

Review

Aerobic dive limit: how often does it occur in nature? ☆

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Abstract

Diving animals offer a unique opportunity to study the importance of physiological constraint in their everyday behaviors. An important component of the physiological capability of any diving animal is its aerobic dive limit (ADL). The ADL has only been measured in a few species. The goal of this study was to estimate the aerobic dive limit from measurements of body oxygen stores and at sea metabolism. This calculated ADL (cADL) was then compared to measurements of diving behavior of individual animals of three species of otariids, the Antarctic fur seal, *Arctocephalus gazella*, the Australian sea lion, *Neophoca cinerea*, and the New Zealand sea lion, *Phocartos hookeri*. Antarctic fur seals dove well within the cADL. In contrast, many individuals of both sea lion species exceeded the cADL, some by significant amounts. Australian sea lions typically dove 1.4 times longer than the cADL, while New Zealand sea lions on average dove 1.5 times longer than the cADL. The tendency to exceed the cADL was correlated with the dive pattern of individual animals. In both Antarctic Fur Seals and Australian sea lions, deeper diving females made longer dives that approached or exceeded the cADL ($P < 0.01$, $r^2 = 0.54$). Australian and New Zealand sea lions with longer bottom times also exceeded the cADL to a greater degree. The two sea lions forage on the benthos while the fur seals feed shallow in the water column. It appears that benthic foraging requires these animals to reach or exceed their aerobic dive limit. © 2001 Elsevier Science Inc. All rights reserved.

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1. Introduction

As a discipline, physiological ecology aims to place the physiology of an organism into the context of its environment. It is fundamentally different from comparative physiology in that it goes beyond documenting the animal's extreme

physiological capacity, to understanding the relative importance of a physiological trait to the animal's life history (Feder and Block, 1991). In this way, we can examine whether a physiological trait confers a selective advantage by increasing fitness, by how much, and we can also ask how did this trait evolve (Bennett et al., 1990; Bennett, 1991). The simplest way to determine whether a trait confers a selective advantage is to ask how often, if ever, does physiology constrain or enable the animals behavior, distribution, abundance or habitat selection (Bennett et al., 1991). A graphi-

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cal representation of the physiological capability of different organisms is given in Fig. 1. The *y*-axis represents the range or scope of physiological responses and is likely to correspond to some abiotic factor such as environmental temperature, pressure or availability of water. The *x*-axis represents different taxonomic or phylogenetic groups that have different physiological capabilities. Within each taxonomic group, four possible scenarios define the range of physiological capacity employed. Response 1 shows an animal that routinely exists well within its physiological capability and rarely, if ever, is it limited by it. Response 2 shows an animal that routinely reaches both its upper and lower physiological limits. Responses 3 and 4 shows an animal that routinely reaches either its lower or upper physiological limit. In scenarios 2, 3 and 4, physiology is a major determinant of the animals behavior, distribution and/or abundance, while it plays a minimal role in scenario 1. A more sophisticated representation of the above model would replace the simple arrows with a curve that represents the frequency distribution of a given response, and would incorporate the variation in physiological capacity between individuals within the population (Bennett et al., 1989; Garland et al., 1990; Garland and Adolph, 1991). An example appropriate to this symposium would be if group A represented the diving ability of otariids (sea lions and fur

seals), then group C would represent the diving ability of phocids (true seals). Both groups are capable of very short or shallow dives, but due to differences in their physiology and anatomy, phocids are capable of deeper longer dives than are otariids (Costa, 1991b, 1993a).

Pinnipeds have provided a unique system to study the relative importance of physiology in determining their foraging behavior. They are tractable, large enough to carry instrumentation, can be studied in captivity and, in some cases, allow for repeated sampling of physiological processes in the field (Zapol et al., 1979; Falke et al., 1985; Hill et al., 1987; Kooyman et al., 1980; Ponganis et al., 1990a,b,c, 1993a,b). As a result of these and other studies, we now have a reasonable understanding of the basic physiological processes that occur during diving in these animals. Following the framework outlined in Fig. 1, we know that the dive capability is constrained by physiology, but that the behavior within these limits is determined by the other aspects of the animals ecology such as the distribution, abundance, depth, and energy content of the prey (Costa, 1991a,b, 1993a). The development of time depth recorders, pioneered by Gerry Kooyman, has resulted in a wealth of information on the diving behavior of freely living marine mammals and seabirds (Kooyman, 1989; Costa, 1993b; Boyd and Croxall, 1996). These studies have recorded a

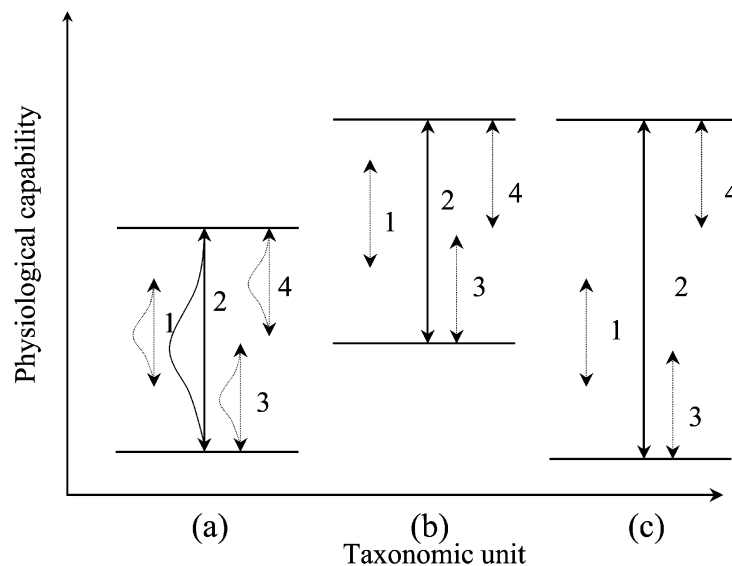


Fig. 1. Four different situations are described for how the physiological capacity of an animal determines its behavior habitat utilization or other aspect of its life history. (a), (b) and (c) refer to potential differences between taxonomic groups. These taxonomic categories could represent any taxonomic grouping from species, orders, to class.

wide range of foraging strategies and have implicated physiology as a limiting or enabling feature (Kooyman et al., 1983, 1980; Kooyman, 1989; Costa, 1993b; Boyd and Croxall, 1996). The diving capability of a marine mammal is determined by its total metabolic stores and the rate that they are used (Kooyman, 1989). These metabolic stores can be separated into aerobic and anaerobic components. The aerobic component of diving metabolism is thought to be the major determinant of diving ability (Kooyman et al., 1980, 1983; Kooyman, 1989; Ponganis et al., 1993a, 1997c). The aerobic dive limit (ADL) has been experimentally defined as the dive duration beyond which blood lactate levels begin to rise above resting levels. When Weddell seals, *Leptonychotes weddelli*, exceed the aerobic threshold, the post-dive surface interval increases disproportionately faster than dive duration (Kooyman et al., 1980, 1983). An increased surface interval is required to clear the lactic acid accumulated during the dive. One of the disadvantages of anaerobic metabolism during diving is that while a diver may increase the duration of a single dive, the total accumulated time spent underwater is reduced, because the animal must spend proportionately more time at the surface clearing lactic acid.

Given the difficulty of measuring post-dive blood lactate levels in free ranging animals it is not surprising that ADL measurements have only been carried with trained animals or animals diving in unique environments. To date, such measurements have been carried out on Weddell seals (Kooyman et al., 1980, 1983; Ponganis et al., 1993a; Burns and Castellini, 1996), California sea lions, *Zalophus californianus* (Ponganis et al., 1997c), Baikal seals, *Phoca sibirica* (Ponganis et al., 1997a), emperor penguins, *Aptenodytes forsteri*, (Ponganis et al., 1997b), Beluga whales, *Delphinapterus leucas* (Shaffer et al., 1997), and bottlenose dolphins, *Tursiops truncatus* (Williams et al., 1993). Irrespective of the difficulty of getting actual measurements of ADL in nature, the concept has received considerable discussion (Butler and Jones, 1982; Kramer, 1988; Ydenberg and Forbes, 1988; Kooyman, 1989; Butler 1991; Houston and Carbone, 1992; Boyd and Croxall, 1996; Carbone and Houston, 1996; Boyd, 1997; Schreer and Kovacs, 1997).

As one of the goals physiological ecology is to understand, when physiology limits behavior it would be instructive to observe how often and

under what conditions animals diving in nature, stay within or exceed the ADL. The aim of this review was to examine the diving behavior of three species of oatriids, the Antarctic fur seal, *Arctocephalus gazella*, the Australian sea lion, *Neophoca cinerea*, and the New Zealand sea lion, *Phocarcos hookeri* with respect to whether individuals dive within the aerobic dive limit. Following the conceptual model proposed in Fig. 1, we examine differences in diving behavior and physiology both within and between taxonomic units. The three species represent the extremes of diving behaviors reported for otariids. The Antarctic fur seal makes short shallow dives, while the two sea lions make deep prolonged dives to the benthos (Fig. 2). The diving behavior of these three species was examined by comparing the individual specific calculated aerobic dive limit (cADL) to individual specific diving behavior. In this way, we can elucidate intra and interspecies variation in the tendency of these animals to reach or exceed their cADLs and, thus, gain insight into how often the ADL is reached by freely diving animals in nature.

2. Materials and methods

Individual specific ADL of 11 Australian sea lions, 15 Antarctic fur seals and 11 New Zealand sea lions were determined by dividing each animals total O₂ stores by their specific diving metabolic rate (DMR), assumed to be the at sea field metabolic rate (FMR) measured by O-18 doubly-labeled water. It is important to note that at-sea FMR integrates the costs of highly variable surface swimming, diving and resting and, therefore, the actual DMR could be higher or lower. However, DMR estimated in this way should reflect relative differences in metabolic effort between individuals. Total oxygen stores were calculated following the method of Davis and Kanatous (1999) and Gentry et al. (1986), with the incorporation of data on blood volume (Costa et al., 1998; Sterling et al., 1998) and muscle myoglobin (Reed et al., 1994; Costa et al., unpublished data) content for each species (Table 1) and the specifics are as follows. Blood oxygen stores were estimated as the sum of arterial and venous oxygen stores using the equation:

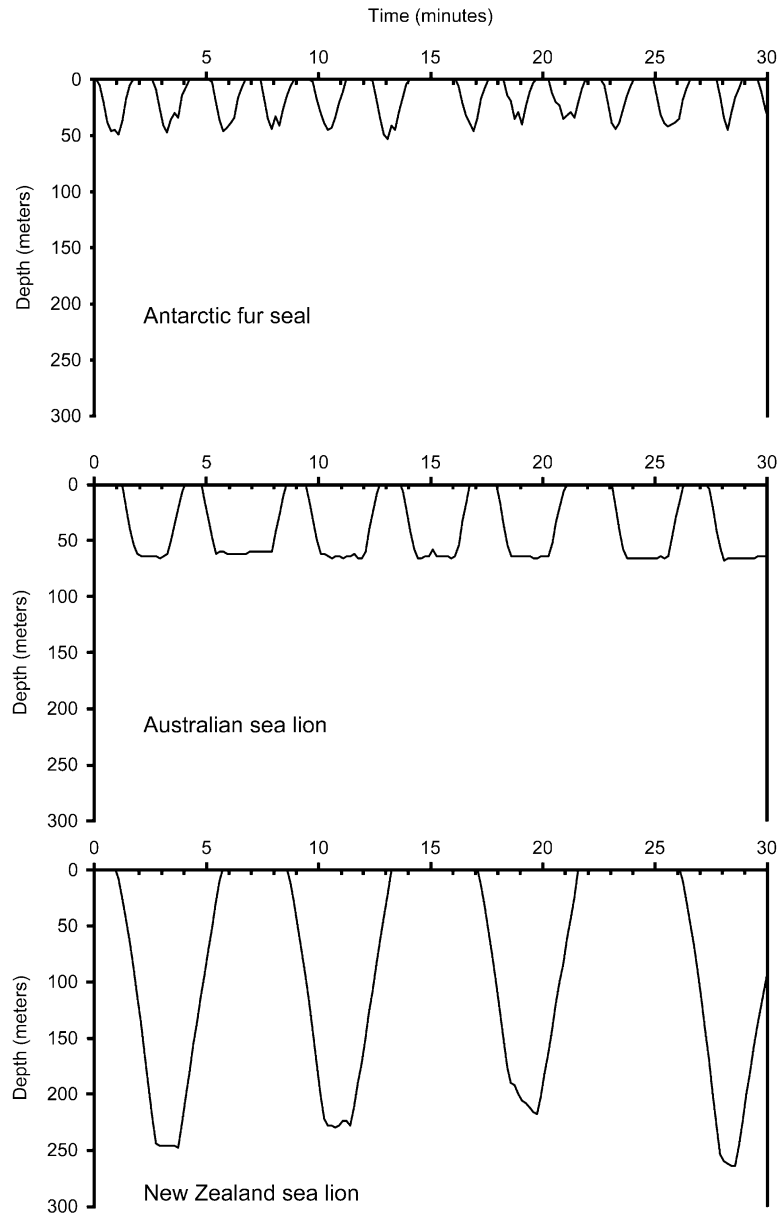


Fig. 2. A 30-min depth vs. time profile from a representative Antarctic fur seal, Australian sea lion (W-C2) and New Zealand sea lion are presented. The same scale was used for the three dive patterns to emphasize the differences in the depth, timing and shape of the dives.

$$\text{Arterial O}_2 = (0.33 \times Vb) \\ \times (0.95 \text{ to } 0.20 \text{ saturation})$$

$$+ \text{Venous O}_2 = (0.66 \times Vb) \\ \times (\text{arterial content} - 5 \text{ vol}\%)$$

where 0.33 = percentage of arterial blood, 0.66 = percentage of venous blood, Vb = blood volume (ml), 0.95 to 0.20 saturation is the amount of

oxygen extracted during a dive assuming an oxygen capacity of 23.0 ml (100 g^{-1}) (Lenfant et al., 1970), and (arterial content — 5 vol%) is the amount of oxygen extracted during a dive (Kooyman et al., 1983). Muscle oxygen stores were estimated using the equation:

$$\text{Muscle O}_2 = (Mb \times 1.34 \text{ ml} \\ \times \text{O}_2 \text{ g}^{-1} \text{ Mb} \times \text{mass} \times 0.3),$$

Table 1

Blood volume, hemoglobin and muscle myoglobin content for the three species are presented; there are no data for hemoglobin and myoglobin concentrations for New Zealand sea lions so the values are estimates from other species (Costa et al., 1998)

	Antarctic fur seal	Australian sea lion	New Zealand sea lion
Blood volume l	13.2 ^a	14 ^d	15.3 ^e
Hemoglobin (g%)	17.95 ^b	17.6 ^d	17.2
Myoglobin (mg g ⁻¹)	22.5 ^c	28 ^d	32
Total O ₂ stores l	44.7	47	50.9

^aSterling, Costa and Goebel (1998).

^bCosta, Burns and Goebel (unpublished).

^cReed et al. (1994).

^dCrocker, Costa, Gales and Burns (unpublished).

^eCosta et al. (1998).

where Mb is a myoglobin concentration (Lenfant et al., 1970) and 0.3 is the fraction of muscle mass in the body (Kooyman et al., 1983).

Diving lung oxygen stores were estimated using the equation:

$$\text{Lung O}_2 = (V_i \times \text{mass} \times 0.15 \text{ FO}_2),$$

where V_i = diving lung volume, $0.50 \times (0.10 \times$

mass^{0.96}) liters (Kooyman, 1989), and 0.15 FO₂ is the oxygen extracted from the air in the lungs (Kooyman et al., 1971).

An estimated aerobic dive limit (ADL) was calculated as:

$$\text{ADL (min)} = \text{available O}_2 \text{ stores} / \text{DMR}.$$

Data on dive behavior and at-sea metabolism were taken from published reports on each species (Costa et al., 2000; Costa and Gales, 2000; Costa and Gales, in review). All studies employed concurrent measurements of metabolic rate and diving behavior on the same individuals. Studies on Australian sea lions were carried out at Seal Bay Kangaroo Island, South Australia during 1989 and 1990. Work on New Zealand seal lions at Sandy Bay, Enderby Island, Auckland Islands Group, New Zealand (50°30'S, 166°17'E) during January and February 1997. Fieldwork with Antarctic fur seals was carried out from the US-AMLR field camp at Cape Shirreff, Livingston Island (62°29'S 60°47'W) during February 1998. Measurements of foraging energetics and diving behavior were completed while females were lactating with pups of between 1 and 6 months old. Metabolic rate (CO₂ production) was measured using the oxygen-18 doubly labeled water method

Table 2

Mass, FMR, oxygen stores, calculated aerobic dive limit (cADL), and the ratio of measured mean dive duration to cADL for individual Antarctic fur seals are presented

Animal	Mass (kg)	FMR ^a (O ₂ ml min ⁻¹)	O ₂ stores (O ₂ ml)	cADL	Dive ^a duration (min)	Dive ^a duration (cADL)
F-36	43.6 ^b	1824 ^b	1949 ^b	1.1 ^b	1.5 ^b	1.4 ^b
F-40	40.6	1461	1815	1.2	1.2	1.0
F-41	36.7	965	1640	1.7	1.1	0.6
F-42	36.6	1388	1636	1.2	1.0	0.9
F-44	39.2	1055	1752	1.7	1.5	0.9
F-45	43.6 ^b	1730 ^b	1949 ^b	1.1 ^b	1.5 ^b	1.3 ^b
F-46	46.5	1243	2079	1.7	1.3	0.8
F-47	42.7	923	1909	2.1	1.3	0.6
F-49	53.5	1377	2391	1.7	0.8	0.5
F-67	41.0	1249	1833	1.5	1.3	0.9
F-69	47.9	759	2141	2.8	1.0	0.4
F-79	39.7	1029	1775	1.7	1.2	0.7
F-84	41.9	1416	1873	1.3	1.0	0.7
F-85	41.0	1145	1833	1.6	0.9	0.6
F-87	32.6	1025	1457	1.4	0.9	0.6
Mean (S.D.)	41.9 (5.0)	1239 (297)	1869 (225)	1.6 (0.4)	1.2 (0.2)	0.8 (0.3)

^aDive and FMR are data from Costa et al. (2000).

^bMean dive durations greater than 1.3 times the cADL.

(Lifson and McClintock, 1966; Nagy, 1980; Nagy and Costa, 1980; Costa, 1987; Speakman, 1997). Field metabolic rate (FMR) data were normalized to estimate FMR while at-sea, by correcting for the portion of time and, hence, FMR spent on-shore (Costa et al., 1989; Costa and Prince, 1987). A variety of wildlife computer time depth recorders (MK 3, 5, 6 and 7) were used to measure diving behavior. Dive records were analyzed using Wildlife Computers software.

Means are followed by ± 1 S.D. Unless otherwise stated, differences between means were tested using a two-sample *t*-test and relations were tested by using least squares linear regression analysis.

3. Results

The mass, FMR, oxygen store, cADL and ratio of measured dive duration to predicted cADL of the three species are given in Tables 2–4. Antarctic fur seals dove well within the cADL. Typically, they dove to 80% of the cADL with only two (F-36, F-45) of fifteen animals exceeding the cADL and then by only 1.3 and 1.4 times (Table 2). In contrast, many individuals of both sea lion species exceeded the cADL, some by significant amounts. Australian sea lions typically dove 1.4 times longer than the cADL, with four females,

S-51, S-139, S-C2, S-141 making dives close to the cADL, while seven, W-P, W-14, W-C2, W-AD, S-AD, S-102 and S-138 made dives ranging from 1.4 to 1.9 times longer (Table 3). New Zealand sea lions, on average, dove 1.5 times longer than the cADL, with four, E-41, E-52, E-55, and E-59 making dives close to the predicted ADL, while seven others E-40, E-42, E-43, E-53, E-56, E-58 and E-61 routinely exceeded their predicted ADL, and one (E-40) by 2.6 times!

The tendency to exceed the cADL was correlated with the dive pattern of individual animals. In Antarctic Fur Seals, deeper diving females made longer dives that approached or exceeded the cADL ($P < 0.01$, $r^2 = 0.54$) (Fig. 3). Similarly, deeper diving Australian sea lions were also more likely to exceed the cADL (Fig. 4). Australian sea lion females with longer bottom times also exceeded the cADL (Fig. 4). New Zealand sea lions showed a slightly different pattern. Individuals that made dives with long bottom times also exceeded their cADL ($r^2 = 0.59$, $P < 0.01$) (Fig. 5). However, there was no relationship between the depth of dive and cADL ($r^2 = 0.08$, $P = 0.5$).

4. Discussion

Our data support the hypothesis that there is significant inter- and intra-specific variation in the

Table 3

Mass, FMR, oxygen stores, calculated aerobic dive limit (cADL) mean dive duration, mean surface interval and the ratio of measured mean dive duration to cADL for individual Australian sea lions are presented

Animal	Mass (kg)	FMR ^a (O ₂ ml min ⁻¹)	O ₂ stores (O ₂ ml)	cADL	Dive ^a duration (min)	Surface interval (min)	Dive ^a duration (cADL)
W ^c -P	89.8 ^b	1987 ^b	4218 ^b	2.12 ^b	4.1 ^b	1.3 ^b	1.9 ^b
W ^c -14	93.9 ^b	2113 ^b	4411 ^b	2.09 ^b	3.2 ^b	1.3 ^b	1.6 ^b
W ^c -C2	66.9 ^b	1581 ^b	3144 ^b	1.99 ^b	3.0 ^b	1.5 ^b	1.5 ^b
W ^c -AD	94.4 ^b	1942 ^b	4434 ^b	2.28 ^b	3.3 ^b	1.7 ^b	1.5 ^b
S ^d -AD	89.0 ^b	1870 ^b	4183 ^b	2.24 ^b	3.9 ^b	1.6 ^b	1.8 ^b
S ^d -102	64.0 ^b	1569 ^b	3008 ^b	1.92 ^b	3.1 ^b	1.1 ^b	1.6 ^b
S ^d -138	59.8 ^b	1345 ^b	2811 ^b	2.09 ^b	2.8 ^b	1.4 ^b	1.4 ^b
S ^d -51	66.4	1213	3121	2.57	3.1	1.0	1.2
S ^d -139	81.6	1383	3835	2.77	2.9	1.0	1.1
S ^d -C2	76.3	1327	3584	2.70	2.8	1.2	1.0
S ^d -141	73.8	1159	3466	2.99	2.2	1.9	0.7
Mean (S.D.)	77.8 (12.6)	1590 (337)	3656 (594)	2.34 (0.36)	3.1 (0.5)	1.4 (0.3)	1.4 (0.4)

^aData from Costa and Gales (in review).

^bMean dive durations greater than 1.3 times the cADL.

^cAnimals studied during the winter of 1989.

^dAnimals studied during the summer of 1991.

Table 4

Mass, FMR, oxygen stores, calculated aerobic dive limit (cADL), mean dive duration, mean surface interval and the ratio of measured mean dive duration to cADL for individual New Zealand sea lions are presented

Animal	Mass (kg)	FMR ^a (O ₂ ml min ⁻¹)	O ₂ stores (O ₂ ml)	cADL	Dive ^a duration (min)	Surface interval (min)	Dive ^a duration (cADL)
E-40 ^b	84.4 ^b	2394 ^b	4001 ^b	1.7 ^b	4.3 ^b	3.2 ^b	2.6 ^b
E-41	109.6	2035	5186	2.5	3.0	4.6	1.2
E-42 ^b	106.7 ^b	2315 ^b	5058 ^b	2.2 ^b	3.0 ^b	3.5 ^b	1.4 ^b
E-43 ^b	123.9 ^b	2510 ^b	5870 ^b	2.3 ^b	4.0 ^b	2.7 ^b	1.7 ^b
E-52	105.5	2236	5001	2.2	2.6	2.5	1.2
E-53 ^b	119.8 ^b	2373 ^b	5679 ^b	2.4 ^b	3.3 ^b	2.6 ^b	1.4 ^b
E-55	109.3	2193	5181	2.4	2.6	3.3	1.1
E-56 ^b	109.4 ^b	1907 ^b	5186 ^b	2.7 ^b	4.1 ^b	6.3 ^b	1.5 ^b
E-58 ^b	118.9 ^b	2290 ^b	5636 ^b	2.5 ^b	3.5 ^b	9.8 ^b	1.4 ^b
E-59	154.8	2644	7338	2.8	3.4	8.6	1.2
E-61 ^b	93.6 ^b	2199 ^b	4437 ^b	2.0 ^b	3.8 ^b	3.9 ^b	1.9 ^b
Mean	112.4	2281	5325	2.3	3.4	4.6	1.5
(S.D.)	(18.1)	(206)	(857)	(0.3)	(0.6)	(2.5)	(0.4)

^a Dive and FMR are data from Costa et al. (2000).

^b Mean dive durations greater than 1.3 times the cADL.

tendency of otariids to reach their maximum physiological capability. The different responses of the three species correlate with their very different diving patterns and foraging ecologies (Fig. 2). These species represent the extremes of

diving behavior found in the family Otariidae. At least at South Georgia and Livingston Islands, Antarctic fur seals make short (mode = 0.9 min, max = 2.8–10 min) shallow dives (19 m) that are typically V-shaped with no bottom time. These

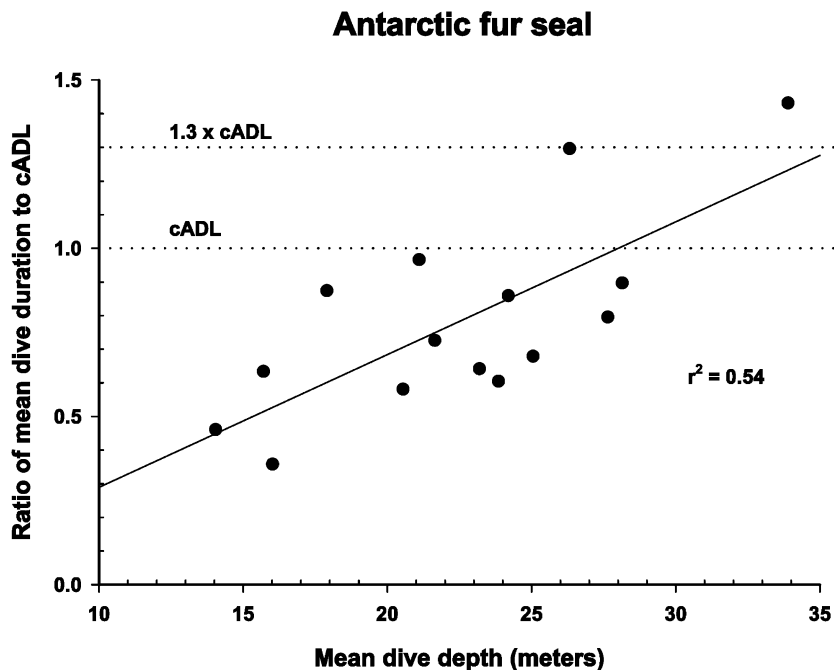


Fig. 3. The ratio of calculated aerobic dive limit (cADL) is plotted as a function of the mean dive depth for 15 individual Antarctic fur seals. Data on cADL and dive duration are matched data from each individual animal. The horizontal dotted lines show the cADL and $1.3 \times$ cADL, to compensate for the 30% underestimate of actual ADL when using the DLW method to estimate diving metabolic rate (Ponganis et al., 1997c).

Australian sea lion

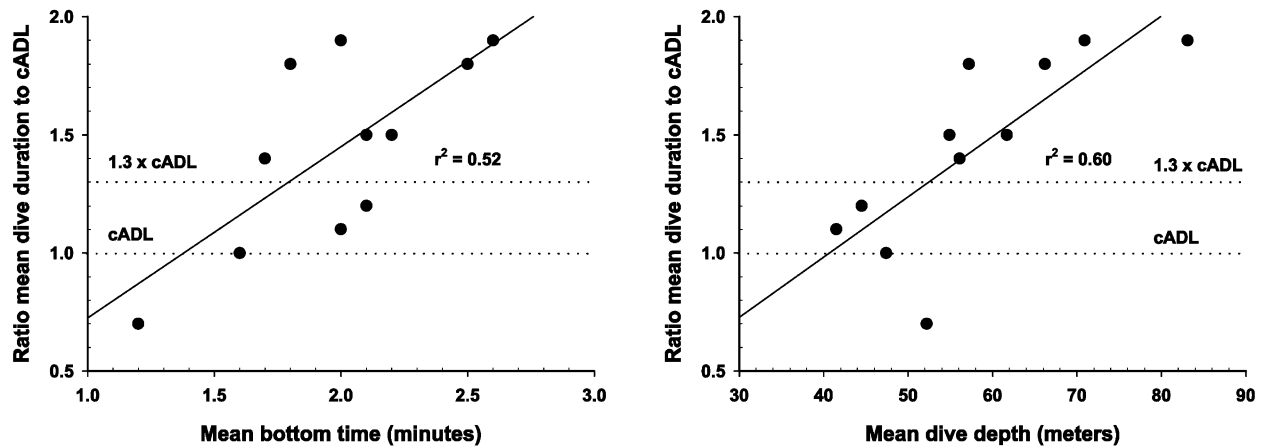


Fig. 4. The ratio of calculated aerobic dive limit (cADL) is plotted as a function of the mean dive depth and mean bottom time for 11 individual Australian sea lions. Data on cADL, dive duration and bottom time are matched data from each individual animal. The horizontal dotted lines show the cADL and $1.3 \times \text{cADL}$ to compensate for the 30% underestimate of actual ADL when using the DLW method to estimate diving metabolic rate (Ponganis et al., 1997c).

animals prey predominately at or near the surface on krill, and to a lesser degree fish and squid (Boyd and Croxall, 1992; Reid and Arnould, 1996; Goebel et al., 2000) and spend considerable time surface swimming between prey patches (Boyd et al., 1995b). In contrast, both Australian and New Zealand sea lions feed predominately on the ben-

thos and spend most of their time at sea diving (Gales and Costa, 1997; Gales and Mattlin, 1997). Lactating Australian sea lions average dives to 61 m, with an average maximum depth of 86 m. Their dives average 3.4 min with a maximum recorded duration of 8.3 min (Gales and Costa, 1997). The highly benthic nature of their diving is

New Zealand sea lion

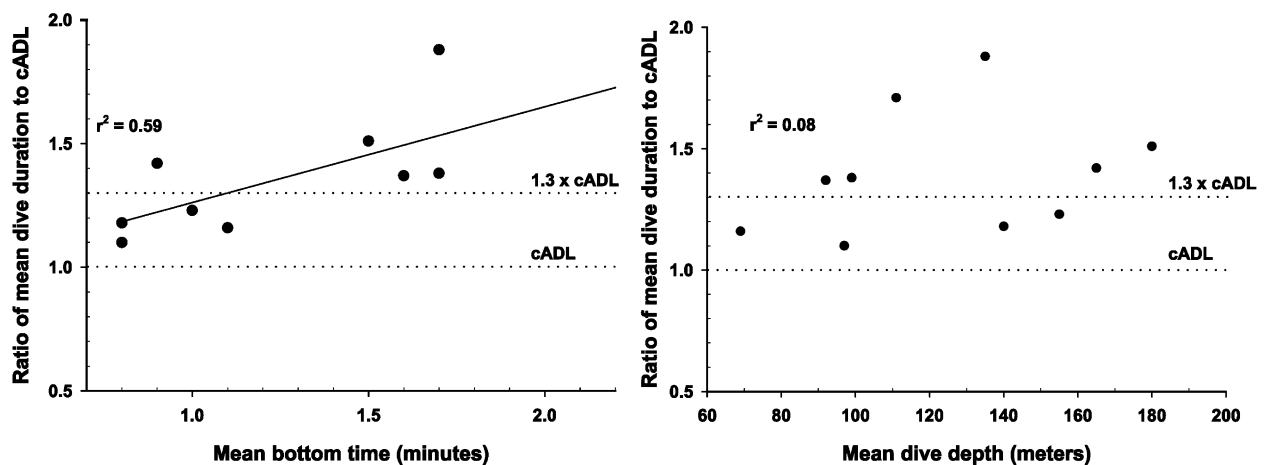


Fig. 5. The ratio of calculated aerobic dive limit (cADL) is plotted as a function of the mean dive depth and mean bottom time for 11 individual New Zealand sea lions. Data on cADL, dive duration and bottom time are matched data from each individual animal. The horizontal dotted lines show the cADL and $1.3 \times \text{cADL}$ to compensate for the 30% underestimate of actual ADL when using the DLW method to estimate diving metabolic rate (Ponganis et al., 1997c).

demonstrated by the fact that 60% of their time is spent on the bottom portion of a dive. Lactating New Zealand sea lions have been reported to be the deepest and longest diving otariid (Gales and Mattlin, 1997). They typically dive for 3.9 min (median = 4.3) and routinely attain depths of 123 m with a maximum depth of 474 m. Some females routinely dive to depths of 187 m with mean dive durations of 4.7 min. This diving pattern is characterized by almost continual dives, most of which are to the benthos, where 39% of their time underwater is spent.

The three species show three different foraging patterns with respect to the tendency to exceed the cADL. The first and simplest is that employed by the Antarctic fur seal, where as a group they normally dove to only 80% of their cADL. Given the pattern described in Fig. 1, Antarctic fur seals would follow line 1 in taxonomic group A. In this case, the primary determinant of the foraging behavior is the optimal solution to finding multiple small prey and not the aerobic dive limit. This is in marked contrast to the sea lions that routinely (Australian sea lion 1.4 times and New Zealand sea lion 1.5 times) exceeded the cADL. The sea lions would appear to follow the pattern described by line 4 taxonomic group C in Fig. 1. In this case physiological capacity is an important determinant of behavior, and plays an important role in the solution to foraging optimally.

Even though the cADL is rarely exceeded in Antarctic fur seals, the range of performance of individual animals followed a significant pattern where some individuals operated closer to their aerobic limit than others (Fig. 3). Deeper diving animals worked closer to their aerobic limit than shallow divers. Although, Australian sea lions routinely operated at or above their aerobic limit they also showed a similar pattern that deeper diving individuals exceeded their cADL to a greater extent than shallower diving individuals (Fig. 4). New Zealand sea lions differed from the other two, in that there was no relationship between mean depth dive and cADL, but a significant correlation between bottom time and the tendency to exceed the cADL (Fig. 5).

The major difference between the sea lions and the fur seal was that the sea lions were diving to the benthos. Benthic diving increases the total amount of time an animal must remain submerged (Fig. 2). Unlike a V-shaped bounce dive the animal must not only get to the maximum

depth, but also must have time to search for prey at the bottom of a dive. The deeper the dive, the longer the time spent in transit with proportionately less time available to search for prey (Costa and Williams, 1999). This relationship probably accounts for the difference between Australian and New Zealand sea lions. New Zealand sea lions on average, dive to twice the depth of Australian sea lions and, as such, proportionately more of their dives are spent in transit (61% in NZSL compared to 40% in ASL). The greater dive depth of New Zealand sea lions appears to limit their options and they adjust their diving physiology in order to maximize bottom time.

Other workers have also reported a tendency for benthic divers to exceed the ADL. Blue-eyed shags, *Phalacrocorax atriceps*, feeding on fish and invertebrates on or near the benthos routinely exceed the ADL and most likely rely on a significant component of anaerobic metabolism (Croxall et al., 1991). Australian fur seals, *Arctocephalus pusillus doriferus*, have recently been shown to forage to the benthos in a manner similar to Australian sea lions, with mean dive durations of 2.9 min and mean depths of 58 m (Arnould and Hindell, 2000). Using a conservative estimate of ADL for otariids derived by Gentry et al. (1986), it was estimated that Australian fur seals exceeded the ADL on at least 17% of their dives. This is comparison to the conspecific South African fur seal, *A. p. pusillus*, that feeds shallow in mid-water and only exceeded a similarly estimated ADL on 3.4% of the dives. Northern fur seals, *Callorhinus ursinus*, exhibit both shallow short and long deep dives (Gentry et al., 1986). Long surface durations associated with deep dives (mean = 120 m, 3 min) compared to shallow dives (mean = 30 m, 1.2 min) in Northern fur seals coupled with swim velocity data, led (Ponganis et al., 1992) to conclude that deep dives involve a significant component of anaerobic metabolism. Furthermore, deep divers only spent 11 min/h diving compared to 27 min/h for shallow divers. In northern fur seals, deep dives are associated with feeding at or near the benthos (Loughlin et al., 1987).

Whereas Australian and New Zealand sea lions appear to exceed their ADLs, this does not appear to be the case in California sea lions. Although California sea lions dive as deep as 274 m and stay submerged for up to 9.9 min, the majority of their dives are less than 3 min in dura-

tion and 80 m in depth. An ADL of 2.3 min was measured in 40-kg juvenile, California sea lions (Ponganis et al., 1997c). Using a scaling factor of $\text{Mass}^{0.25}$ yields an ADL of 2.7 min for adult California sea lion females (80 kg). California sea lions feed on mid-water fish and squids, and typically do not have a bottom component (Antonelis et al., 1983; Feldkamp et al., 1989). Although we do not have concurrently collected data on metabolic rate and diving behavior, it is likely that these animals routinely dive within their ADL.

Among diving birds and mammals, it appears that deep diving is limited to the pursuit of large prey where only a few are required per dive. In contrast, the pursuit of many small prey is limited to the shallow end of the divers capability (Costa, 1991a). Unfortunately, the information of the diet of New Zealand and Australian sea lions are limited, but the information we have suggests that they prey on relatively large prey such as octopus and large arrow tooth squids (Gales and Cheal, 1992; Gales and Fletcher, 1999). These are relatively large prey and once spotted, are probably worth pursuing well beyond the ADL.

The number of sea lions that routinely exceeded cADL makes one wonder about the efficacy of calculating ADL is this way. Our approach is supported by work on California sea lions (Ponganis et al., 1997c). Aerobic thresholds were measured in freely-diving trained sea lions. They found an increase in the formation of lactic acid that corresponded with dives lasting greater than 2.3 min. The predicted ADL of these animals was based on similar estimates of body oxygen stores coupled with FMRs derived from doubly-labeled water measurements on wild adult female California sea lions (Costa et al., 1990). ADLs calculated in this way yielded cADLs of between 1.8 and 2.0 min, whereas ADLs calculated from metabolic rates estimated from flume studies yielded much longer cADLs of 3–3.5 min. Although, ADLs estimated from FMR data derived from double-labeled water underestimated the actual ADL of these animals, it was far closer than metabolic rates estimated in other ways. Given that cADLs were only 1.2–1.3 times greater, we feel that our calculations of ADL presented here (Tables 2–4) are quite reasonable. This lends support to the conclusion that all of the fur seals and some of the sea lions dove aerobically, while

none of the fur seals and many of the sea lions routinely dove beyond their ADL. It is likely that these individuals included some proportion of anaerobic metabolism while diving. Regardless, it is safe to conclude that New Zealand and Australian sea lions routinely push or exceed their aerobic dive limit, while Antarctic fur seals do not.

Such measurements are not just of academic interest, but have relevance to wildlife managers as well. For example, it is important to know whether a species in decline is operating at or close to, its maximum physiological capacity. This is because if it is, it will be less capable of compensating to normal environmental or human-made fluctuations in food availability or other changes in its environment. In contrast, an animal that is operating well within its physiological capacity will be more capable of responding to environmental fluctuations (Boyd, 1999; Boyd et al., 1994). Such animals would be able to draw on a greater physiological reserve to pursue prey deeper, dive longer or forage for greater periods (Boyd et al., 1994). From this perspective, it is important to note that both New Zealand and Australian sea lions are endemic species with the lowest populations of any sea lion and probably of any otariid (Gales and Fletcher, 1999; Gales et al., 1994). In contrast, Antarctic fur seals and California sea lions, two species that operate well within their cADLs, have populations that are large and expanding (Boyd et al., 1995a; Sydeman and Allen, 1999).

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