

When does physiology limit the foraging behaviour of freely diving mammals?

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Abstract. Diving animals offer a unique opportunity to study the importance of physiological constraint and the limitation it can impose on animal's behaviour in nature. This paper examines the interaction between physiology and behaviour and its impact on the diving capability of five eared seal species (Family Otariidae; three sea lions and two fur seals). An important physiological component of diving marine mammals is the aerobic dive limit (ADL). The ADL of these five seal species was estimated from measurements of their total body oxygen stores, coupled with estimates of their metabolic rate while diving. The tendency of each species to exceed its calculated ADL was compared relative to its diving behaviour. Overall, our analyses reveal that seals which forage benthically (i.e. on the sea floor) have a greater tendency to approach or exceed their ADL compared to seals that forage epipelagically (i.e. near the sea surface). Furthermore, the marked differences in foraging behaviour and physiology appear to be coupled with a species demography. For example, benthic foraging species have smaller populations and lower growth rates compared to seal species that forage epipelagically. These patterns are relevant to the conservation and management of diving vertebrates. © 2004 Published by Elsevier B.V.

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1. Introduction

While comparative physiology documents the range of physiological variation across organisms, field physiology provides insight into the homeostatic mechanisms that animals

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actually employ in nature. In addition, understanding an animal's natural history is a prerequisite for designing meaningful field investigations that integrate physiology with behaviour and ecology [1]. In this context, pinnipeds (seals and sea lions) provide a unique system to study the role of physiology and its impact or constraint on the foraging ecology and behaviour of diving vertebrates. Pinnipeds are tractable study organisms because they have an amphibious life style so they can be captured on shore multiple times to deploy and recover instrumentation to study their behaviour at sea as well as to collect measurements for physiological evaluation [2–4]. Consequently, there is a reasonable understanding of the basic physiological processes that occur when animals dive. We know that the ultimate constraint on diving ability is determined by an animal's physiological performance. However, within these limits, the range of diving behaviour is determined by ecological factors such as the distribution, abundance, depth, and energy content of prey [5]. Technological developments over the last two decades have significantly increased our ability to study the behaviour of diving animals in nature [6–8]. These studies as well as many others have recorded a wide range of behavioural patterns, and have implicated physiology as a limiting or enabling feature of a species performance [3,6,7,9,10].

The diving capability of a marine mammal is determined by its available oxygen and fuel stores and the rate they are consumed by metabolic processes [6]. The quantity of oxygen and metabolic fuels stored in tissues can differ substantially among marine mammals, but their consumption occurs via aerobic or anaerobic pathways [6]. The time required to consume fuels aerobically while diving is thought to be the major determinant of diving performance [3,4,6,7,10]. Hence, the aerobic dive limit (ADL) has been experimentally defined as the dive duration beyond which blood lactate levels increase above resting levels due to anaerobic metabolism [3]. When Weddell seals (*Leptonychotes weddelli*) exceed the aerobic threshold, the post-dive surface interval increases disproportionately faster than dive duration [3,11]. An increased surface interval is required to clear lactic acid accumulated during the previous dive. One of the disadvantages of exceeding the ADL is that, while a diver may increase the duration of a single dive, the total accumulated time spent underwater in a bout of dives is reduced because more time at the surface is required to clear lactic acid. Although the relationship between physiology and behaviour is fairly well documented for Weddell seals, the relationship is far less clear among other pinniped species.

In this paper, we extend our earlier examination [12] of this relationship between aerobic dive limit and foraging behaviour to include new information on other species of otariids (i.e. eared seals). More importantly, we review our analyses in light of both ecological and demographic implications. In total, our analyses include data for five otariid species that represent the extremes of diving behaviours reported for otariids. The Antarctic fur seal (*Arctocephalus gazella*) makes short shallow dives, while the Australian (*Neophoca cinerea*) and New Zealand (*Phocarctos hookeri*) sea lions and the Australian fur seal (*A. pusillus doriferus*) make deep prolonged dives to the benthos [13–17]. We also include data from California sea lions (*Zalophus californianus*) foraging off the California coast where they dive epipelagically [18], and from the Sea of Cortez where they forage quite deep on mesopelagic prey [Kuhn, Aurioles-Gamboa, Costa unpublished]. Like our earlier study [12], we compare the differences in diving behaviour and calculated aerobic dive limit (cADL) between individual animals. In this way, we elucidate intra- and inter-

specific variation in the tendency of individuals to reach or exceed their cADLs and, thus, gain insight into the diving performance of free-ranging animals in nature.

2. Methods and materials

Individual specific cADL for adult females of 11 Australian sea lions, 11 New Zealand sea lions, 10 California sea lions, 9 Australian fur seals and 15 Antarctic fur seals were determined by dividing each animal's total available oxygen stores by its specific diving metabolic rate (DMR). DMR was assumed to be equivalent to the at-sea field metabolic rate (FMR), which can be measured by oxygen-18 doubly labelled water [19]. It is important to note that at-sea FMR integrates the costs of highly variable surface swimming, diving and resting. Therefore, true DMR could be higher or lower. Nevertheless, DMR estimated in our analyses should reflect relative differences in metabolic effort between individuals. Furthermore, no measures of blood lactate were collected to confirm the true ADL of our study animals so we refer to our estimates as cADL.

The total available oxygen store of each animal was calculated following methods described elsewhere [20,21] with the incorporation of data on blood volume [22] [Weise, Arnould, Shaffer and Costa unpublished data] and muscle myoglobin [23], [Costa, Gales, Weise, Arnould, Shaffer, Crocker and Burns, unpublished data] content for each species (Table 1).

The data on diving behaviour of Antarctic and Australian fur seals, and Australian and New Zealand sea lions were taken from published reports on each species [14–17]. Information on the diving behaviour of California sea lions comes from recently acquired unpublished data from six females at San Nicolas Island, Channel Islands, California, and from four females at Los Islotes Island, Bay of La Paz, Baja California [Kuhn, Auriolles-Gamboa, and Costa unpublished data]. Measurements of metabolic rate and diving behaviour for Australian and New Zealand sea lion, and Antarctic fur seals were collected concurrently on the same individuals [14–16]. DMR of California sea lions were obtained from previously published FMR data [5] and DMR for Australian fur seals were derived from FMRs acquired on Antarctic fur seals normalized for differences in body mass [24].

Table 1
The summary of parameters used to determine cADL of otariids

Species	Mass (kg)	Diving behaviour		O ₂ stores (ml O ₂ kg ⁻¹)	FMR (kJ kg ⁻¹ min ⁻¹)	cADL (min)
		Depth (m)	Duration (min)			
<i>Epi/Mesopelagic</i>						
Antarctic fur seal	41.8	23	1.16	38.1	29.6	1.6
California sea lion	85.3	42.2	1.93	42.7	15.6	2.7
<i>Mesopelagic</i>						
California sea lion	102.0	125	4.18	58.6	15.6	3.8
<i>Benthic</i>						
Australian fur seal	77.7	64	3.20	49.9	29.6	1.7
Australian sea lion	79.2	59	3.21	41.9	22.0	2.3
New Zealand sea lion	112.5	124	3.40	45.7	20.2	2.3

3. Results

The results show that oxygen storage capacity differs between each species of otariid (Table 1). As oxygen storage capacity increases among species, there is a significant increase in dive duration (Fig. 1). Concomitantly, all five species exhibit differences in their tendency to exceed the cADL according to their foraging mode (Fig. 2). That is, otariid species that forage benthically appear to operate well above the cADL whereas the species that forage epipelagically appear to operate well within the cADL. Furthermore, our data not only support this general pattern but also they shows that diving performance varies within a species, reflecting the different environments that these animals forage within. For example, California sea lions foraging off the Southern California coast (i.e. San Nicolas Island) routinely make relatively short shallow (epipelagic) dives and forage on surface prey [25], whereas sea lions foraging off Los Islotes consistently make deeper, longer dives to feed on mesopelagic prey (Fig. 2 and Ref. [26]).

4. Discussion

Our data support the hypothesis that there is significant inter- and intra-specific variation in the tendency of otariids to reach their maximum physiological capability while diving. Interestingly, the different responses of the five species relate more to their very different diving patterns and foraging ecologies than their phylogenies (i.e. fur seals versus sea lions; Fig. 2). Our data exemplify the pattern that benthic hunters maximize the time they spend at the benthos (Fig. 3). When foraging in deep water, benthic hunters may operate at levels closer to their maximum physiological capacity than epipelagic foragers. Unlike epipelagic or near-surface feeders, benthic foragers must have enough oxygen to get to the bottom of a dive as well as to search for prey once there. The deeper the dive, the longer the time spent in transit with proportionately less time available to search for prey [27].

Animals that operate at or near their maximum physiological performance are less likely to have the capacity to increase their foraging effort in response to reductions in

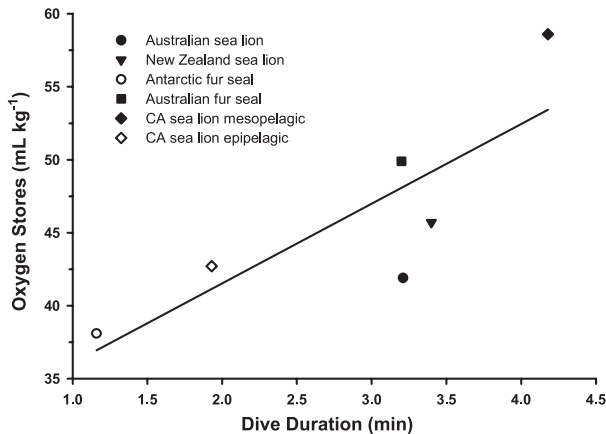


Fig. 1. Relationship between oxygen storage capacity and dive duration in five species of otariids. Open symbols are for epipelagic (near surface) foragers and solid symbols for benthic or mesopelagic foragers. $R^2=0.68$.

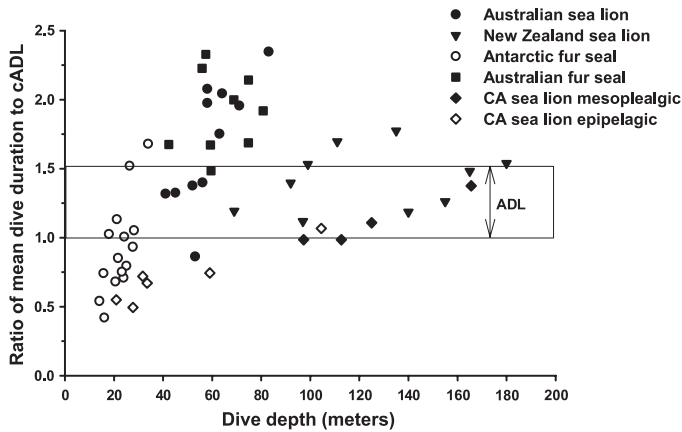


Fig. 2. Dive performance defined as the ratio between average dive duration and the predicted aerobic dive limit as a function of dive depth in five pinnipeds species. Open symbols are for epipelagic (near surface) foragers and solid symbols for benthic or mesopelagic foragers. Range of cADL outlined by the box is the cADL plus 50% to account for the variability in FMR estimates.

food availability whether due to environmental changes, fishery related activities, or both. However benthic prey are a more predictable resource that are less influenced by oceanographic perturbations such as El Niños compared to epipelagic prey. Animals that operate within their physiological capacity would be able to draw upon a greater energy reserve to pursue prey at deeper depths. Moreover, they could dive longer than normal if need be, or forage for longer periods, to accommodate the variability in prey resources [12,16].

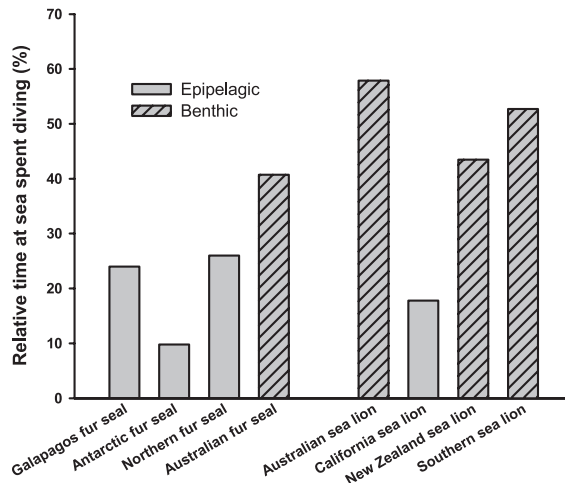


Fig. 3. The relative time spent diving while at sea compared across otariid species. Data for Galapagos fur seals (*Arctocephalus galapagoensis*) are from Ref. [28]; data for Northern fur seals (*Callorhinus ursinus*) are from Ref. [29], data for California sea lions are from Ref. [18]; and data for Southern sea lion (*Otaria flavescens*) are from Ref. [30].

Table 2

Pinniped population numbers and trends for epipelagic, mesopelagic, and benthic foraging species (see Ref. [34] for review)

Common name	Species	Population size	Trend
<i>Epi/Mesopelagic</i>			
Antarctic fur seal	<i>Arctocephalus gazella</i>	1,600,000	increasing
California sea lion	<i>Zalophus californianus</i>	237,000–244,000	increasing
Cape fur seal	<i>A. pusillus pusillus</i>	1,700,000	increasing
Subantarctic fur seal	<i>A. tropicalis</i>	>310,000	increasing
<i>Benthic</i>			
Australian sea lion	<i>Neophoca cinerea</i>	9300–11,700	stable or increasing
Australian fur seal	<i>A. pusillus doriferus</i>	60,000	slowly increasing
New Zealand sea lion	<i>Phocarctos hookeri</i>	13,000	stable
South American sea lion	<i>Otaria flavescens</i>	275,000	decreasing
Steller sea lion	<i>Eumatopias jubatus</i>	<75,000	decreasing ^a

^a Stock specific.

Other data on diving behavior further this argument. Benthic foragers, whether fur seal or sea lion, expend more effort foraging by spending >40% of their time at sea underwater compared to epipelagic species that spend <30% of their time at sea underwater (Fig. 3). These findings may explain why many fur seal species (and the epipelagic foraging California sea lion) have experienced substantial population growth. In contrast, all the sea lion species that feed on or near the sea bottom (e.g. Steller, *Eumatopias jubatus*; Australian; southern, *Otaria byronia*; and New Zealand sea lion) and the Australian fur seal (a benthic forager), have stable or declining populations [31–33], and (Table 2) despite the fact that many sympatrically breed with near-surface feeding fur seals [16].

A further compounding dilemma for benthic foragers is the possibility that juvenile animals may experience lower survival than adults. Given that adults operate at or near their physiological limit, juveniles who have less physiological capabilities than adults due to their small body size and inexperience would have an even harder time foraging benthically. If correct, juvenile survival would be reduced in these species and thus, decrease recruitment in the population. These patterns are relevant to the conservation and management of diving vertebrates.

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