10 The aerobic dive limit

The aerobic dive limit (ADL) has become the most fundamental concept in the interpretation of the diving physiology, diving behavior, and foraging ecology of marine mammals and diving birds. The ADL, as originally defined by Kooyman and co-workers, is the dive duration associated with the onset of post-dive blood lactate accumulation (Kooyman, 1985, Kooyman *et al.*, 1980, 1983). Studies of adult Weddell seals (*Leptonychotes weddellii*) diving at an isolated dive hole demonstrated that post-dive blood lactate concentration was distinctly elevated after dives of 26-min duration and that blood lactate began to rise after dives of about 20-min duration (Fig. 10.1). Furthermore, 97% of dives of Weddell seals were under 26 min. Thus, most dives were completely aerobic, and it was the efficiency of aerobic metabolism that allowed frequent, repetitive dives to depth.

Since these landmark publications in the early 1980s, the ADL hypothesis (dives are primarily aerobic) has become fundamental in the interpretation of diving behavior and foraging ecology, as well as diving physiology (Boyd and Croxall, 1996, Butler, 2004, 2006, Costa *et al.*, 2001, 2004, Davis and Kanatous, 1999). The number of species in which an ADL has been estimated are too numerous to cite. The concept of an aerobic limit re-emphasized the importance of hypoxic tolerance and the rate of oxygen store depletion that had been so well demonstrated by Scholander and Elsner (see prior chapters). In addition, the emphasis in biochemical investigations also shifted – from glycolysis and anaerobic capacity to aerobic metabolism and the magnitude of oxygen stores. Later studies of Weddell seals have also reaffirmed this finding, with post-dive increases in blood lactate concentration after dive durations of 17–23 minutes in adults and 4–5 minutes in pups (Burns and Castellini, 1996, Guppy *et al.*, 1986, Williams *et al.*, 2004).

Although the ADL may be one of the most frequently cited concepts in diving physiology and behavior, it has been rarely measured due to technical limitations. In this chapter, ADLs that have been determined by measurements of blood lactate levels in different species will first be reviewed. Then, various indirect methods to estimate the ADL will be assessed. Lastly, the physiological basis of the ADL will be examined.

10.1 Aerobic dive limits determined by blood lactate measurements

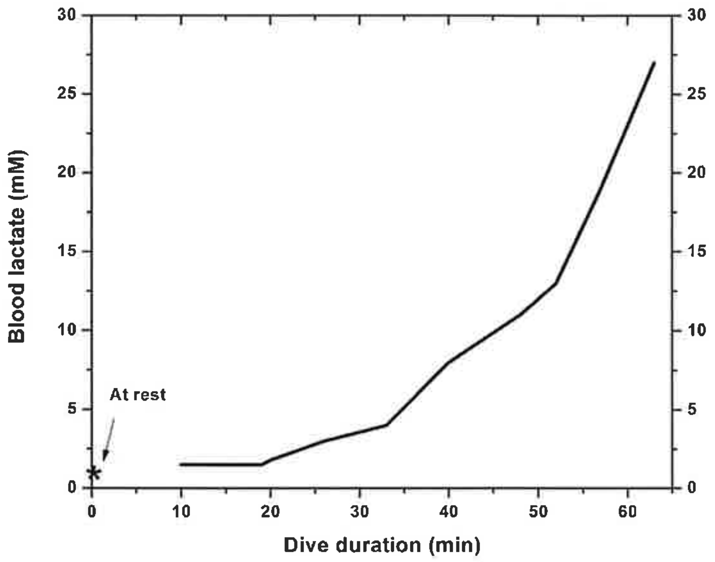

Figure 10.1 The lactate endurance curve for the Weddell seal (*Leptonychotes weddellii*) documented the rise in post-dive blood lactate concentration after dives of various duration, and established the basis for the aerobic dive limit concept. Adapted from Kooyman, 2006, Kooyman et al. (1980a).

In addition to the Weddell seal, an ADL has been determined by post-dive blood lactate measurements in five other species under various conditions (Table 10.1). A 5.6-min ADL for emperor penguins (*Aptenodytes forsteri*) was measured in birds diving at an isolated dive hole on the sea ice of McMurdo Sound (Ponganis *et al.*, 1997c). The experimental approach was basically similar to that used for Weddell seal. In Baikal seals (*Phoca sibirica*), a 15-min aerobic submersion limit was measured during spontaneous submersions of captive animals in shallow tanks (Ponganis *et al.*, 1997b). The term *submersion limit* was used because the seals were not actively swimming; they merely submerged and lay on the bottom of the tank. These seals had been captured in the wild and were untamed. If humans were in sight, they would stay underwater as long as 25 minutes, with heart rates as low as 5 bpm for the last 5 min.

The three other ADL measurements involved captive, trained animals. A 2.3-min ADL was measured in young California sea lions (*Zalophus californianus*), trained to swim submerged following a target in the ring tank that had been built as part of Scholander's Physiological Research Lab at Scripps Institution of Oceanography (Ponganis *et al.*, 1997d). This again was not actual diving as the animals were not descending to depth and undergoing pressure-related changes in lung volume and buoyancy. A 3.3-min ADL was measured in bottlenose dolphins (*Tursiops truncatus*) trained to dive to a target as deep as 210 m (Williams *et al.*, 1999). These animals were trained for fluke presentation to allow blood sampling from blood vessels in the fluke. In a similar experiment, two beluga whales (*Delphinapterus leucas*) were trained to dive and station at a target at up to 300-m depth for dive durations as long as 11 min (Shaffer *et al.*, 1997). An ADL as long as 9–10 min for the beluga whale was reported on the basis of elevated blood lactate concentrations after dives of 9–11 min. However, it is unknown if lactate might begin to increase after shorter dive durations of beluga whales

Table 10.1 Aerobic limits determined with post-dive blood lactate measurements in different divers.

Species	Aerobic limit (min)	Technique	Reference
Weddell seal		Isolated dive hole	
Leptonchotes weddellii			
Adult	17–23		A
Juvenile	10–13		B
Pup	4–5		C
Emperor penguin	5.6	Isolated dive hole	D
Aptenodytes forsteri			
Bottlenose dolphin	3.3	Trained dives	E
Tursiops truncatus			
Beluga whale	≤9–11	Trained dives	F
Delphinapterus leucas			
Baikal seal	15	Stationary, voluntary dives in a tank	G
Phoca sibirica			
California sea lion	2.3	Submerged swimming	H
Zalophus californianus			
(juvenile)			
Sea otter	>1.6	Voluntary dives in a tank	I
Enhydra lutris			

References: A: Guppy *et al.*, 1986, Kooyman *et al.*, 1980, Williams *et al.*, 2004; B: Kooyman *et al.*, 1983; C: Burns and Castellini, 1996; D: Ponganis *et al.*, 1997c; E: Williams et al., 1999; F: Shaffer *et al.*, 1997; G: Ponganis *et al.*, 1997b; H: Ponganis *et al.*, 1997d; I: Yeates *et al.*, 2007.

Results for beluga whales and sea otters represent upper and lower limits, respectively, for an aerobic dive limit. In beluga whales, lactate was elevated after 9–11-min dives, but no data were obtained for dives of lesser duration. In sea otters, lactate was not elevated after dives up to 1.6 min in duration, but no data were obtained for dives of longer duration.

as there were no dives of shorter duration in the study. Lastly, although an ADL$_M$ has not been determined in sea otters, it is at least 1.6 minutes as blood lactates did not rise after dives as long as 100 sec in captive otters (Yeates *et al.*, 2007).

These studies were remarkable technical achievements that have provided the best available estimates of the duration of predominant aerobic metabolism during diving. Nonetheless, potential limitations have been raised in application of these data to animals diving freely in the wild. First, for seals and penguins diving at an isolated dive hole, it could be questioned whether these animals are primarily searching for an escape hole and that physiological responses during such dives are different than in animals diving in a completely unrestricted situation. Although such search or "escape" dives undoubtedly occur, both seals and penguins appear to adapt to the situation and begin feeding regularly (Davis *et al.*, 1999, Kooyman, 1968, Ponganis *et al.*, 1993a, 2000, Williams *et al.*, 2004). It should also be noted that emperor penguins at the isolated dive hole predominantly dive to less than 50-m depth, so the ADL of 5.6 min may not be applicable to deep dives because of potential differences in buoyancy, stroke rate, diving air volume, and cardiovascular responses (Sato *et al.*, 2011, Williams *et al.*, 2012, Wright *et al.*, 2014). The submerged swimming sea lion study is also subject to the same limitation. Heart rate responses during submerged swimming were similar to those during trained dives to shallow depths at sea, but were higher than during deep (400 m) dives (McDonald and Ponganis, 2014, Ponganis *et al.*, 1997d).

Lastly, a potential criticism of techniques involving trained dives is that the cardiovascular responses and oxygen depletion patterns may be different between a natural dive and a dive in which the animal may not know the depth of the target or the duration it may have to station at the target. On the other hand, a foraging animal searching for prey may also not know the depth or duration of dive needed to find its prey. In conclusion, despite such potential limitations, these studies remain remarkable accomplishments and still provide the best available data on the duration of aerobic metabolism and onset of lactate accumulation during diving. In the future, development and refinement of an intravascular blood lactate sensor (Baker and Gough, 1995) may allow investigations in the wild.

10.2 Behavioral and calculated aerobic dive limits: indirect techniques

Due to the difficulty of actually measuring an ADL with blood lactate determinations (i.e., a measured ADL, ADL$_M$), many researchers have resorted to other approaches to examine the ADL. The first technique is the estimation of a behavioral ADL (ADL$_B$). This is based upon the original observations of Kooyman and co-workers that 92–96% of dives were less than the ADL$_M$, and that dives beyond the ADL had longer surface intervals (Kooyman *et al.*, 1980, 1983). Thus, the ADL$_B$ has been estimated as the dive duration below which 95–97% of dives occur (Burns and Castellini, 1996, Hindle *et al.*, 2011). Alternatively, although many factors may contribute to the duration of a surface interval, the ADL$_B$ can be considered the dive duration after which surface intervals begin to increase (Burns, 1999, Cook *et al.*, 2008, Kooyman and Kooyman, 1995). Analysis of minimum surface intervals in relation to dive duration provided an ADL$_B$ of 8 min in emperor penguins at sea, about 2.4 min longer than the ADL$_M$ at the isolated dive hole (Kooyman and Kooyman, 1995). Only about 4% of foraging dives of emperor penguins at sea were greater than that ADL$_B$. A similar type of analysis was used to estimate ADL$_B$ in different age groups of Weddell seals (Burns, 1999). A recent elegant constraint line analysis of scattergrams of dive durations and surface intervals has been used to estimate an ADL$_B$ of 3.2 minutes in adult, female Galapagos fur seals (*Arctocephalus galapagoensis*) (Horning, 2012).

The ADL has also been calculated (ADL$_C$) by dividing total body oxygen stores by the diving metabolic rate. This approach was again based on the findings of Kooyman and co-workers. They made such calculations from prior measurements of body oxygen stores and diving metabolic rate in Weddell seals and found that it was quite close to the inflection point in their lactate concentration–dive duration curve (Kooyman *et al.*, 1980, 1983). Although this formula has become the most common technique to estimate an ADL, there are several limitations to its use. First, as reviewed in Chapter 4, accurate assessment of oxygen stores is dependent not just on myoglobin concentration, hemoglobin concentration, and blood volume, but also on the less frequently documented respiratory volume and muscle mass. Second, and probably most important, what diving metabolic rate should be used in the formula? As originally calculated, as reaffirmed in a subsequent study of Weddell seals, and as demonstrated for submersions of Baikal seals, the dive event metabolic rate (total oxygen consumed during the surface interval divided by the sum of the dive duration plus surface interval) was used to correctly calculate the ADL (Kooyman *et al.*, 1980, Ponganis *et al.*, 1993a, 1997b,). In the Weddell seal studies, that diving metabolic rate was approximately two times the allometrically predicted resting metabolic rate. Note that neither the field metabolic rate, the estimated metabolic rate during a dive (based on accelerometry, heart rate, or excess oxygen consumption above baseline during the surface interval divided by dive duration), nor the actual oxygen store depletion rate during a dive were used. As reviewed in Chapter 9, dive event metabolic rates have been determined in few species. Consequently, the diving metabolic rate in the denominator of the $\mathrm{ADL_C}$ formula is the least documented variable in the equation. For mammalian divers, investigators will often use a value twice the allometrically predicted resting metabolic rate (as found in the Weddell seal data). Based on the most recent estimates of oxygen stores in emperor penguins, the 5.6-min $\mathrm{ADL_M}$ is also best predicted by a calculation with a diving metabolic rate twice the allometrically predicted resting metabolic rate (Ponganis *et al.*, 2010a).

It has been emphasized many times that the $\mathrm{ADL_C}$ formula should be considered to simply predict the dive duration with the onset of post-dive blood lactate accumulation (Kooyman and Ponganis, 1998, Kooyman *et al.*, 1999, Ponganis, 2011, Ponganis *et al.*, 1997d, 2003a, 2010a). The formula does not define the status of the oxygen stores at the ADL. Physiologically, the ADL has been a black box. Certainly, there is at least some localized depletion of oxygen and subsequent glycolysis at the ADL, but all oxygen stores are not necessarily depleted. After all, animals can dive much longer than the ADL. The formula, however, is convenient to at least begin to estimate the duration of aerobic dive time without resort to increased glycolysis and lactate accumulation. It should be remembered, however, that the accuracy of the formula has only been demonstrated in two species.

Because of the confusion over the physiological implications of the $\mathrm{ADL_C}$ formula, a new terminology was suggested in the late 1990s (Butler and Jones, 1997). The $\mathrm{ADL_M}$, the ADL measured with lactate determinations, was labeled the diving lactate threshold (DLT). The dive duration calculated by the $\mathrm{ADL_C}$ formula, and at which all oxygen stores were consumed, was termed the calculated ADL or cADL. A diving lactate threshold is similar in concept to lactate thresholds in exercise studies of terrestrial mammals. The suggested cADL represents the point of complete oxygen depletion and is quite different from earlier use of the $\mathrm{ADL_C}$ to simply predict the onset of post-dive blood lactate accumulation. Although these new terms are now used in the literature, they have not gained universal use. Consequently, readers should be aware which terminology is being used. In order to avoid confusion and be consistent with the wording in earlier research, the suggested change in terminology is not used in this book.

10.3 Physiological basis of the aerobic dive limit

In order to examine the physiological basis of the aerobic dive limit and eliminate confusion caused by various interpretations of the $\mathrm{ADL_C}$ formula, oxygen store management was investigated in emperor penguins. In a series of projects, indwelling $\mathrm{P_{O2}}$

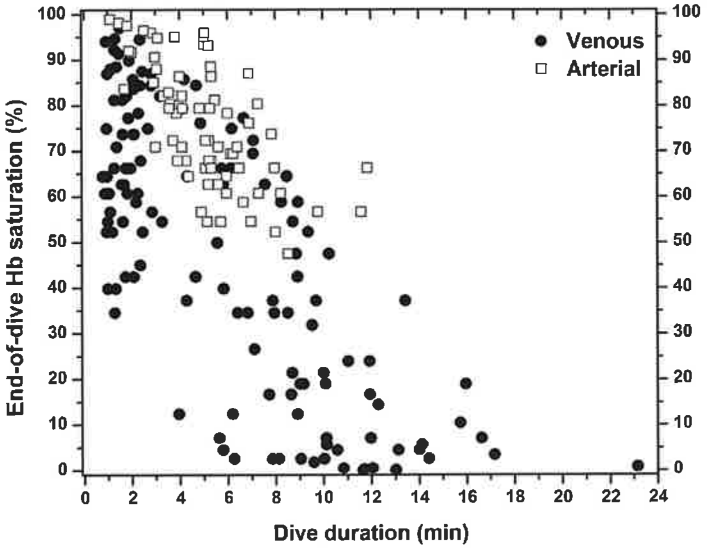

Figure 10.2 End-of-dive arterial and venous hemoglobin (Hb) saturations of the emperor penguin (*Aptenodytes forsteri*) were highly variable but demonstrated that blood oxygen was not completely depleted even in dives beyond the 5.6-min aerobic dive limit determined with post-dive blood lactate measurements. Adapted from Meir and Ponganis (2009).

electrodes and near-infrared myoglobin saturation probes were utilized to monitor O_2 store depletion in emperor penguins diving at an isolated dive hole (Meir and Ponganis, 2009, Ponganis *et al.*, 2007, 2009, Stockard *et al.*, 2005, Williams *et al.*, 2011a). This model was ideal because the 5.6-min $\mathrm{ADL_M}$ had been determined previously with post-dive blood lactate measurements (Ponganis *et al.*, 1997c).

Investigation of air sac, arterial, and venous $\mathrm{P_{O2}}$ revealed a wide range of end-of-dive values at the 5.6-min $\mathrm{ADL_M}$. For example, end-of-dive respiratory O_2 fractions at the ADL ranged from 1% to 8% (Stockard *et al.*, 2005). Similarly, venous hemoglobin saturations ranged from 5% to 50% while arterial hemoglobin saturations were 55% to 95% (Fig. 10.2) (Meir and Ponganis, 2009). During two dives greater than 10 min, end-of-dive arterial hemoglobin saturations were still 60–65% (Fig. 10.2). Clearly, the respiratory and blood O_2 stores were not depleted at the ADL. However, myoglobin saturation profiles, although also variable, demonstrated complete depletion in some dives of 5–6-min duration (Fig. 10.3), close to the 5.6-min $\mathrm{ADL_M}$ (Williams *et al.*, 2011a). Given that muscle lactate accumulation begins at 10–20% saturation in seals (Scholander *et al.*, 1942a, Williams *et al.*, 2012), these investigations supported the hypothesis that the depletion of muscle oxygen is the physiological basis of the ADL (Kooyman and Ponganis, 1998). Near-complete myoglobin desaturation in the primary locomotory muscle results in increased glycolysis, accumulation of muscle lactate, and subsequent wash-out of lactate into the blood during the post-dive interval.

Further evidence for the lack of complete blood O_2 store depletion at the ADL was also found in hemoglobin saturation profiles of diving elephant seals and sea lions

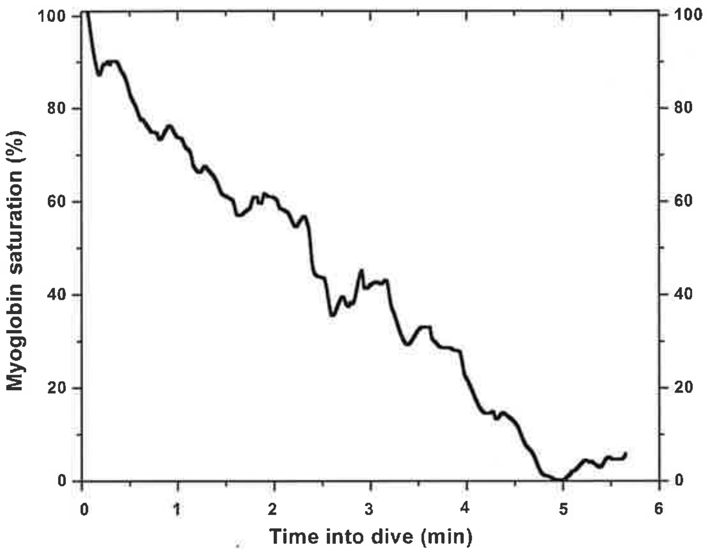

Figure 10.3 Myoglobin (Mb) saturation in the emperor penguin (*Aptenodytes forsteri*) demonstrated almost complete muscle oxygen depletion in dives near the 5.6-min aerobic dive limit consistent with the hypothesis that muscle oxygen depletion and subsequent lactate accumulation provided the physiological basis of the aerobic dive limit. Adapted from Williams et al. (2011a).

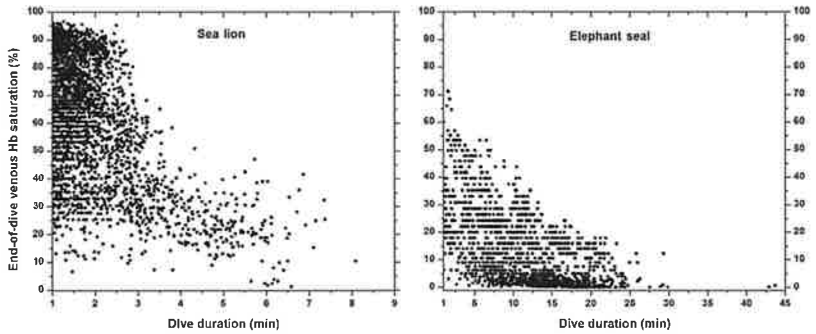

Figure 10.4 End-of-dive venous hemoglobin (Hb) saturations in lactating California sea lions (*Zalophus californianus*) and young northern elephant seals (*Mirounga angustirostris*) were highly variable, especially for dives of shorter duration. However, blood oxygen depletion was often incomplete even for longer dives. Sea lion data were from the posterior vena cava; elephant seal data from the hepatic sinus and extradural vein. Adapted from McDonald and Ponganis (2013), Meir et al. (2009).

(McDonald and Ponganis, 2012, 2013, Meir *et al.*, 2009). Although an at-sea ADL has not been determined with post-dive lactate measurements, end-of-dive venous hemoglobin saturations ranged as high as 40% in dives longer than 6 min in sea lions and 20 min in elephant seals (Fig. 10.4). End-of-dive arterial hemoglobin saturations were as high as 30% during dives of 20–22-min duration in elephant seals, and were greater than 80% during dives as long as 7 min in sea lions. For the sea lions, back calculation of alveolar P_{O_2} from the measured arterial P_{O_2} results in a lung oxygen fraction near 10%; approximately half of the lung O_2 store was not consumed in some of the deepest, longest dives of these sea lions. All these findings reinforce the fact that the calculation of an ADL based on O_2 stores and a diving metabolic rate does not represent the physiological basis of the onset of post-dive blood lactate accumulation. The calculated ADL may be useful in ecological models and prediction of the dive duration associated with the onset of lactate accumulation, but it does not address the physiological/biochemical processes underlying the ADL. Hence, the importance of recent research addressing myoglobin saturation, the degree of muscle perfusion and linkage of heart rate/stroke rate during diving (Chapter 5).

As already pointed out in many reviews and studies, the ADL probably has some variability, dependent on the physiological responses, locomotory effort, digestive processes, and ultimately metabolic rate during a dive (Kooyman and Ponganis, 1998, Meir and Ponganis, 2009, Ponganis, 2011, Ponganis *et al.*, 1993a, Sato *et al.*, 2011, Williams *et al.*, 2004, 2011a,). In surfacers such as elephant seals, even sleep may occur and potentially prolong the ADL by decreasing metabolic rate during a dive (Crocker *et al.*, 1997, Mitani *et al.*, 2010).

In a theoretical model, it has also been argued that the ADL can be optimized by coupling heart rate and muscle perfusion with muscle workload so as to simultaneously deplete the blood and muscle O_2 stores (Davis and Kanatous, 1999). Again, this emphasizes the significance of the linkage of heart rate (and perfusion) with flipper stroke rate during diving (see Chapter 5). However, the above findings in emperor penguins are not consistent with such a model of simultaneous depletion of the blood and muscle O_2 stores. Ideally, O_2 store management strategies and the onset of post-dive blood lactate accumulation can be further examined in other species with use of recorders and sensors for continuous P_{O_2}, myoglobin saturation, and even lactate profiles. Translocated elephant seals, otariids on maternal foraging trips, trained cetaceans, and isolated dive hole studies of Weddell seals and emperor penguins are all feasible models.