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Graphical Review

The aerobic dive limit: After 40 years, still rarely measured but commonly used

Gerald L. Kooyman [a], Birgitte I. McDonald [b], Cassondra L. Williams [c], Jessica U. Meir [d], Paul J. Ponganis [a,*]

[a] Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92093, USA
[b] Moss Landing Marine Laboratories, California State University, 8272 Moss Landing Road, Moss Landing, CA 95039, USA
[c] National Marine Mammal Foundation, 2240 Shelter Island Drive, #200, San Diego, CA 92106, USA
[d] NASA Johnson Space Center, Houston, TX, 77058, USA

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ABSTRACT

The aerobic dive limit (ADL) and the hypothesis that most dives are aerobic in nature have become fundamental to the understanding of diving physiology and to the interpretation of diving behavior and foraging ecology of marine mammals and seabirds. An ADL, the dive duration associated with the onset of post-dive blood lactate accumulation, has only been documented with blood lactate analyses in five species. Applications to other species have involved behavioral estimates or use of an oxygen store / metabolic rate formula. Both approaches have limitations, but have proved useful to the evaluation of the dive behavior and ecology of many species.

1. Introduction

The physiological adaptations, metabolism, and dive capacity of marine mammals have long fascinated physiologists, including August Krogh, who speculated on the physiology and metabolism of the blue whale (*Balaenoptera musculus*) (Krogh, 1934). As recently reviewed, it was in this era that Irving and Scholander conducted their seminal laboratory studies of diving physiology (Ponganis et al., 2011). The collaboration of Irving and Scholander was fostered, in part, through interactions with Krogh. In the 1930s, Irving, already an established investigator, had visited Krogh in Copenhagen (Fig. 1), and also hosted Krogh at Swathmore College for a series of lectures that eventually formed the basis of Krogh's comparative physiology textbook (Scholander, 1990). While at Swathmore, Krogh, who was familiar with Scholander's laboratory investigations of seals, suggested that they seek a Rockefeller Foundation fellowship for Scholander to study with Irving (Scholander, 1990). However, in 1939, the Foundation suddenly decided to stop funding European fellowships because of the impending start of World War II. At that time, Krogh quickly sent a note to Scholander to leave Norway immediately for the United States even without confirmation of a fellowship, and with instructions not to inform Irving of his travel until he reached the United States. Scholander departed the next evening on the last ship from Oslo to New York with little more than "my violin, my tuxedo, and manuscript" (Scholander, 1990). After Scholander's arrival, Irving pleaded to the Foundation for funding. In the end, the Foundation relented and awarded the fellowship because its cancellation letter had arrived in Oslo one day after Scholander's departure. And that was the beginning of the Irving-Scholander collaboration, which included pioneering, landmark laboratory studies on the diving physiology of seals.

Investigation of free-diving seals and "physiology without restraint" awaited the development of the isolated dive hole protocol for Weddell seals (*Leptonychotes weddellii*) in the 1960s-1970s (Kooyman, 1985) (Fig. 2). And it was at Scholander's Physiological Research Laboratory at Scripps Institution of Oceanography that Kooyman continued his diving physiology research with Weddell seals and embarked upon studies of many other species.

The aerobic dive limit (ADL) and the hypothesis that most dives are predominantly aerobic in marine mammals and seabirds was introduced in 1980 (Kooyman et al., 1980). Over the past 40 years, the ADL has become fundamental to interpretations of diving physiology and behavior. Here, we review a) the origin of the ADL, b) its documentation

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* Corresponding author.
E-mail address: pponganis@ucsd.edu (P.J. Ponganis).

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Fig. 1. Drs. August Krogh, Marie Krogh and Laurence Irving enjoy breakfast during Irving's visit to Copenhagen.

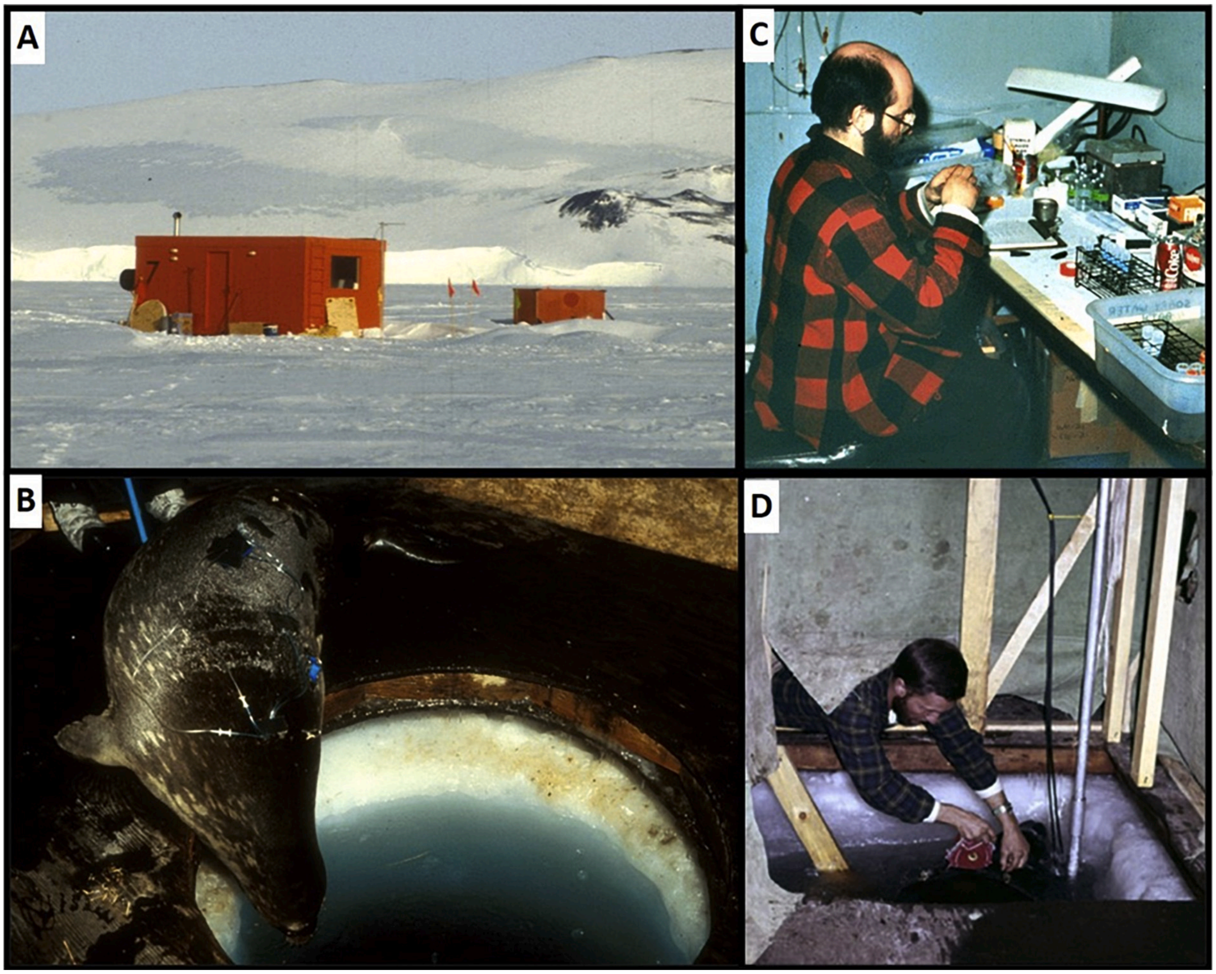


Fig. 2. Research at the isolated dive hole. **A.** Research hut and a seal transport sled on the sea ice of McMurdo Sound Antarctica; **B.** Weddell seal about to enter dive hole below floor of hut; **C.** M. Castellini processing blood samples; **D.** G. Kooyman attaching a time depth recorder to a seal in the dive hole. (Photos: A-C: R. Davis, D: C. Drabek, with permission).

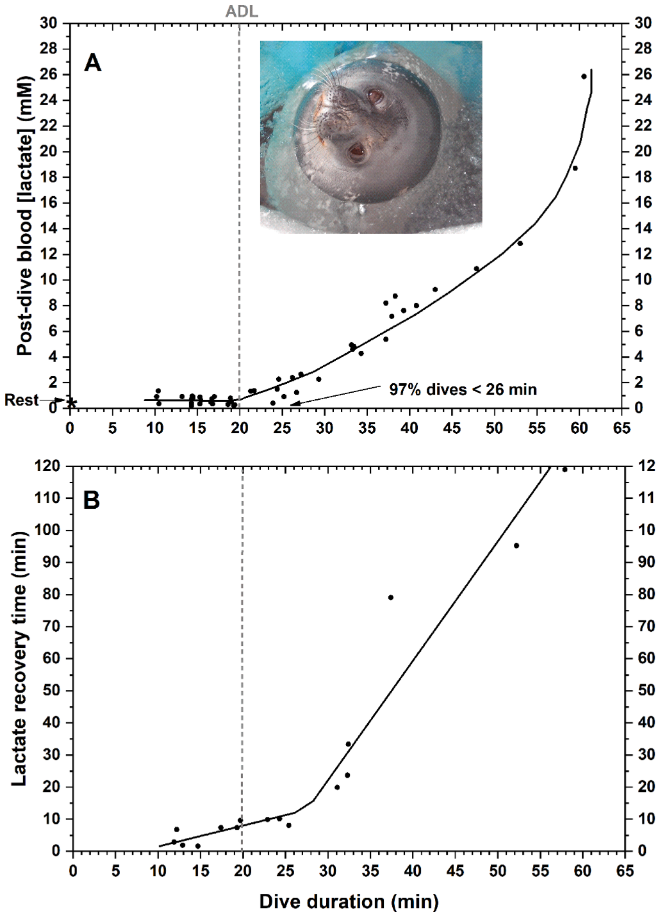


Fig. 3. A. Post-dive blood lactate concentrations of Weddell seals remained near resting levels until a dive duration of about 20 min; this is the aerobic dive limit (ADL - indicated by the dashed line). Lactate concentrations became consistently elevated by 26 min and increased rapidly as dive duration increased. 97% of free-ranging dives of seals were less than 26 min, supporting the concept that most dives of Weddell seals were aerobic in nature. **B.** Due to the progressive rise in post-dive lactate with dive duration, the recovery time for lactate to return to baseline increased as dive duration increased. Adapted from Kooyman et al., 1980. (Photo: P. Ponganis).

in select species, c) the hypothesis that muscle oxygen depletion triggers the ADL, and d) the widespread application of the ADL to diving behavior and ecology.

2. Origin of the ADL concept – Weddell seals

The ADL, the dive duration associated with the onset of post-dive blood lactate accumulation, was first documented in Weddell seals diving at an experimental dive hole in the sea ice of McMurdo Sound, Antarctica (Kooyman et al., 1980). Post-dive arterial blood lactate concentrations of adult seals began to rise above resting levels, and became consistently elevated after dive durations of about 20 min, and 26 min, respectively (Fig. 3A). Notably, 97% of dives of free-ranging seals were less than 26 min. As post-dive blood lactate concentrations became higher with longer dives, more time was required for blood lactate to decrease to baseline (Fig. 3B).

In contrast to prolonged surface intervals after longer dives, surface intervals between the serial shorter dives of free-ranging seals were brief (Kooyman et al., 1980). It was concluded that reliance on aerobic metabolism during dives < ADL allowed for more efficient diving with frequent, repetitive dives to depth when foraging pelagically. At the time, this conclusion represented a paradigm shift in research on diving metabolism from investigation of glycolytic and anaerobic capacity to examination of the magnitude and management of oxygen stores (Castellini and Castellini, 2004). Of note, this hypothesis on aerobic metabolism during most dives and the need for anaerobic metabolism only during longer dives had been suggested almost 40 years earlier (Scholander et al., 1942).

3. Post-dive blood lactate analyses and ADLs in other species

Further studies of Weddell seals at experimental dive holes have confirmed an ADL of about 17–20 min in adults, 10–13 min in juveniles, and 4–5 min in pups (Burns and Castellini, 1996; Kooyman et al., 1983; Qvist et al., 1986; Williams et al., 2004). An ADL has been determined through post-dive blood lactate analyses in only four other species (Fig. 4). The studies have included: emperor penguins (*Aptenodytes forsteri*, 5.6-min ADL) diving at an experimental dive hole, Baikal seals (*Phoca sibirica*, 15-min ADL) during spontaneous inactive submersions in pools, juvenile California sea lions (*Zalophus californianus*, 2.3-min ADL) during trained submerged swims in a tank, and bottlenose dolphins (*Tursiops truncatus*, 3.3-min ADL) trained to dive to depth at sea (Ponganis et al., 1997a; Ponganis et al., 1997b; Ponganis et al., 1997c; Williams et al., 1999). Investigations in trained belugas (*Delphinapterus leucas*) and sea otters (*Enhydra lutris*) have not established ADLs, but have provided evidence that the ADL is ≤9–11 min in belugas, and > 1.6 min in otters (Shaffer et al., 1997; Yeates et al., 2007). Despite the significance of the ADL, the technological challenges and difficulties of post-dive blood lactate sampling have prevented its measurement in other species.

A literature search of dive durations in the wild for these five species revealed that dive durations and measured ADLs were longer in species with larger O_2 stores and that most dive durations in the wild (> 60%) were less than the measured ADL in each species (Fig. 5). The available data support the concept that most dives are aerobic in these species. However, a precise estimate of the percentage of dives less than the ADL in each species was limited because of the study conditions required for lactate measurements and the available dive data sets. Only in the Weddell seal were the age classes and dive behavior of research subjects similar in both the blood lactate study and in the dive distribution survey (Kooyman et al., 1980). Nonetheless, the evaluations of dive duration distribution in Fig. 5 provide insights into the complexity of the interpretation of the ADL and dive behavior.

For example, elevated hemoglobin concentrations documented in off-shore bottlenose dolphins probably increase available O_2 stores and the ADL in those dolphins of the dive study used for Fig. 5 relative to those of coastal dolphins and those under managed care used for the lactate study (Klatsky et al., 2007; Williams et al., 1999). This is not to say that anaerobic dives never occur in off-shore bottlenose dolphins, but simply that the true percentage of aerobic dives is not known.

In juvenile California sea lions (Fig. 5), blood/muscle O_2 store development, the volume of air inhaled prior to deeper dives, and the utilization rate of O_2 stores probably differ between sea lions actively diving to forage at depth in the wild and those under managed care that were used for lactate measurements after submerged swims (McDonald and Ponganis, 2012; McHuron et al., 2018; Ponganis et al., 1997c). Again, the precise percentage of dives under the ADL is not known. Similarly, larger air volumes inhaled prior to deeper dives of emperor penguins (Sato et al., 2011) *versus* the probable lower air volumes of shallow-diving penguins at the isolated dive hole may increase the ADL during deeper, longer dives at sea (Fig. 5).

Lastly, the ADL of the Baikal seal serves to emphasize that the ADL is not necessarily a fixed value in a given species. The ADL determined in Baikal seals (Ponganis et al., 1997a) probably represents a maximum ADL for a dive because the seals were not swimming (Fig. 5). In addition, the dive duration data set was from a juvenile Baikal seal, approximately two-thirds the size of those in the lactate study (Stewart et al., 1996). The ADL of the juvenile seal may well be less due to body size, age, O_2 store development, and swimming activity.

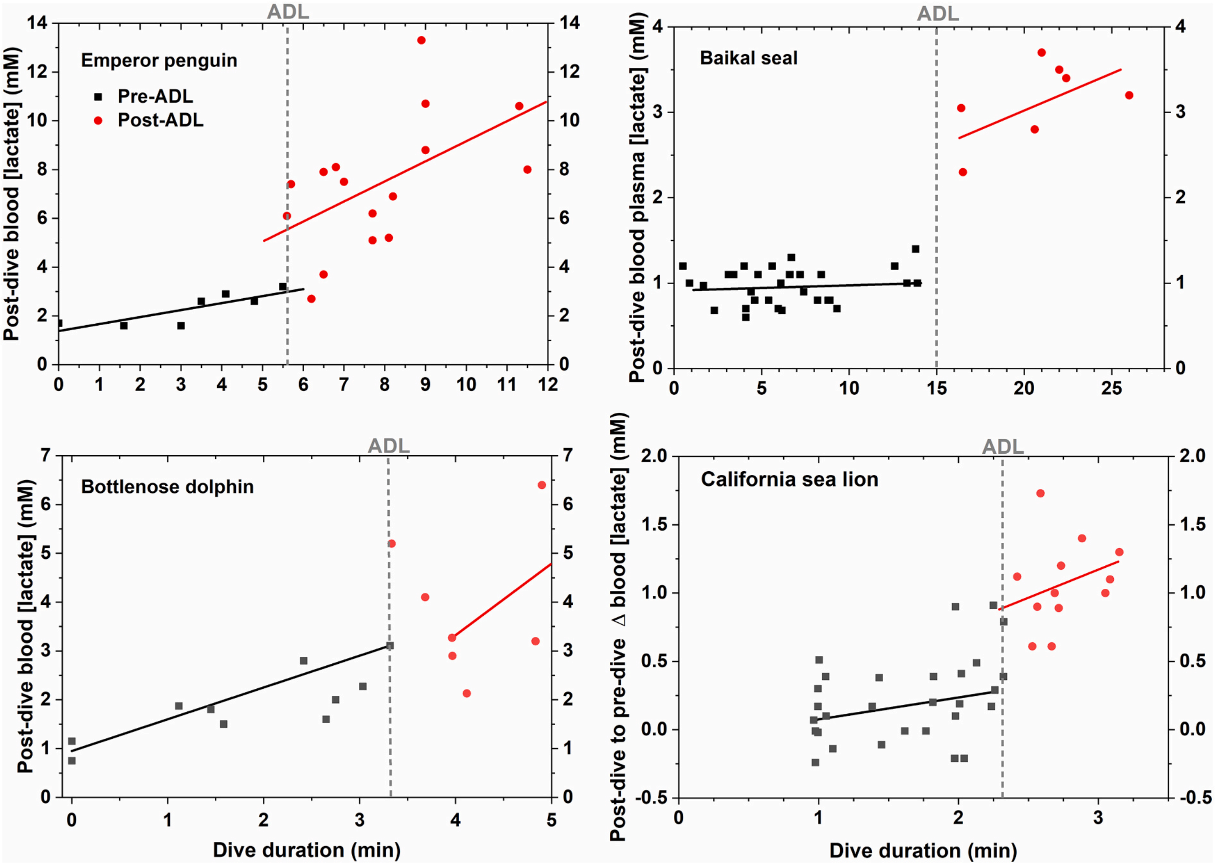


Fig. 4. Two-phase regression analyses of post-dive blood lactate concentration and dive duration resulted in aerobic dive limits (ADLs) of 5.6 min in emperor penguins diving at an experimental dive hole, 15 min in Baikal seals during spontaneous, inactive dives in a pool, 3.3 min in bottlenose dolphins trained to dive to depth at sea, and 2.3 min in juvenile California sea lions during trained underwater swims. Abbreviation: Δ = difference. Adapted from Ponganis et al., 1997a, 1997b, 1997c and Williams et al., 1999.

4. Muscle oxygen depletion and the ADL

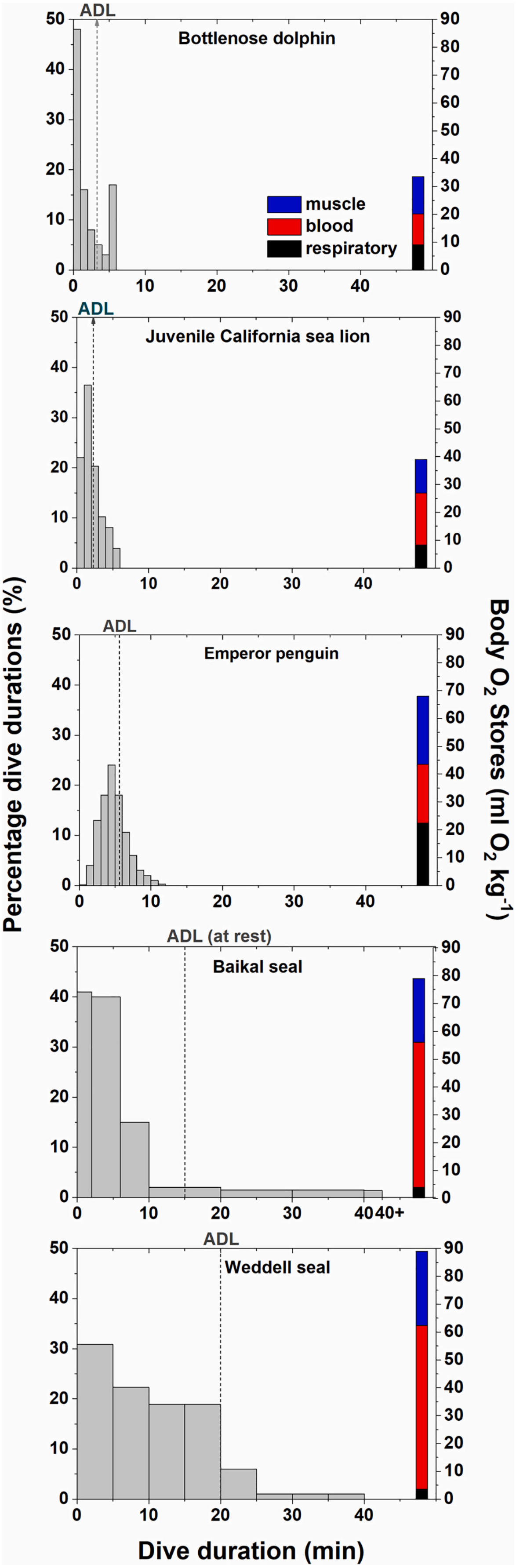
As emphasized in the prior section, the ADL is dependent on the magnitude and utilization of the body O_2 stores during a dive. Oxygen is stored in the respiratory system, blood, and muscle. The pattern and depletion rate of those stores are dependent on the locomotory effort in a dive, temperature regulation and the cardiovascular dive response (Butler, 2006; Ponganis et al., 2011). This response consists of a decrease in heart rate and cardiac output, peripheral constriction of arteries, and a redistribution of blood flow throughout the body that decreases tissue perfusion and may even isolate organs from the circulation (Ponganis et al., 2011). The intensity of the dive response is variable and most likely dependent on dive behavior (depth, duration, effort, feeding/digestion). In dives beyond the ADL, localized tissue oxygen depletion and the associated increase in glycolysis during the dive are hypothesized to result in tissue lactate accumulation. Blood lactate levels obtained by intermittent sampling during dives in three species were consistent with this hypothesis (Fig. 6). Intra-dive blood lactate concentrations remained low even as dives progressed beyond the ADL in emperor penguins, Weddell seals, and Baikal seals (Ponganis et al., 1997a; Ponganis et al., 2009; Qvist et al., 1986). As in Scholander's forced submersion experiments, increased heart rate and tissue reperfusion during the post-dive period account for the washout of lactate and elevation in blood lactate concentration after long dives (Scholander et al., 1942). Although aerobic glycolysis presumably occurs in tissues of these diving animals, local lactate metabolism and lactate shuttles to other tissues under aerobic conditions likely prevent large increases in lactate concentrations (Brooks, 2009).

Investigations of hemoglobin and myoglobin desaturation during dives of emperor penguins at an experimental dive hole have revealed that the primary locomotory muscles were the most probable source of the elevation in blood lactate after dives beyond the ADL (Meir and Ponganis, 2009; Williams et al., 2011). Although desaturation profiles were variable, it was myoglobin that was often completely desaturated at the 5.6-min ADL (Williams et al., 2011) (Fig. 7). In contrast, arterial hemoglobin saturations were 55–95% at the end of 6-min dives, and remained near 100% for most of the dive even in dives as long as 10 min (Meir and Ponganis, 2009).

It must be emphasized that the ADL may be variable, dependent on both the intensity of the dive response and the locomotory effort expended during a given dive. For example, any sprint-type swimming would be expected to result in muscle lactate accumulation regardless of dive duration. It should also be noted that not all muscles may be fully desaturated at the ADL. In Weddell seals, myoglobin did not completely desaturate even in dives beyond the ADL; however, the muscle investigated was not a primary locomotory muscle involved in hind flipper stroke effort (Guyton et al., 1995).

5. Application of the ADL to diving behavior and ecology

The ADL, although only measured in five species, has been applied to the interpretation of the diving behavior and ecology of many species of marine mammals, seabirds, and diving reptiles. A search for "aerobic dive limit" in Google Scholar® yielded 1280 citations. Estimations of the ADL for many species have been based on behavioral criteria or by a calculation (the division of total body O_2 stores by diving metabolic rate). These behavioral estimates and calculations are based on observations and calculations in the original ADL papers (Kooyman et al.,



(caption on next column)

Fig. 5. The aerobic dive limits (ADLs), distribution of dive durations, and magnitude of body oxygen stores in the five species with measured ADLs. Dive durations and ADLs were longer in species with higher total body oxygen stores. In all species, most dives (> 60%) were aerobic (under the ADL). Of note, the emperor penguin dives were "foraging" dives; if short duration, shallow dives (travelling dives) were included, 96% of all dives were < ADL. ADLs were determined with post-dive blood lactate measurements as described in the text. Available dive data included those for off-shore bottlenose dolphins, two juvenile California sea lions, emperor penguins on foraging trips to sea, a juvenile Baikal seal, and Weddell seals in McMurdo Sound, Antarctica. Oxygen store measurements were conducted on bottlenose dolphins and sea lions that were under managed care, and on emperor penguins, Baikal seals and Weddell seals in the wild. Adapted from multiple references for each species: dolphins (Klatsky et al., 2007; Noren et al., 2012; Williams et al., 1999), sea lions (McHuron et al., 2018; Ponganis et al., 1997c), emperor penguins (Kooyman and Kooyman, 1995; Ponganis et al., 1997b; Sato et al., 2011), Baikal seals (Ponganis et al., 1997a; Stewart et al., 1996), and Weddell seals (Kooyman et al., 1980; Ponganis et al., 1993).

1983; Kooyman et al., 1980). For example, behavioral criteria have included a) a dive duration threshold below which 95% of dives occur (Burns and Castellini, 1996), and b) the inflection point at which minimum surface intervals begin to increase in the surface interval-dive duration relationship (Horning, 2012).

The surface interval inflection approach for ADL estimation is at least partially based on the assumption that a "recovery" from a long dive must occur before the resumption of diving. It is often assumed that blood lactate concentrations must return to resting levels or at least decrease prior to the resumption of diving. However, seals will resume diving with elevated blood lactate concentrations, and those concentrations can decrease during the subsequent dive (Kooyman et al., 1980; Ponganis et al., 1997a). As already mentioned, lactate is routinely oxidized under aerobic conditions. Indeed, it has been proposed that such "recovery" occurs during the short duration, relatively shallow dives that occur between long, deep, foraging dives of beaked whales and emperor penguins (Kooyman et al., 2020; Tyack et al., 2006). The inter-deep-dive interval is usually prolonged in those species. However, the continuous deep diving behavior of the elephant seal (*Mirounga sp.*) is exceptional and still remains a physiological mystery (Butler, 2006; Hindell et al., 1991; Le Boeuf et al., 1988). Deep dives and short surface intervals continue even after the longest dives recorded in these seals.

The oxygen store / metabolic rate calculation approach to estimate the ADL is subject to the accuracy of oxygen store estimates and, most importantly, to the accuracy of the dive metabolic rate measurement (Butler, 2006). Nonetheless, the calculation has been widely used to predict the ADL, which we emphasize is the dive duration associated with the onset of post-dive blood lactate accumulation. It must be remembered that the formula does not reflect physiological processes and the status of total body oxygen stores at the ADL. As discussed above for the emperor penguin, total body oxygen stores are not depleted at the ADL. Because of the formula, it had been suggested that the ADL determined with post-dive lactate analyses be called the diving lactate threshold (DLT), and that the calculated ADL be considered the dive duration at which all oxygen stores are depleted (Butler, 2006). That terminology, however, has not gained wide acceptance. We prefer the term, ADL, because it emphasizes that diving metabolism of most dives is primarily aerobic and that was the original intention of the terminology. As in many prior publications, we again repeat that the formula for the calculated ADL is used to estimate the dive duration associated with post-dive blood lactate accumulation, but not to describe the status of total body oxygen stores.

Although the ADL concept and calculations of aerobic limits emphasize aerobic diving, this hypothesis has also provided the framework to interpret diving behaviors and foraging strategies of species that appear to dive frequently beyond their calculated ADLs. Among these species are Australian and New Zealand sea lions (*Neophoca cinerea*,

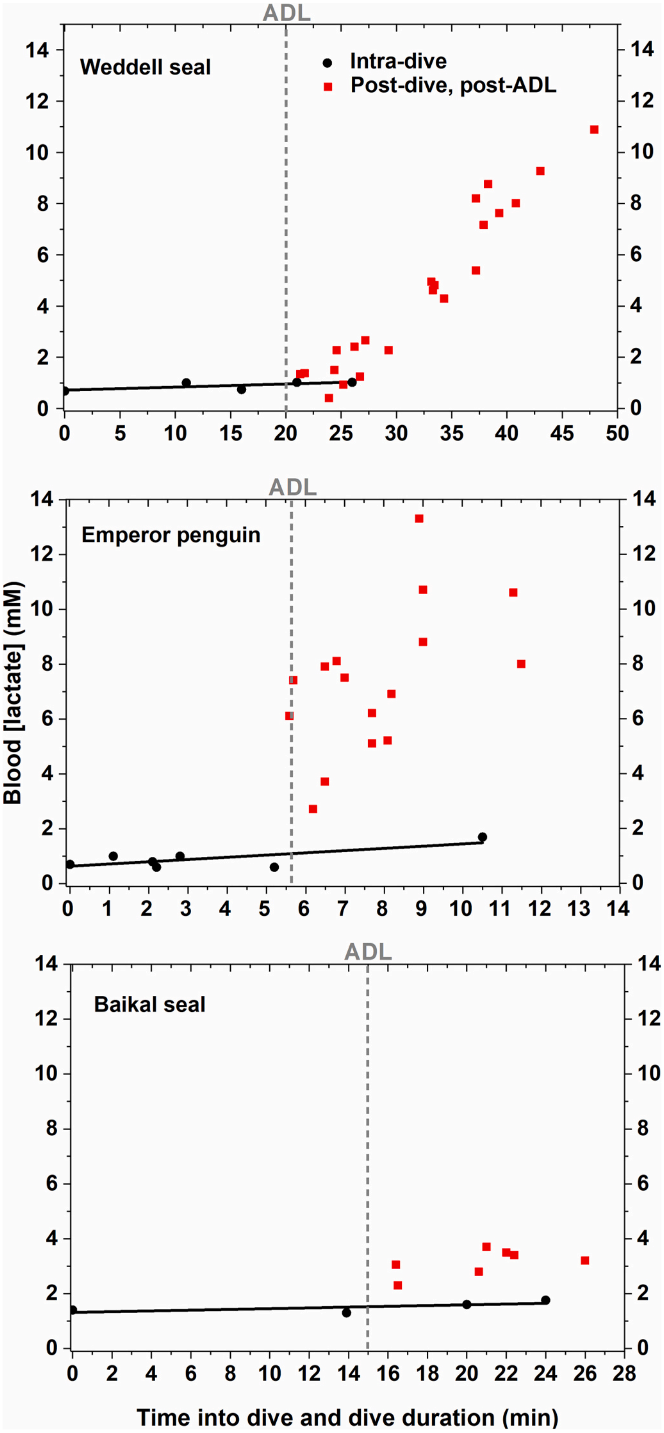


Fig. 6. Comparison of intra-dive blood lactate concentrations with post-dive blood lactate concentrations in three species revealed that intra-dive blood lactate remained near resting levels even as dives progressed beyond the aerobic dive limit (ADL). Intra-dive data for emperor penguins and Weddell seals were obtained with backpack blood samplers while the Baikal seal data were obtained with intermittent manual blood sampling. Intra-dive data adapted from Qvist et al., 1986 and Ponganis et al., 1997a, 2009. Post-dive data adapted from Kooyman et al., 1980, Ponganis et al., 1997a, 1997b.

Phocarctos hookeri), blue-eyed and South Georgian shags (*Phalacrocorax atriceps*, *Phalacrocorax georgianus*), and gentoo and king penguins (*Pygoscelis papua*, *Aptenodytes patagonicus*) (Butler, 2004; Chilvers et al., 2006; Costa and Gales, 2003; Croxall et al., 1991).

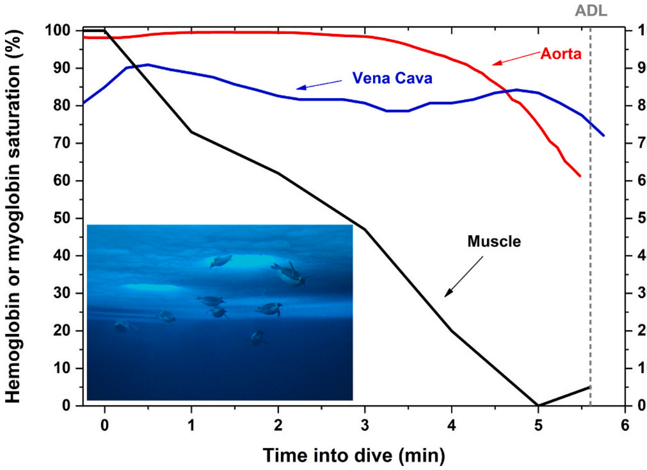


Fig. 7. Myoglobin saturation profiles and arterial and venous hemoglobin saturation profiles of emperor penguins diving at an experimental dive hole revealed that the muscle oxygen store, but not the blood oxygen store was depleted at the previously measured 5.6-min aerobic dive limit (ADL) (Ponganis et al., 1997b). Oxygen depletion and subsequent glycolysis in the primary locomotory muscle are postulated to account for the elevations in post-dive blood lactate concentration after dives beyond the ADL. Data were obtained from dives of 5.5- to 6-min duration in different penguins diving at an experimental dive hole; adapted from Meir and Ponganis, 2009, Williams et al., 2011. (Photo: K. Ponganis, with permission).

6. Summary

Since its introduction 40 years ago, the hypothesis that most dives are aerobic in nature has become fundamental to the understanding of diving physiology and to the interpretation of diving behavior and foraging ecology. An ADL has only been documented with blood lactate analyses in five species. Applications to other species have involved behavioral estimates or use of an oxygen store / metabolic rate formula. Both approaches have limitations, but are useful for the evaluation of the dive behavior and ecology of many species. This is not to say that anaerobic dives never occur or are not important. Deep foraging dives of emperor penguins and beaked whales are probable examples of such anaerobic dives. And physiological mysteries still exist. The continuous deep dives of elephant seals are a prime example. The concept of an ADL provides the framework to further examine the physiology underlying such dive behavior with investigation of a) cardiovascular responses, b) oxygen storage, transport and utilization, c) the role of carbon dioxide, d) temperature regulation, and e) cost of transport. Perhaps most valuable for future research would be the development of an *in vivo* tissue/ blood lactate sensor.

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Declaration of Competing Interest

The authors have no conflicts of interest.

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