

## REVIEW

# Postnatal development of diving physiology: implications of anthropogenic disturbance for immature marine mammals

Shawn R. Noren\*

**ABSTRACT**

Marine mammals endure extended breath-holds while performing active behaviors, which has fascinated scientists for over a century. It is now known that these animals have large onboard oxygen stores and utilize oxygen-conserving mechanisms to prolong aerobically supported dives to great depths, while typically avoiding (or tolerating) hypoxia, hypercarbia, acidosis and decompression sickness (DCS). Over the last few decades, research has revealed that diving physiology is underdeveloped at birth. Here, I review the postnatal development of the body's oxygen stores, cardiorespiratory system and other attributes of diving physiology for pinnipeds and cetaceans to assess how physiological immaturity makes young marine mammals vulnerable to disturbance. Generally, the duration required for body oxygen stores to mature varies across species in accordance with the maternal dependency period, which can be over 2 years long in some species. However, some Arctic and deep-diving species achieve mature oxygen stores comparatively early in life (prior to weaning). Accelerated development in these species supports survival during prolonged hypoxic periods when calves accompany their mothers under sea ice and to the bathypelagic zone, respectively. Studies on oxygen utilization patterns and heart rates while diving are limited, but the data indicate that immature marine mammals have a limited capacity to regulate heart rate (and hence oxygen utilization) during breath-hold. Underdeveloped diving physiology, in combination with small body size, limits diving and swimming performance. This makes immature marine mammals particularly vulnerable to mortality during periods of food limitation, habitat alterations associated with global climate change, fishery interactions and other anthropogenic disturbances, such as exposure to sonar.

**KEY WORDS:** Acidosis, Blood, Bradycardia, Cetacean, Dive response, Heart rate, Hypercarbia, Hypoxia, Metabolism, Muscle, Oxygen stores, Pinniped, Sonar

**Introduction**

The lifestyles of marine mammals, and the habitats in which they reside, are diverse, resulting in a range of diving capabilities as measured by maximal achieved dive depth or duration. For example, Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) and Australian sea lions (*Neophoca cinerea*) only hold their breath for about 6 min (Black, 1994; Costa and Gales, 2003), whereas bottlenose whales (*Hyperoodon ampullatus*) and southern elephant seals (*Mirounga leonina*) are capable of holding their breath for over 2 h (Hooker and Baird, 1999; Slip et al., 1994). Regardless of their

diving capability, it is generally accepted that marine mammals prefer to dive within aerobic dive limits (see Glossary) that are established by the magnitude of the body's oxygen stores and the rate at which those stores are used (Kooyman, 1989).

Irving (1934, 1939) and Scholander (1940) were among the first to reveal the physiological attributes that enable cetaceans (dolphins, porpoises and whales) and pinnipeds (seals, sea lions, fur seals and walrus) to hold their breath for extended periods of time. Based on these early observations and more recent work, we know that adult marine mammals have evolved enhanced oxygen stores in the blood and locomotor muscle in comparison to terrestrial mammals. In the blood, this is accomplished by elevating levels of hemoglobin (Hb; see Glossary; Kooyman, 1989; Lenfant et al., 1970; Snyder, 1983) and overall blood volume (BV; Kooyman, 1989; Snyder, 1983); whereas, in the muscle, concentrations of myoglobin (Mb; see Glossary) are 10–30 times greater than levels found in terrestrial mammals (Kooyman, 1989). Conversely, oxygen storage in the lungs of marine mammals is considered to be less important in supporting prolonged dive durations because of lung collapse at depth, which for dolphins occurs around 70 m, preventing gas exchange with the circulatory system (Ridgway and Howard, 1979).

In mature marine mammals, enhanced oxygen stores are combined with oxygen-conserving 'tricks' (Irving et al., 1941; Scholander, 1940; Scholander et al., 1942). Upon submersion there is selective peripheral vasoconstriction (see Glossary) that conserves blood oxygen for the central hypoxia-intolerant organs (i.e. heart and brain). Moreover, by altering blood flow while diving, the unloading of endogenous oxygen stores is more effective, as blood and muscle oxygen reserves are depleted in parallel because reperfusion (see Glossary) of hypoxic regions of the muscle enables extraction of more oxygen from the blood (Davis and Kanatous, 1999). Increases in vascular resistance caused by vasoconstriction are matched by proportional decreases in cardiac output via a diving bradycardia (see Glossary), which is a hallmark of the dive response (see Glossary; Alboni et al., 2011; Andrews et al., 1997; Davis and Kanatous, 1999; Elsner, 1965; Elsner et al., 1966; Harrison and Tomlinson, 1960; Irving et al., 1941; 1963; Ponganis et al., 1990; Ridgway et al., 1975; Scholander, 1963; Van Citters et al., 1965).

In some cases, when breath-hold duration surpasses aerobic dive limits, anaerobic metabolism (see Glossary) can become increasingly important (Hochachka and Storey, 1975; Kooyman et al., 1980). Although few adaptations have been identified in the biochemical enzymes that support the anaerobic capacity of marine mammals (Castellini et al., 1981; Kooyman et al., 1981), it is known that the ability to handle acidic products of anaerobic glycolysis (e.g. lactate) is important. Adult pinnipeds and cetaceans have enhanced buffering capacities that can counteract changes in pH that occur as lactic acid is produced during anaerobic metabolism. Enhanced buffering capacity enables locomotor muscles to function

Institute of Marine Science, University of California, Santa Cruz, CA 95060, USA.

\*Author for correspondence (snoren@ucsc.edu)

 S.R.N., 0000-0003-3122-8289

## Glossary

### Acidosis

Increased acidity in the blood or other body tissues.

### Aerobic dive limit

The duration of a dive that is supported by the use of oxygen-based metabolism (aerobic metabolism).

### Anaerobic metabolism

Anaerobic metabolism provides energy in the absence of oxygen; it does not produce as much energy as aerobic metabolism and it produces lactic acid, which can build up in the muscles and degrade muscle function.

### Bradycardia

Reduced heart rate.

### Calculated aerobic dive limit

The ratio of total body oxygen stores to the rate at which oxygen stores are utilized.

### Cytoglobin

A globin molecule that may facilitate diffusion of oxygen through tissues and serve a protective function during oxidative stress.

### Decompression sickness

Also called generalized barotrauma or the bends, decompression sickness refers to injuries caused by a rapid decrease in the pressure that surrounds the animal that results in dissolved gases coming out of solution, forming bubbles inside the body.

### Dive response

A set of physiological responses upon immersion that optimize the distribution of oxygen stores to the heart and brain to enable extended submersion.

### Hematocrit

The ratio of the volume of red blood cells to the total volume of the blood.

### Hemoglobin

The protein in red blood cells that binds with oxygen.

### Hypercarbia

Hypercarbia, or hypercapnia, is when there is too much carbon dioxide in the bloodstream.

### Hypoxia

Low oxygen in the tissue.

### Inter-deep dive interval

The duration between the end of one deep dive and the beginning of the next deep dive.

### Maternal dependency period

Maternal dependency period is defined here as the nursing interval plus any terrestrial post-weaning fast.

### Myoglobin

An oxygen-binding protein in the muscle tissue of vertebrates.

### Neuroglobin

A protein found in neurons that provides some resilience to hypoxia by assisting with the transport of oxygen across the blood–brain barrier.

### Oxidants

Reactive molecules produced inside the body that can react with other molecules in the body, damaging them in the process.

### Oxidative stress

An imbalance between the production of reactive oxygen species and a biological system's ability to detoxify the reactive intermediates or to repair the resulting damage.

### Reperfusion

Restoration of blood flow to a tissue or organ.

### Vasoconstriction

Narrowing of blood vessels due to the contraction of the muscular walls of the vessels; it reduces blood flow through that vessel.

during prolonged breath-hold and burst locomotion when the circulation may be unable to remove lactic acid (Castellini and Somero, 1981; Noren, 2004).

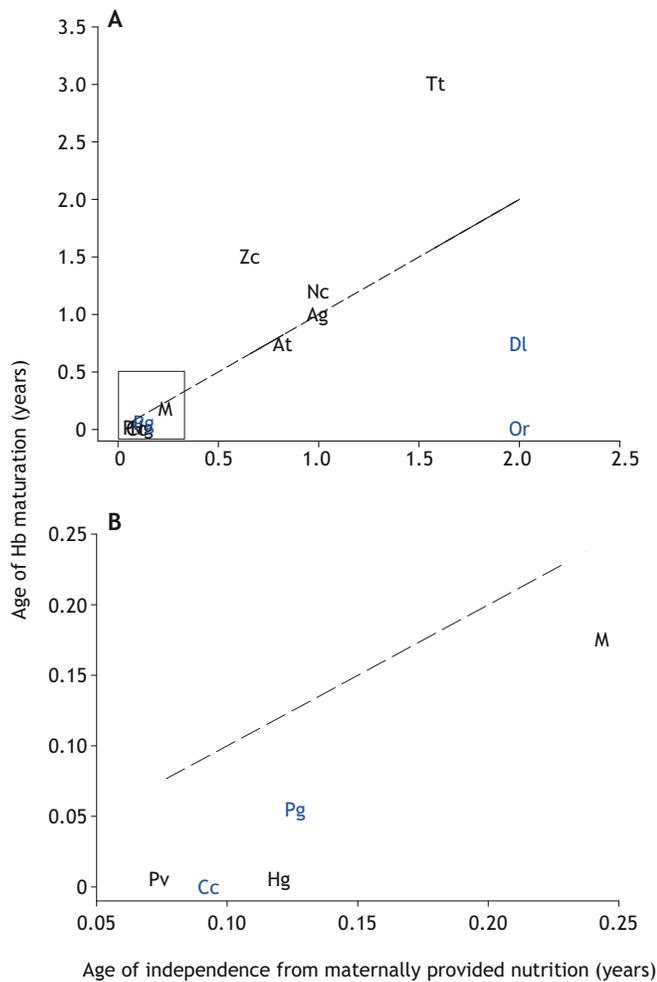
The physiological attributes described above not only support the prolonged dive durations of marine mammals but also typically enable marine mammals to avoid (or tolerate) issues associated with

hypoxia, hypercarbia, acidosis and decompression sickness (DCS; see Glossary). Yet, research over the past few decades has shown that the diving physiology of marine mammals is underdeveloped at birth. Here, I review research on the postnatal development of diving physiology in pinnipeds and cetaceans to explore the magnitude and duration of the development of the blood and muscle oxygen stores. In addition, I report how oxygen consumption rate (metabolism) and heart rate vary throughout ontogeny and explore some additional factors that may also influence diving capacity. By examining the postnatal development of diving physiology across diverse marine mammal species, I have uncovered patterns linking the duration of this development to life-history characteristics and habitat – this has enabled me to approximate developmental patterns for species of marine mammal that are difficult to study, such as beaked whales. By understanding the development of diving physiology and quantifying physiological capacities, scientists can make predictions about the vulnerability of immature marine mammals to alterations in habitat and other anthropogenic disturbances.

## Postnatal development of blood and muscle oxygen stores

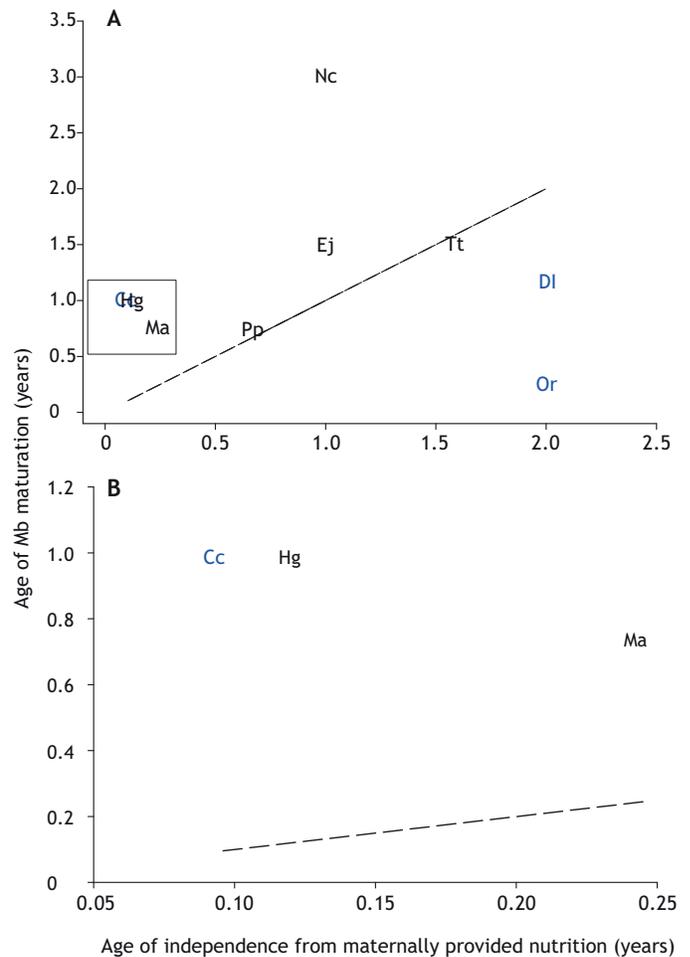
Postnatal maturation and other factors can influence the oxygen-carrying capacity of the blood and muscle. For example, in humans (Rothstein, 1993) and sheep (Potocnik and Wintour, 1996), hematocrit (Hct; see Glossary) and Hb levels initially decrease after birth but then increase as the number of circulating red blood cells increases over time to achieve mature levels. Meanwhile, the expression of Mb seems to be highly variable throughout life; it increases with increased physical activity (Saunders and Fedde, 1991), thermal demands (Morrison et al., 1966) and exposure to hypoxia (MacArthur, 1990; Stephenson et al., 1989), as shown in adult terrestrial and semi-aquatic birds and mammals. Interestingly, despite the demand for elevated oxygen stores, immature marine mammals, like their terrestrial counterparts, possess underdeveloped oxygen stores at birth.

Studies on the postnatal development of body oxygen stores in marine mammals initially focused on pinnipeds, probably because pinnipeds are born on land and are therefore more easily accessible to study than cetacean calves, which are born at sea. Thorson (1993) investigated the ontogeny of body oxygen stores in northern elephant seals (*Mirounga angustirostris*), and found that BV, Hb and Mb levels are low at birth and increase throughout the nursing interval. Subsequent research on other phocids (true seals) demonstrated that even when initial Hb levels are the same as those of adults, Hb levels quickly decline soon after birth as pups enter an ‘anemic period’ (Table S1). Blood samples taken from otariid pups (sea lions and fur seals) also indicate that Hb levels are low compared with those of adults (Table S1). The reductions in Hct and Hb directly after birth could be associated with several factors, including (1) the replacement of fetal Hb with adult Hb (Noren et al., 2002), (2) rapid body growth that outpaces blood production (Bryden and Lim, 1969) as a result of limits in the rate of protein turnover and water balance (Jørgensen et al., 2001), (3) the development of the control by erythropoietin (EPO), the hormone that stimulates the production of red blood cells (Clark et al., 2006, 2007), and/or (4) insufficient iron intake during the nursing interval, which could limit Hb biosynthesis (Burns and Hammill, 2008). Ultimately, the time taken for Hb levels to mature seems to match the maternal dependency period (MDP; see Glossary), such that mature Hb levels are achieved at the end of the MDP, just prior to pinniped pups departing for their first trip to sea. Generally, phocids achieve mature Hb levels earlier in life than otariids; this matches their shorter MDP (28–90 days) compared with the longer MDP (7 months to 2 years) of otariids (Table S1; Fig. 1).



**Fig. 1. Age of hemoglobin maturation in relation to age of independence from maternally provided nutrition.** (A) Independence from maternally provided nutrition occurs for cetaceans when the nursing interval ends, and for pinnipeds at the end of the nursing interval plus any terrestrial post-weaning fast period, during which the pup subsists on the blubber stores it accumulated during the nursing interval. The dashed line is a 1:1 relationship; species below the line obtain mature hemoglobin (Hb) prior to independence from maternally provided nutrition and species above the line obtain mature Hb after the age of independence. Data for phocids and otariids are from Table S1; species were excluded if the age for Hb maturation could not be determined. Phocids clustered within the rectangle (enlarged in B: Pv, harbor seal; Cc, hooded seal; Hg, gray seal; Pg, harp seal; M, northern and southern elephant seal). Otariids clustered within the center of the plot (At, sub-Antarctic fur seal; Zc, California sea lion; Nc, Australian sea lion; Ag, Galapagos fur seal), while the Pacific walrus (Or; Noren and Edwards, 2020), bottlenose dolphin (Tt; Noren et al., 2002) and beluga whale (Dl; Noren et al., 2018) data fell individually. Arctic ice-associated species (Cc, Pg, Or, Dl) are indicated by blue font. This figure was adapted from Noren and Edwards (2020).

In contrast, mass-specific BV (Burns et al., 2005, 2007; Fowler et al., 2007; Noren et al., 2005; Thorson, 1993; Weise and Costa, 2007) and Mb (Table S1; Fig. 2) are not mature at the end of the MDP. For example, 40 day old gray (*Haliocoerues grypus*) and 90 day old northern elephant seal pups depart to sea with only 62% (Noren et al., 2005) and 68% (Thorson, 1993) of adult mass-specific BV, respectively. More generally, 1.5–3.5 month old phocids and 2.5–14.5 month old otariids depart for their first foraging trip with only 68–76% and 48–70% of adult Mb levels, respectively (Table S1). Yet, interestingly, despite differences in chronological age as the pups depart for their first trip to sea, total oxygen storage



**Fig. 2. Age of myoglobin maturation in relation to age of independence from maternally provided nutrition.** (A) Independence from maternally provided nutrition occurs for cetaceans when the nursing interval ends, and for pinnipeds at the end of the nursing interval plus any terrestrial post-weaning fast period, during which the pup subsists on the blubber stores it accumulated during the nursing interval. The dashed line is a 1:1 relationship; species below the line obtain mature myoglobin (Mb) prior to independence from maternally provided nutrition and species above the line obtain mature Mb after the age of independence. Cetaceans include beluga whale (Dl), bottlenose dolphin (Tt) and harbor porpoise (Pp); data from Table S2. For pinnipeds, final Mb maturation takes place when the pups are out to sea in their first, second or even third year (see Table S1). This makes it difficult to determine the age when Mb matures, because pups are not sampled at sea. To be able to include pinnipeds in this graph, I included species that had data for pups nearly approaching adult Mb levels. Phocids clustered within the rectangle (enlarged in B) and include the age at which the hooded seal (Cc), gray seal (Hg) and Northern elephant seal (Ma) obtained 81%, 80% and 85% of adult Mb levels, respectively. Otariids are represented by the age at which Australian sea lion (Nc) and Steller sea lion (Ej) obtained 81% and 86% of adult Mb levels, respectively. This compares to the one odobenid, Pacific walrus (Or) that obtained 79% of adult Mb levels by 3 months. Arctic ice-associated species (Cc, Or, Dl) are denoted by blue font.

capacity as a proportion of adult levels falls within a narrow range across species: 45 day old grey seal pups, 90 day old northern elephant seals and 1 year old Steller sea lions (*Eumetopias jubatus*) have 67% (Noren et al., 2005), 73% (Thorson, 1993; Thorson and Le Boeuf, 1994) and 83% (Richmond, 2004) of adult total mass-specific oxygen stores, respectively. After a year at sea, BV appears to be mature (Burns et al., 2005, 2007; Fowler et al., 2007; Noren et al., 2005; Thorson, 1993; Weise and Costa, 2007), whereas Mb

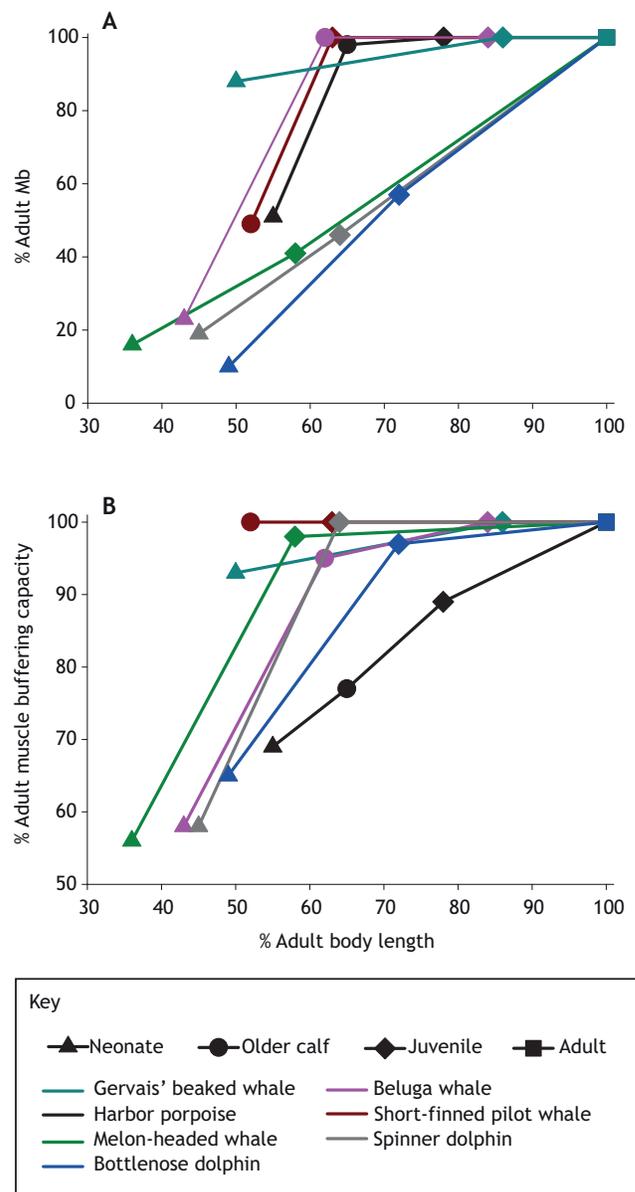
levels in most pinniped species are still lower than those of adults (Table S1).

However, there is a third group of pinnipeds, odobenids (walruses; *Odobenus rosmarus*), that does not adhere to the pattern described above. Walruses are genetically more related to otariids than to phocids (Agnarsson et al., 2010; Fulton and Strobeck, 2010; Schröder et al., 2009), and they have one of the longest MDPs across pinnipeds. Walruses are attended to by their mothers for 2–3 years and have been observed nursing for up to 35 months post-parturition (Fay, 1982; Kovacs and Lavigne, 1992). Given these facts, it might be expected that walruses have a prolonged postnatal maturation period, but surprisingly their maturation period is extremely truncated (Noren et al., 2015; Noren and Edwards, 2020; Table S1). Hb levels at 2 weeks after birth are equivalent to adult levels and do not change throughout ontogeny (Noren and Edwards, 2020), and neonates have 44% of adult Mb levels, such that by 3 months of age calves have nearly obtained mature Mb levels (Noren et al., 2015). This rapid postnatal maturation of body oxygen stores undoubtedly supports the unique behavior of walrus mother–calf pairs. Within 2 days of birth, walrus calves enter the water (Fay, 1982), nurse underwater (Reeves et al., 1992) and are submerged underwater by their mother when she perceives a threat (Reeves et al., 1992). Within months of birth, the calf must transit alongside its mother under sea-ice, where breathing holes are patchily distributed and ephemeral. This early exposure to prolonged hypoxia likely promotes the comparatively rapid Hb and Mb maturation of young walruses.

Cetaceans are also exposed to hypoxia early in life, as they are born directly into water. Thus, one might expect cetaceans to have rapid maturation of body oxygen stores like walruses, but surprisingly this is not the case. To date, the postnatal development of Hb has only been fully examined in two cetacean species, beluga whales (*Delphinapterus leucas*) and bottlenose dolphins (*Tursiops truncatus*), where both longitudinal and cross-sectional sampling were performed on neonatal through to sexually mature adult animals (Noren et al., 2002, 2018). In both species, Hb levels decrease after birth, then increase rapidly from 1.5 to 6 months, and continue to increase more gradually until mature levels are achieved at 9 months and 3 years after birth for beluga whales (Noren et al., 2018) and bottlenose dolphins (Noren et al., 2002), respectively (Fig. 1).

The postnatal development of Mb has been explored in several cetacean species (Table S2). For all cetacean species studied to date, Mb levels are initially low at birth, and the neonates of most species have less than a quarter of adult Mb levels (Table S2). Unfortunately, small sample sizes combined with a lack of life-history knowledge limits us to only use three of these species [harbor porpoises (*Phocoena phocoena*), bottlenose dolphins and beluga whales] to explore how Mb maturation varies in relation to weaning age in cetaceans (see table 3 in Noren and West, 2017). Of these three species, Mb maturation varies in accordance with weaning age in only two; Mb matures at 0.75–0.83 years in harbor porpoises (Noren et al., 2014), in accordance with their 0.7 year weaning age (Evans, 1987), and Mb matures at 1.5–3.4 years in bottlenose dolphins (Noren et al., 2001), in accordance with their 1.6 year weaning age (Evans, 1987). The Arctic-dwelling beluga whale is the exception; for this species, Mb matures at 1.7 years (Noren and Suydam, 2016), well before their 2–3 year weaning age (Suydam, 2009; Fig. 2).

By examining how Mb varies with body length across life-history classes (Fig. 3A), it becomes apparent that deep-diving cetaceans [Gervais' beaked whale (*Mesoplodon europaeus*) and short-finned



**Fig. 3. Proportion of adult muscle Mb and non-bicarbonate buffering capacity in relation to proportion of adult body length in seven cetacean species.** The relationship is shown for Mb (A) and muscle buffering capacity (B). Each species is shown in a different color, and each life history class – neonate, older calf, juvenile and adult – is denoted by a unique symbol. Only species with data for both Mb and buffering capacity from three or more age classes were included; the fetal age class was excluded because the focus is on postnatal development. See Table S2 for data and references.

pilot whale (*Globicephala macrorhynchus*; Velten, 2012] are similar to the Arctic-dwelling beluga whale (Noren and Suydam 2016); Mb levels for these three species mature earlier in life compared with the three delphinid species. This commonality is likely because deep-diving and Arctic cetacean neonates both endure prolonged bouts of hypoxia early in life that must be supported by large endogenous oxygen stores as they accompany their mothers foraging in the bathypelagic zone and under sea-ice, respectively. Like the findings for walrus, early exposure to prolonged hypoxia promotes rapid oxygen store maturation, uncoupling body oxygen store maturation from weaning age in these cetacean species. As a result, beluga whale calves attain 70%

of adult mass-specific oxygen stores by 6 months of age (calculated from Noren and Suydam, 2016). In contrast, a delphinid (bottlenose dolphin) does not achieve this proportion of adult mass-specific oxygen storage capacity until 12 months of age (calculated from Noren et al., 2002).

#### Postnatal development of metabolic rate and heart rate

Understanding the ability of marine mammals to alter oxygen consumption and heart rate while diving is another key component in elucidating diving capability. Young animals typically have elevated metabolic rates in comparison to adults; this is likely associated with costs of growth as they synthesize and store new tissue in the body (Kleiber, 1975). Moreover, rather than being an innate feature of mammalian physiology, the ability to adjust heart rate in response to respiratory events requires refinement throughout maturation. For example, human infants have irregular cardiorespiratory patterns for up to 6 months after birth (Patzak et al., 1996). It appears that postnatal development of a sinus arrhythmia, in which heart rate is higher during inhalation and lower during exhalation, is a normal pattern in mammals (Katona et al., 1980; Leistner et al., 1990; Schubert et al., 1987).

There have been few studies on how oxygen is utilized while diving, particularly for immature marine mammals. For diving Weddell seals (*Leptonychotes weddelli*), it was found that immature seals have higher oxygen consumption rates than adults (based on experimentally determined aerobic dive limits), such that diving metabolism is 4, 2 and 1 times basal metabolic rate for pups, yearlings and adults, respectively (for a review of these data, see Schreer et al., 2001). Given the paucity of data on this subject, an examination of how resting metabolism varies with age can provide some insight into how diving metabolism may vary throughout ontogeny. Many studies show that the mass-specific resting metabolism of immature marine mammals is higher than that of adult conspecifics. For example, the resting metabolic rate of juvenile gray seals is 35% higher than that predicted for adults, and it decreases with age until 3–5 years post-parturition, when sexual maturity is attained (Boily and Lavigne, 1997). Immature otariids also have higher metabolic rates than adults (Donohue et al., 2000; Fowler et al., 2007; Ladds et al., 2017; Verrier et al., 2011), and in some species these differences are evident for up to 5 years post-parturition (Ladds et al., 2017). However, there are some exceptions to this pattern. Resting metabolic rates of newly weaned elephant seal pups (Noren, 2002a,b) and juvenile and sub-adult California sea lions (*Zalophus californianus*; Liwanag et al., 2009) and Southern sea lions (South American; *Otaria flavescens*; Dassis et al., 2012) do not differ from those of adults. The limited number of studies and disparate conclusions make it difficult to predict how oxygen utilization patterns vary throughout ontogeny, particularly while diving.

In the absence of direct measurements of metabolism, and therefore oxygen utilization rates, the degree of bradycardia while diving could be a good relative measure of oxygen consumption at depth. The degree of bradycardia is related to the degree of peripheral vasoconstriction, and as bradycardia increases, muscle blood flow decreases, with a consequent reduction in overall oxygen consumption (Butler and Jones, 1997). Initial studies on postnatal changes in heart rate in immature marine mammals focused on pinnipeds. It was found that fetal seals are capable of bradycardia, both spontaneously (Bacon et al., 1985) and during maternal dives, which likely protects the developing fetus from hypoxia (Elsner et al., 1970). Likewise, neonatal elephant seals (Castellini et al., 1994b; Falabella et al., 1999), harbor seals (*Phoca vitulina*; Lapierre

et al., 2004) and Australian fur seals (*Arctocephalus pusillus doriferus*; Deacon and Arnould, 2009) can lower their heart rate during the respiratory cycle, but changes in heart rate in young pups are smaller, more gradual and more variable than those observed in older pups and adults. The ability to alter heart rate during respiration is indicative of the cardiac control that would be required during diving, as the pattern of accelerating and decelerating heart rate during respiration on land and at the water's surface is similar to that observed (albeit in an exaggerated form) during the dive cycle. Indeed, harbor seal pups can reduce their heart rate while diving, but heart rate becomes more consistent and the level of bradycardia increases with age (Greaves et al., 2005). In forced diving studies, harbor seal (Harrison and Tomlinson, 1960) and fur seal (*Callorhinus ursinus*; Irving et al., 1963) pups also increase the degree of bradycardia with age. Thus, heart rate regulation during normal sinus arrhythmia, sleep apnea and diving apnea are likely to be under one common homeostatic control mechanism (Castellini et al., 1994a,b; Irving et al., 1935). For elephant seals (Castellini et al., 1994b; Falabella et al., 1999) and harbor seals (Greaves et al., 2005), the refinement of cardiac control occurs prior to the end of the MDP.

Investigations on immature cetaceans, including California gray whales (*Eschrichtius robustus*; Ponganis and Kooyman, 1999), harbor porpoises (Reed et al., 2000) and bottlenose dolphins (Noren, 2002a,b; Noren et al., 2004), also show the presence of a sinus arrhythmia early in life, but cardiac control is further refined during the postnatal period. Minimum heart rate and mean steady-state minimum heart rate during diving in young dolphin calves (1.5–2.5 and 2.5–3.5 year olds) are greater than those of older dolphin calves (3.5–4.5 and 4.5–5 year olds), whereas the ability to lower heart rate while diving does not differ between 3.5–4.5 and 4.5–5.5 year old dolphins (Noren, 2002a,b; Noren et al., 2004); these results were based on longitudinal and cross-sectional analyses of the five longest-duration dives (amongst hundreds of dives) for each dolphin. These results indicate that diving bradycardia in dolphins is not fully developed until 3.5 years post-parturition, which is after the age of weaning (Noren, 2002a,b; Noren et al., 2004). Of note, across age classes for both dolphins (Noren, 2002a,b; Noren et al., 2004) and seals (Greaves et al., 2005), maximum heart rates at the surface do not differ, whereas minimum heart rates while diving do; this suggests that the improved ability to reduce heart rate during diving is not simply attributable to the lowering of heart rate that occurs with age (Dittmer and Grebe, 1959), because maximum and minimum heart rate would both be affected if this was the case. Rather, developmental changes appear to be impacting the physiological and/or psychogenic processes that control the ability to reduce heart rate while diving (Noren, 2002a,b; Noren et al., 2004). See Kooyman (1989) and Ponganis (2015) for a review of the processes that control heart rate.

#### Postnatal development of other physiological attributes that impact diving capability

This Review, thus far, has examined the postnatal development of the variables used to determine calculated aerobic dive limits (cADLs; see Glossary; Kooyman, 1989), that enable us to make predictions about the at-sea behaviors of marine mammals. However, there are several other factors that can influence the diving ability of marine mammals. Some of these factors have been shown to require postnatal maturation, and these are discussed below.

An important factor for supporting the metabolic needs of the working locomotor muscles while diving is the activity of the

enzymes involved in the aerobic [citrate synthase (CS) and  $\beta$ -hydroxyacyl-coenzyme A dehydrogenase (HOAD)] and anaerobic [lactate dehydrogenase (LDH)] metabolic pathways. An examination of these enzymes in the muscles of seals revealed that neonatal muscles have significantly lower metabolically scaled CS and HOAD activity compared with that of adults, and the developmental increases in LDH activity are slower than those of the aerobic enzymes (Burns et al., 2015). Until mature enzyme concentrations are achieved, the locomotor muscles of seal pups cannot support strenuous aerobic exercise or rely heavily on anaerobic metabolism while diving. It is unknown whether there are postnatal changes in metabolic enzymes in cetaceans, and this warrants additional research.

Also under the influence of postnatal development is the ability of the muscle to buffer against changes in pH that occur as carbon dioxide accumulates during breath-hold. Changes in pH also result from the accumulation of lactic acid during prolonged breath-holds, as there is an increased reliance on anaerobic metabolism. In general, the buffering capacity of the muscle in marine mammals is not mature until weaning or soon after weaning, as evident in two phocid seal species [hooded seal (*Cystophora cristata*) and harp seal (*Pagophilus groenlandicus*); Lestyk et al., 2009], the Pacific walrus (Noren et al., 2015) and several cetacean species (see Table S2). Without adequate buffering capacity, dramatic alterations in pH can disrupt cellular function. Interestingly, the two deep-diving cetacean species (Gervais' beaked and short-finned pilot whales) are distinct from all other cetaceans examined to date (Table S1; Fig. 3B), in that they attain mature muscle buffering capacity soon after birth (Velten, 2012).

Another important characteristic required to support repetitive extended breath-holds is the ability to mitigate the buildup of oxidants (see Glossary). After a dive, as ventilation restores oxygen to hypoxic cells, marine mammals could experience an increase in oxidant production and be susceptible to oxidative stress (see Glossary; Elsner et al., 1998; Zenteno-Savín et al., 2002), as blood reoxygenation after hypoxemia and ischemia–reperfusion has been shown to increase oxidant production and oxidative damage in terrestrial mammals (McCord, 1985). Yet, despite routine and chronic exposure to apnea-induced hypoxemia and ischemia–reperfusion, adult seals do not exhibit higher levels of oxidative damage in their tissues or red blood cells compared with terrestrial mammals (Vázquez-Medina et al., 2007). An enhanced antioxidant capacity likely contributes to the seal's tolerance of apnea-induced hypoxemia and ischemia–reperfusion (Hermes-Lima and Zenteno-Savín, 2002; Zenteno-Savín et al., 2002). Meanwhile, the ability of immature pinnipeds to mitigate the buildup of oxidants that occurs during bouts of hypoxia is limited as a consequence of non-existent or ineffective antioxidant defenses (Vázquez-Medina et al., 2011). It is unknown whether there are postnatal changes in antioxidant defenses in cetaceans, and this warrants additional research.

#### **Postnatal changes in at-sea behaviors: how might these influence the vulnerability of immature marine mammals to disturbance?**

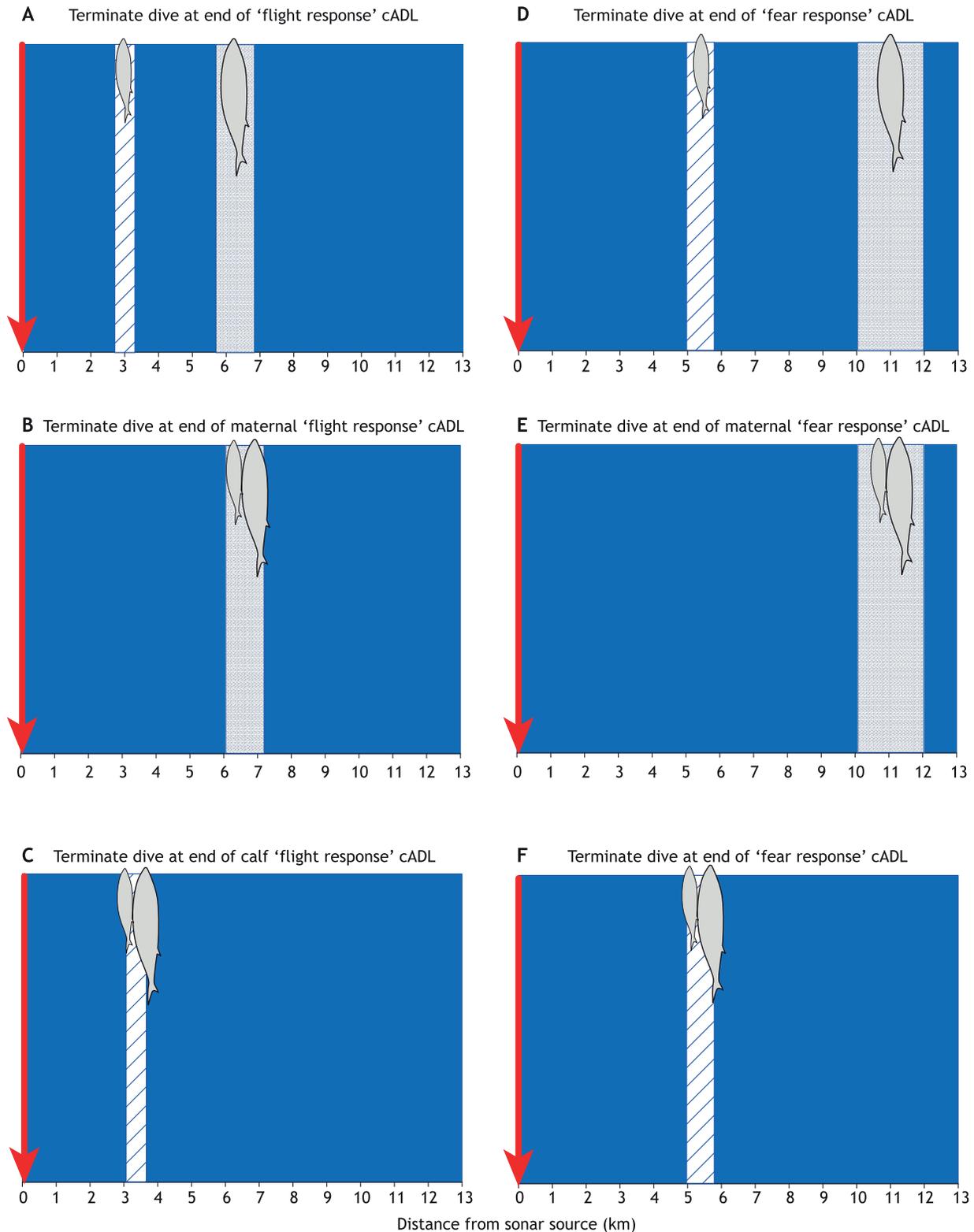
The underdeveloped diving physiology of immature marine mammals will shape their at-sea behaviors and could heighten their vulnerability to habitat alteration and other anthropogenic disturbances; thus, it is crucial to understand their physiological limitations. Compared with adults, immature pinnipeds exhibit shallower dives, shorter dive durations, a lower percentage of time spent diving and shorter distances traveled. As their postnatal maturation progresses, their onshore apnea durations, at-sea submergence times, dive durations and home-range sizes increase

(Bowen et al., 1999; Burns and Castellini, 1996; Burns et al., 1997, 1998; Burns, 1999; Castellini et al., 1994b; Costa et al., 1998; Falabella et al., 1999; Fowler et al., 2006, 2007; Greaves et al., 2005; Harrison and Tomlinson, 1960; Horning and Trillmich, 1997; Irving et al., 1963; Kooyman et al., 1983; Lapierre et al., 2004; Lowther et al., 2013; Lydersen and Hamill, 1993; Lydersen et al., 1994; McCafferty et al., 1998; Rehberg and Burns, 2008; Thorson, 1993). Likewise, compared with adults, immature bottlenose dolphins have shorter dive durations (Lockyer and Morris, 1986; Noren, 2002a,b; Noren et al., 2004) and slower swim speeds (Noren et al., 2006) that increase with age in accordance with ontogenetic enhancements in muscular and cardiorespiratory physiology. Ontogenetic differences in at-sea behaviors and performance are associated with inter-age class variations in diet (Bowen et al., 1993, 1999; Field et al., 2007; Jeglinski et al., 2012), and immature animals show heightened mortality during prey-limited periods (Trillmich et al., 1991) and fishery interactions (Archer et al., 2006; Noren and Edwards, 2007; Noren and West, 2017), as well as increased vulnerability as a result of alterations in prey distribution patterns associated with global climate change (Noren et al., 2015; Noren and Suydam, 2016). The underdeveloped diving physiology of immature marine mammals undoubtedly puts them at risk when faced with anthropogenic disturbances.

Among the myriad of anthropogenic disturbances marine mammals face daily is noise pollution. The past two decades have seen multi-species mass strandings of marine mammals coincident with United States naval exercises utilizing mid-frequency active (MFA) sonar (1–10 kHz), which the navy uses to detect submarines. Stranded species have included beaked whales (Jepson et al., 2003), with Cuvier's beaked whale (*Ziphius cavirostris*) accounting for 69% of all recorded strandings (D'Amico et al., 2009). Some stranded animals possess gas and fat emboli that are consistent with DCS (Jepson et al., 2003, 2005; Fernandez et al., 2004, 2005), which was thought to not occur in marine mammals (Scholander, 1940). The behavioral responses of beaked whales to MFA sonar are thought to play an important role in the series of events that lead to beaked whales stranding (Cox et al., 2006; Hooker et al., 2012).

When exposed to sonar, beaked whales extend dive duration and increase swim speed as they rapidly evade the sound source (DeRuiter et al., 2013). Increased swim speed could reduce the level of diving bradycardia, as shown in bottlenose dolphins (Noren et al., 2012a; Williams et al., 2015). Conversely, fear can increase the level of diving bradycardia, as exhibited by 'alarmed' narwhals (*Monodon monoceros*; Williams et al., 2017b). These two disparate responses, elevated heart rate and dramatically reduced heart rate, would result in different oxygen utilization and carbon dioxide production rates throughout the dive. To date, heart rate data have not been collected from beaked whales. Thus, we can only speculate about how the heart rate of diving beaked whales may respond to sonar disturbance, and what that might mean for their risk of the consequences of hypoxia, hypercarbia and acidosis, as well as their potential to suffer from DCS.

With underdeveloped diving physiology combined with small body size, immature beaked whales exposed to MFA sonar are likely to be most at risk of the consequences of hypoxia, hypercarbia and acidosis, and could have an increased susceptibility to DCS. The higher mass-specific metabolic rate of immature animals (Kleiber, 1975) results in relatively higher oxygen consumption and carbon dioxide production rates. At the same time, lung collapse at depth will prevent gas exchange with the circulatory system (Ridgway and Howard, 1979) so that the lung is no longer available as a sink for carbon dioxide. Carbon dioxide could build



**Fig. 4. Possible scenarios for beaked whale mother–neonate pairs disturbed by sonar.** The red arrow is a sonar disturbance that occurs at the start of the dive, which the whales perceive immediately. The mother–neonate pair then swim in the same direction in a straight-line path away from the sonar source at the same speed. The hatched bar (neonate) and stippled bar (mother) show the horizontal underwater distances covered by the time the dive is terminated at the end of their calculated aerobic dive limit (cADL), assuming swim speed varied from 2.6 to 3.1 m s<sup>-1</sup> as observed for beaked whales evading sonar. Two cADLs were used to estimate subsurface duration: A–C assume a 'flight response' diving metabolism and D–F assume a 'fear response' diving metabolism (Table S3). For A and D, the whales surfaced at the end of their own cADLs, resulting in the mother–neonate pair being separated by 3–3.5 km and 5.1–6.1 km, respectively. For B and E, the whales surfaced together at the end of the mother's cADL, which could make the calf especially prone to issues associated with hypoxia, hypercarbia and acidosis. For C and F, the whales surfaced together at the end of the calf's cADL, which could be problematic because it leaves the mother–neonate pair close to the origin of the disturbance.

up in the blood, increasing the risk of gas emboli (Harris et al., 1945), as well as potentially overwhelming buffering capacity, which would result in a lowering of the pH of the blood. Moreover, if immature beaked whales dive beyond their aerobic dive limit, the accumulation of lactic acid (Kooyman, 1989) will further lower blood pH. Interestingly, inter-deep dive intervals (see Glossary) of MFA sonar-exposed adult beaked whales are at the upper end of their normal range, suggesting that even adult beaked whales need a recovery period at the surface after sonar exposure (Schorr et al., 2014).

In addition to concerns about the consequences of hypoxia, hypercarbia and acidosis, and increased susceptibility to DCS, sonar disturbance could possibly separate mother–neonate pairs or force neonates to dive well beyond their aerobic dive limit. To explore this, I calculated aerobic dive limits of adult females and neonates; the general assumptions for these calculations are provided elsewhere (Noren and Suydam, 2016; Ponganis, 2011), and the inputs that I used specifically for Cuvier’s beaked whale cADLs are provided in Table S3. I calculated two cADLs for adults and two cADLs for neonates; one based on a diving metabolism that could be associated with an elevated heart rate (‘flight response’) and the other based on a diving metabolism that could be associated with a dramatically reduced heart rate (‘fear response’). The cADLs for adult female Cuvier’s beaked whale ranged from 39 to 65 min and were in agreement with the routine diving behaviors of Cuvier’s beaked whales, where 48–68 min dives are followed by short post-dive surface intervals, indicating that dives of this duration are supported by aerobic metabolism (Baird et al., 2006). The cADLs of neonates are half the duration of adult cADLs, which could be problematic during MFA sonar exposure, because adult beaked whales respond by prolonging dive duration.

For each of the two cADLs, there are three possible outcomes for sonar-exposed mother–neonate pairs (Fig. 4). One scenario is that each whale surfaces at the end of its own cADL. If this is the case, mother–neonate pairs could become separated from each other by 2.96–3.53 km to 5.15–6.14 km based on the ‘flight response’ and ‘fear response’ cADL, respectively, assuming swim speeds of 2.6–3.1 m s<sup>-1</sup> as exhibited by MFA sonar-disturbed beaked whales (DeRuiter et al., 2013). Mother–neonate separations can result in offspring mortality, because neonatal cetaceans are highly dependent on their mothers for nourishment and protection (Noren and Edwards, 2007). In the second scenario, a neonate may surpass its cADL as it is pulled along in its mother’s slipstream (Weihs, 2004; Weihs et al., 2006; Noren et al., 2008). If the mother surfaces at the end of her cADL, the neonate will be forced to hold its breath for twice as long as its cADL. This could make neonates especially prone to issues associated with hypoxia, hypercarbia and acidosis (as described above). Adult marine mammal tissues survive under these conditions because of a number of adaptations including: (1) high capillary density and high glycogen concentrations in the brain, (2) alterations in neuroglobin/cytoglobin (see Glossary) concentration or function, (3) scavenging of reactive oxygen species and (4) elevated tissue buffering capacity (for review see Ponganis, 2011). However, the underdeveloped diving physiology of neonatal beaked whales may preclude neonates from functioning under extreme hypoxia, owing to the fact that they may be unable to mitigate large alterations in carbon dioxide, pH and lactic acid levels, as well as oxidant production. Neonates may also be at a higher risk of DCS: it is generally accepted that beaked whales strand with DCS-like symptoms after physiological exertion associated with extreme diving (Cox et al., 2006; Hooker et al., 2012). A third scenario is that

the mother opts to surface at the end of her neonate’s cADL. However, it is unclear what cues the mother would rely on to terminate the dive, and this response requires the mother to abort her ‘startle’ response, which is to prolong dive duration in order to swim as far away from the disturbance as possible. With this scenario, upon surfacing, the pair remains close to the origin of the disturbance.

### Conclusions and future directions

Even though physiologists have been fascinated by the breath-holding capability of marine mammals for over a century, there are still large gaps in our basic understanding of their diving physiology, and even less is known about the diving physiology of immature marine mammals.

As discussed in this Review, over the past three decades we have made progress in identifying that marine mammals require a period of postnatal maturation in order to attain mature diving physiology; this involves maturation of their blood and muscle oxygen stores, as well as an enhanced ability to reduce heart rate while diving, and the development of buffering capacity, antioxidant systems and key enzymes associated with metabolism. The time taken for complete maturation of the diving physiology can be prolonged (over 2 years), even for cetaceans that are born in the water and experience the demands of hypoxia immediately. For some aspects of diving physiology, the duration of the maturation period varies across species in accordance with the MDP. Arctic marine mammals and deep-diving cetaceans appear to be exceptions to this pattern, where postnatal maturation of the body’s oxygen stores is comparatively rapid, such that this physiological metric of diving is mature prior to weaning. Yet, there is still much to learn. It is unknown how heart rate varies during diving in relation to exercise intensity and dive duration during disturbance events, and how heart rate relates to oxygen consumption rate while diving. Given the experimental approaches that would be required to elucidate these relationships, investigations of marine mammals in aquaria, particularly cetaceans, are warranted. This area of research deserves more attention, especially given the vulnerability of marine mammals to disturbance. Moreover, the underdeveloped diving physiology of young marine mammals, coupled with their small body size, ultimately increases their vulnerability to disturbance, as my theoretical analysis suggests is the case for MFA sonar-disturbed neonatal beaked whales.

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