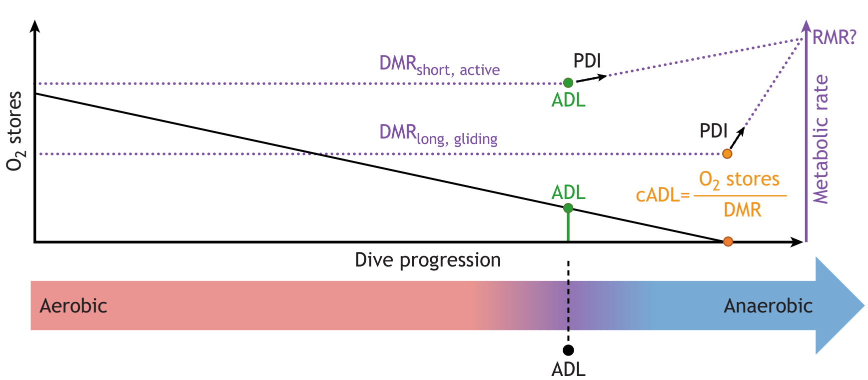

Fig. 6. A simplistic depiction of the depletion of oxygen stores throughout a dive and how that translates to different values for the calculated versus true ADL. It has been suggested that not all oxygen stores are depleted at the ADL (the dive duration at which post-dive lactate increases; green circles), leading to overestimation of their calculated ADL (cADL; orange) (Butler, 2006; Davis and Kanatous, 1999). These calculations depend on the value used for diving metabolic rate (DMR; dotted purple lines), which can vary by dive type and duration, but is generally assumed to be a constant value. Whether DMR and metabolism during the PDI are generally above or below resting metabolic rate (RMR) is still unclear.

sea lions and fur seals more than adults (i.e. *Neophoca cinerea*, *Zalophus californianus*, *Callorhinus ursinus*) as they are smaller, lack experience and are still developing their oxygen stores (Fowler et al., 2007; Shero et al., 2012; Weise and Costa, 2007). However, the difficulties experienced by juveniles to survive and recruit is likely an essential factor in benthic-foraging species exhibiting low recruitment and declining populations (Arnould and Costa, 2006; Costa and Valenzuela-Toro, 2021; Williams et al., 2011a,b).

Linking individual measurements to the population level

Knowledge of the ecological context is critical and has important implications for conservation. Humans rely on the ocean for food, transportation, mineral extraction and recreation, which are increasingly disturbing marine life. When a disturbance reduces an animal's ability to forage, all other life functions can be compromised. Specifically, reduced foraging can compromise maternal condition (see Glossary) by reducing energy gain (interrupting foraging behavior) and increasing energy expenditure (avoidance costs). This eventually leads to a compromised condition, reduced energy delivery to offspring, higher rates of offspring mortality and increased adult mortality (e.g. Keen et al., 2021; Pirotta et al., 2018, 2022a). The disturbance may change time–energy budgets if animals spend more time in energetically costly behaviors such as foraging and searching for prey (increasing energy requirements).

Bioenergetic models have been developed to examine when a disturbance has a population consequence (e.g. McHuron et al., 2021, 2018; Pirotta et al., 2022b). Unfortunately, many of the critical physiological input parameters (e.g. SMR, FMR, cost of reproduction, starvation threshold) required for these bioenergetic models are currently unavailable (McHuron et al., 2022). Nevertheless, the tools and approaches to obtain these data are available or, in some cases, are under development. In some instances (e.g. for ocean 'giants'), we may need to broaden our approaches and adopt qualitative proxies for physiological parameters that cannot be directly measured or validated (Goldbogen and Madsen, 2021; Watanabe and Goldbogen, 2021).

An acute response to disturbance may also result from maladaptive neurocognitive fear responses, putting the animal in physiological distress. Extreme reactions may exaggerate the appropriate behavioral responses to predator avoidance (Aguilar de Soto et al., 2020; Beltran et al., 2021). For instance, animals may react and flee from the disturbance in ways that put them in physiological jeopardy (Cox et al., 2005). Indeed, several mass-strandings of beaked whales have been associated with seismic surveys or naval sonar (D'Amico et al., 2009; Filadelfo et al., 2009). As noted earlier, beaked whales routinely perform extreme dives. It has been hypothesized that an exaggerated escape response upsets their typical dive pattern, resulting in decompression sickness (Cox et al., 2005; Hooker et al., 2019). This is a reasonable hypothesis, as it is still unclear how marine mammals avoid decompression sickness under normal conditions (Hooker et al., 2012). Another example is the response of narwhals to a seismic survey where narwhals went into extreme bradycardia (heart rate $\leq$4 beats min^{-1}) and rapidly swam away at >25 strokes min^{-1} (Williams et al., 2022). Such a contradictory response should rapidly deplete their oxygen stores, severely compromising their physiological state.

It is essential to recognize that these stressors are not confronted alone (Pirotta et al., 2022b). For example, when exposed to a disturbance, a female may be lactating, nutritionally depleted or have a high pollutant load (Peterson et al., 2023). While this increased complexity is challenging to study, a promising approach may be found in 'stress physiology' (Atkinson et al., 2015): the animal's stress response integrates its response to all the stressors it faces. Studying population demographics in tandem with individual stress physiology will be necessary for linking these individual measurements to population consequences.

Concluding remarks

From the earliest work in laboratories to recent investigations in the field, we have made significant progress in understanding the diving behavior and physiology of diving mammals. However, there remain unknowns about many aspects of these animals' daily lives. There is an urgency to understand the capabilities of these animals as their habitat changes as a result of climate change. Many of the unexplained deviations and unanswered questions can be addressed using existing technologies. For example, there are few metabolism measurements in adult marine mammals, but these could be carried out at zoos or aquaria (Ponganis and Kooyman, 1999; Worthy et al., 2014). For the largest and most elusive marine mammals (e.g. sperm and baleen whales), we can overcome the inability to perform these measurements by using physical and theoretical approaches to develop suitable proxies (Goldbogen and Madsen, 2021; Watanabe and Goldbogen, 2021). Integrating existing sensors to obtain a variety of data streams simultaneously and within the same space can provide context that could not be achieved when the instruments are deployed alone (Goldbogen et al., 2017). However, some questions will only be answered as new technologies and sensors are developed. For example, fundamental anaerobic and aerobic diving questions will only be answered when we can measure lactate levels in freely diving animals. While work on such a sensor is underway, developing sensors that can withstand the saltwater environment and associated pressures that these animals routinely experience is challenging. Additionally, understanding how these animals avoid decompression sickness will require creative solutions. Finally, understanding the physiology of stress in these animals and how multiple stressors interact to affect their health and behavior will be crucial for their conservation and management.

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Competing interests
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