

## REDUCTIONS IN OXYGEN CONSUMPTION DURING DIVES AND ESTIMATED SUBMERGENCE LIMITATIONS OF STELLER SEA LIONS (*EUMETOPIAS JUBATUS*)

GORDON D. HASTIE<sup>1</sup>

DAVID A. S. ROSEN

ANDREW W. TRITES

Marine Mammal Research Unit,  
Aquatic Ecosystems Research Laboratory,  
University of British Columbia,  
Vancouver, British Columbia V6T 1Z4, Canada  
E-mail: gdh10@st-andrews.ac.uk

### ABSTRACT

Accurate estimates of diving metabolic rate are central to assessing the energy needs of marine mammals. To circumvent some of the limitations inherent with conducting energy studies in both the wild and captivity, we measured diving oxygen consumption of two trained Steller sea lions (*Eumetopias jubatus*) in the open ocean. The animals dived to predetermined depths (5–30 m) for controlled periods of time (50–200 s). Rates of oxygen consumption were measured using open-circuit respirometry before and after each dive. Mean resting rates of oxygen consumption prior to the dives were 1.34 ( $\pm 0.18$ ) and 1.95 ( $\pm 0.19$ ) liter/min for individual sea lions. Mean rates of oxygen consumption during the dives were 0.71 ( $\pm 0.24$ ) and 1.10 ( $\pm 0.39$ ) liter/min, respectively. Overall, rates of oxygen consumption during dives were significantly lower (45% and 41%) than the corresponding rates measured before dives. These results provide the first estimates of diving oxygen consumption rate for Steller sea lions and show that this species can exhibit a marked decrease in oxygen consumption relative to surface rates while submerged. This has important consequences in the evaluation of physiological limitations associated with diving such as dive duration and subsequent interpretations of diving behavior in the wild.

Key words: diving metabolism, energy, diving physiology, ADL, otariid.

To exploit resources at depth, pinnipeds possess a suite of physiological mechanisms that increase the depths they can attain and maximize the time they can forage below the surface. A key potential constraint is the amount of time that an animal can

<sup>1</sup> Address for correspondence: Sea Mammal Research Unit, University of St. Andrews, Fife IV11 8LB, Scotland, UK.

utilize aerobic metabolism while underwater, known as the aerobic dive limit (ADL) (Kooyman *et al.* 1980).

Originally defined as the maximum breath-hold that can be supported by available oxygen reserves without a post-dive rise in plasma lactate levels (Kooyman *et al.* 1980), theoretical ADLs have been calculated from the animal's oxygen storage capacity and its rate of oxygen consumption. Therefore, information on diving oxygen consumption rate will not only allow predictions of the energy needs of individuals and populations (*e.g.*, Olesiuk 1993, Winship *et al.* 2002), but will also assist in understanding the physiological constraints (such as submergence limitations) that underlie foraging decisions (*e.g.*, Costa *et al.* 2001, Thompson and Fedak 2001) and the potential impacts of changes in prey distributions or types (*e.g.*, Winship *et al.* 2002).

Early studies of diving metabolism consisted of forced submersions with restrained laboratory harbor seals (*Phoca vitulina*) (*e.g.*, Scholander 1940), which showed that submerged animals dramatically reduced their metabolism and heart rate (by up to 90%) during the submersion period. More recently, a limited number of studies on wild animals (*e.g.*, Kooyman *et al.* 1973, 1980, 1983; Castellini *et al.* 1992; Williams *et al.* 2004), and with freely diving animals in captivity (*e.g.*, Gallivan 1981, Reed *et al.* 1994, Hurley and Costa 2001, Sparling and Fedak 2004), have provided a greater understanding of physiological responses during dives. Evidence from changes in heart rate (*e.g.*, Kooyman and Campbell 1972, Jones *et al.* 1973, Hill *et al.* 1987, Ponganis *et al.* 1997, Webb *et al.* 1998) and direct measurements of oxygen consumption (*e.g.*, Gallivan 1981, Castellini *et al.* 1992, Hurley and Costa 2001, Sparling and Fedak 2004) indicate that unrestrained pinnipeds also appear to exhibit pronounced reductions in metabolic rate during dives. These studies show that, although metabolic reductions are observed, these are generally less intense among freely diving pinnipeds compared to those observed in restrained subjects.

Metabolic changes for diving pinnipeds can also be highly dependent on dive behavior. A unique series of studies in the wild that have greatly furthered our understanding of the links between diving energy and behavior were carried out on Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica (*e.g.*, Kooyman *et al.* 1980, Castellini *et al.* 1992, Williams *et al.* 2004). In these previous studies, the diving metabolism of seals was measured using open-circuit respirometry on a dive-by-dive basis when the seals returned to breathe at the surface in discrete holes in the ice. As reported by Castellini *et al.* (1992) and Williams *et al.* (2004), diving Weddell seals exhibit diving oxygen consumption rates that are highly variable during relatively short dives (<23 min), with no evidence of reduced oxygen consumption rates, and it is only during longer dives that seals show consistent and potentially reduced (Williams *et al.* 2004) rates. These previous studies (*e.g.*, Kooyman *et al.* 1973, Kooyman *et al.* 1980, Gallivan 1981, Kooyman *et al.* 1983, Castellini *et al.* 1992, Reed *et al.* 1994, Hurley and Costa 2001, Sparling and Fedak 2004, Williams *et al.* 2004) highlight that the degree of metabolic response is likely to be highly variable among species, and it is clear that species-specific estimates of diving metabolic rates are required.

One reason for the paucity of information on diving metabolism of pinnipeds is the challenge of collecting these type of data. Although controlled experiments can be carried out in captivity, these are restricted by the physical constraints of a confined environment. In the wild, studies are generally limited to measuring average field metabolic rate (FMR) over a period of days or weeks (*e.g.*, Costa and Gales 2003) and are logistically challenging and often opportunistic in nature. One solution to overcoming these limitations is to combine the best aspects of both wild and captive

studies and use trained animals to carry out experimental trials in the open ocean. This has been employed in the past with success to study aspects of the diving physiology of California sea lions (*Zalophus californianus*) (e.g., Ponganis *et al.* 1997).

Our study measured diving oxygen consumption of Steller sea lions (*Eumetopias jubatus*) at the water surface and during dives using sea lions trained to freely dive to depth in the open ocean. We also examined the relationships between changes in metabolic rates during dives and dive depth and duration. Finally, we combined these data with existing information on oxygen storage capacity to estimate submergence duration limits for Steller sea lions.

## METHODS

### *Animals*

Two female Steller sea lions (F00BO; 4 yr of age, with a mean weight of 117.6 kg, and F97SI; 7 yr of age with a mean weight of 193.6 kg.) were used to measure oxygen consumption during dives. The animals had been brought into captivity as pups and had participated in numerous previous research studies. The sea lions were housed in a specially designed floating pen (Hastie *et al.* 2006) located in a coastal inlet in British Columbia, Canada. It allowed the sea lions access to seawater and provided a base for studies in the surrounding waters. The sea lions freely chose to cooperate with all data collection and were never restrained or confined during any of the trials. Research was conducted under University of British Columbia Animal Care Permit A04-0311.

### *Diving Oxygen Consumption*

All trials were performed in the morning, at least 16 h postprandial. Animals were weighed ( $\pm 0.1$  kg) and fitted with a webbing body harness, with a VHF transmitter (Advanced Telemetry Systems, Inc., Isanti, MN, USA) attached (used to locate the sea lion in the event of it leaving the trial area) prior to each daily trial. The lightweight harness (0.76 kg with transmitter) was designed to have minimal effect on the drag and biomechanics on the animals.

A floating respiratory chamber was deployed at the water surface next to the holding pen for dives up to 10-m depth. For deeper dives, the sea lions were transported in a specially designed 6.7-m boat from their holding pen to a dive trial area. A separate 6.7-m research boat carrying the respiratory equipment was anchored at the dive trial area 45 min prior to the arrival of the sea lion, with the respiratory chamber deployed from the bow. The respiratory chamber consisted of a 190-liter Plexiglas dome attached to a 1.5  $\times$  1.5-m floating base.

A light target system was positioned beneath the chamber at a predetermined depth. This consisted of (1) a small white sphere that each sea lion was trained to place its nose against, (2) an underwater light (Multi-Sea Lite P/N 710-040-601; Deep Sea Power and Light Inc., San Diego, CA, USA) with a diffuser filter over the front, and (3) an underwater camera (P/N 740-048-601; Deep Sea Power and Light, Inc.) that allowed the attendance and behavior of the sea lion at the target to be monitored from the surface.

Oxygen consumption at the surface was estimated using open-circuit gas respirometry (Kaufmann *et al.* 1989). Air was drawn through the respiratory chamber at a

constant rate of between 200 and 275 liter/min (depending on experimental dive duration) using a Sable Systems Mass Flow Kit 500H (Sable Systems International, Henderson, NV, USA). This system automatically corrected flow rates to standard temperature and pressure in a dry gas (STPD) despite variations in temperature and barometric pressure. A subsample of excurrent air was drawn through two columns of Drierite and two columns of soda lime to absorb moisture and  $\text{CO}_2$  from the air sample. Oxygen concentrations were continuously measured using a Sable Systems FC-1B Oxygen Analyzer. A data acquisition system recorded an average gas concentration from the analyzer every second. Instantaneous rates of oxygen consumption were estimated using the computation described by Bartholomew *et al.* (1981). This allowed us to correct for the damped response caused by the washout characteristics of the system and to calculate  $\text{O}_2$  depletion volumes.

At the start of each trial, the sea lions left the holding pen, entered the water (either directly or *via* the transport vessel), and remained calm and stationary with their head in the respiratory chamber. They stayed in the chamber for a minimum of 6 min (mean = 7.1, SD = 1.7, range = 6–13 min) to obtain a measure of pre-dive oxygen consumption rate. The mean oxygen consumption rate during the 3-min period prior to the dive was used to establish pre-dive oxygen consumption rate (Fig. 1). A short series of trials where each animal remained in the chamber for a period up to 15 min suggested that oxygen consumption generally reached a steady state and rarely varied significantly after a period of 3 min in the chamber, supporting our experimental approach in establishing the baseline rate. After establishing the baseline, the sea lion swam to depth (between 5 and 30 m) on command and remained

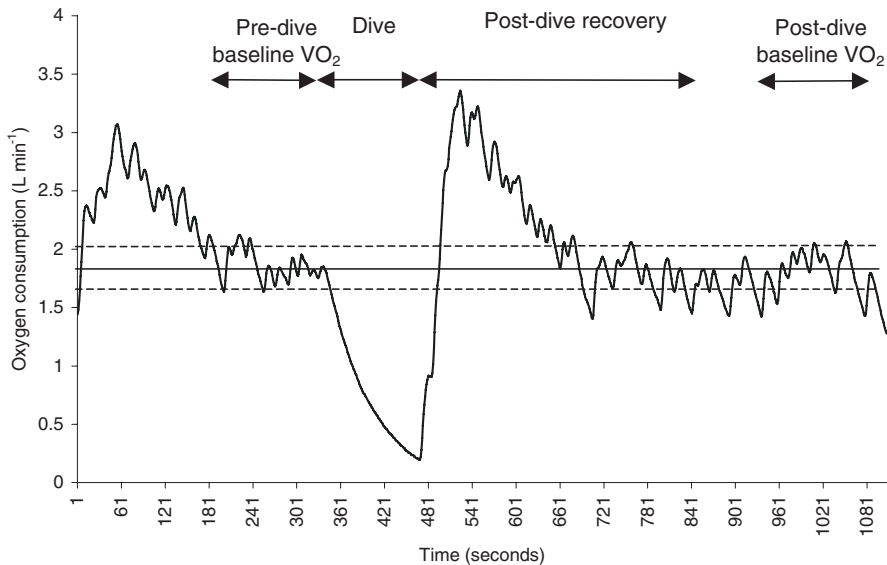


Figure 1. Example of the estimation of diving oxygen consumption rate during a single dive of 137 s to 10 m by sea lion F97SI. Oxygen consumption rate was estimated from the oxygen consumed during the recovery period in excess of the pre-dive baseline rate measured during that trial (pre-dive baseline rate shown by the solid line  $\pm$ SD). These were calculated as the total area under the curve of oxygen consumption *vs.* time. Instantaneous rates of oxygen consumption were estimated using the computation described by Bartholomew *et al.* (1981).

stationary at the target light for a predetermined duration (between 60 and 200 s). A total of thirteen trials were carried out with F00BO (durations between 65 and 176 s), and eighteen trials with F97SI (between 68 and 199 s). These durations were designed to represent a range of realistic dive durations carried out by wild sea lions (*e.g.*, Merrick and Loughlin 1997, Loughlin *et al.* 2003). The sea lion returned to the respiratory chamber at the surface when the light was extinguished, where post-dive oxygen consumption rate was measured (see below). We attempted to run training trials for the sea lions at each specific duration and depth for around 7–10 d prior to data collection.

The sea lions were occasionally fed small amounts of herring (maximum of 0.5 kg) during the trials to facilitate their cooperation. This small amount of food was unlikely to have affected the metabolic measurements due to the short duration of experimental trials (~20 min) in relation to the longer time course for the heat increment of feeding (Rosen and Trites 1997). We could not discount the possibility that our sea lions captured wild fish during the descent and ascent phases of dives. However, it seems unlikely that they would have encountered prey during the direct swim between the surface and depth, and prey captures observed during training periods were usually extremely overt.

The water temperature at the respiratory chamber and at the target light system was monitored during each trial using remote temperature loggers (Onset Computer Corp., Pocasset, MA, USA). Temperatures at the surface ranged from 6.5°C to 19°C, whereas temperatures at depth ranged from 7.6°C to 16.3°C.

Estimates of diving oxygen consumption rate were based on the method described by Castellini *et al.* (1992) and Hurley and Costa (2001). This was calculated as the total oxygen consumption during the post-dive recovery period in excess of the pre-dive baseline measured during that trial, divided by the total dive time (Fig. 1). The post-dive recovery period was defined as the time between the sea lion resurfacing after the dive and the time when oxygen concentrations reached less than 1 SD above the pre-dive baseline level. To ensure that all of the oxygen debt had been accounted for, the oxygen consumption rate over a 3-min period beyond this point was also included (Fig. 1).

To allow for more direct comparisons of surface and diving metabolic rates between this and other studies, we also calculated metabolic rates as a multiplier of Kleiber's prediction of basal metabolic rate for a similarly sized adult animal (Kleiber 1975) (*i.e.*, Metabolism (O<sub>2</sub> liter/min) = 28,944 × mass (kg)<sup>0.75</sup>).

To evaluate the influence of dive characteristics (dive depth and dive duration) on diving oxygen consumption rates, we analyzed the metabolic data for each animal in a generalized linear modeling framework. Selection and fitting of the models began by fitting each variable and its interaction terms to the null model, with the term that resulted in the greatest improvement in the model fit being selected for inclusion in the next step. At each successive step, the remaining variables were again tested individually for possible inclusion. *P*-values were calculated using a chi-squared approximation. Analyses were carried out using the SPLUS 2000 software package (Mathsoft, Inc., Needham, MA, USA).

### *Effects of Training*

The influence of training on oxygen consumption rates during dives was closely monitored throughout the experimental trials. Specifically, we evaluated whether

each sea lion changed its diving oxygen consumption rate as it gained experience in the intended dive duration or depth by examining variation in diving oxygen consumption rate for each sea lion across the period of experimental trials.

#### *ADL Estimates*

ADLs for each sea lion were calculated using the data on diving oxygen consumption together with estimates of their oxygen storage capacity. Oxygen storage capacity was assumed to be 38.8 mL O<sub>2</sub>/kg (Lenfant *et al.* 1970). This is similar to more recent estimates of oxygen storage capacity for California sea lions (40.0 mL O<sub>2</sub>/kg) (Ponganis *et al.* 1997). The theoretical ADL (Castellini *et al.* 1992) was calculated by dividing estimated total oxygen stores by diving oxygen consumption for each sea lion. Results include the range of ADL estimates (resulting from variation in diving oxygen consumption rates) and mean values ( $\pm$ SD) for each sea lion.

## RESULTS

#### *Oxygen Consumption at the Surface*

Mean rates of oxygen consumption during the pre-dive period were 1.34 ( $\pm$ 0.18) liter/min for F00BO and 1.95 ( $\pm$ 0.19) liter/min for F97SI (Table 1). Pre-dive rates were significantly higher for F97SI than for F00BO ( $t_{29} = 9.12$ ,  $P < 0.0001$ ), partly because of differences in body size (Table 1). There was no significant difference between pre-dive oxygen consumption rates and oxygen consumption rates measured during the final 3 min following the post-dive recovery period of each trial (F00BO;  $t_{12} = -1.4$ ,  $P = 0.18$ , F97SI;  $t_{18} = -0.96$ ,  $P = 0.35$ ).

Rates of post-dive oxygen consumption peaked within the first minute after resurfacing. Mean peak rates of oxygen consumption were 2.16 ( $\pm$ 0.13) liter/min for F00BO and 3.25 ( $\pm$ 0.63) liter/min for F97SI. Mean time for the post-dive oxygen consumption to decrease to within 1 SD of pre-dive rates was 101  $\pm$  30 s for F00BO and 140  $\pm$  38 s for F97SI.

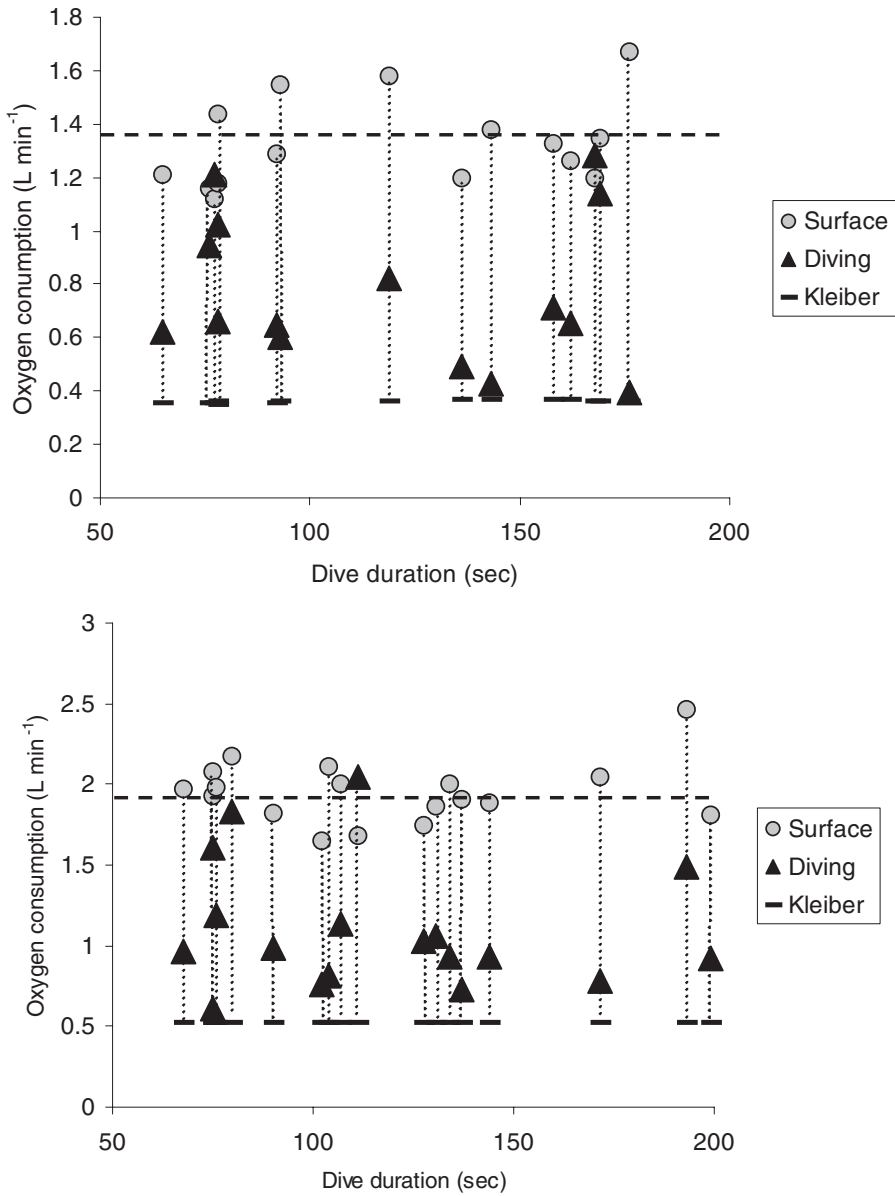
#### *Diving Oxygen Consumption*

Mean rates of oxygen consumption for diving sea lions were 0.71 ( $\pm$ 0.24) liter/min for F00BO and 1.10 ( $\pm$ 0.39) liter/min for F97SI (Table 1). Rates of oxygen consumption for diving sea lions were less than the pre-dive rates on 12 of 13 occasions for F00BO and on 17 of 18 for F97SI (Fig. 2). Overall, rates of oxygen consumption during dives were significantly less than the pre-dive rates (F00BO;  $t_{12} = 6.25$ ,  $P < 0.0001$ , F97SI;  $t_{17} = 8.57$ ,  $P < 0.0001$ ). Diving oxygen consumption rates varied from 122% to 30% of the respective pre-dive oxygen consumption rates, with a mean of 55% ( $\pm$ 24) for F00BO and 57% ( $\pm$ 21) for F97SI. Diving oxygen consumption rate was significantly higher for F97SI than for F00BO ( $t_{29} = -3.19$ ,  $P = 0.003$ ).

Dive duration ranged from 65 to 199 s and was not significantly different for each sea lion. The mean dive duration was 115 ( $\pm$ 39) s. The results of the generalized linear models for each sea lion suggested that neither of the dive characteristic variables (dive depth and dive duration) or their interactions were significant predictors of diving oxygen consumption (Table 2).

*Table 1.* Summary of oxygen consumption rates at the surface and during 31 dives for two Steller sea lions. Dive durations were between 65 and 200 s to depths between 5 and 30 m. All values of mass, and pre-dive and diving oxygen consumption rates are given in means ( $\pm$ SD). Rates of oxygen consumption are calculated in three ways for comparisons to other studies.

Sea lion	<i>n</i>	Mass (kg)	Pre-dive (liter/min)	Pre-dive (mL kg/min)	Pre-dive (Kleiber)	Diving (liter/min)	Diving (mL kg/min)	Diving (Kleiber)
F00BO	13	117.6	1.34 ( $\pm$ 0.18)	11.4 ( $\pm$ 1.5)	3.7 ( $\pm$ 0.47)	0.71 ( $\pm$ 0.24)	6.05 ( $\pm$ 2.08)	1.97 ( $\pm$ 0.67)
F97SI	18	193.6	1.95 ( $\pm$ 0.19)	10.08 ( $\pm$ 0.98)	3.71 ( $\pm$ 0.36)	1.10 ( $\pm$ 0.39)	5.68 ( $\pm$ 2.06)	2.09 ( $\pm$ 0.76)



*Figure 2.* Relationships between oxygen consumption and dive duration for F00BO (top) and F97SI (bottom). Each figure shows diving oxygen consumption, the corresponding values (shown by the vertical dashed lines) of pre-dive surface oxygen consumption, and Kleiber's prediction of basal metabolic rate for a similarly sized adult animal (Kleiber 1975). For comparison, the horizontal dashed line represents the rate of resting oxygen consumption measured for each of the experimental animals resting under standard conditions on land (University of British Columbia; unpublished data).



*Table 2.* Summary of the stepwise generalized linear models describing the influence of dive depth and dive duration on the diving oxygen consumption by two Steller sea lions. Terms include single variables and interactions between variables (denoted by  $\times$ ). *P*-values were calculated using a chi-squared approximation.

Animal	Model term	$\chi^2$	df	<i>P</i>
F00BO	Dive depth	0.03	1	0.86
	Dive duration	0.06	1	0.81
	Dive depth $\times$ Dive duration	0.53	3	0.91
F97SI	Dive depth	0.01	1	0.92
	Dive duration	0.24	1	0.62
	Dive depth $\times$ Dive duration	0.29	3	0.96

### *Effects of Training*

The relationship between diving oxygen consumption and time (in weeks from the start of each new intended duration or depth) was weak for each sea lion (F00BO;  $r^2 = 0.27$ ,  $P = 0.16$ , F97SI;  $r^2 = 0.13$ ,  $P < 0.3$ ) and was inconsistent between sea lions, with diving oxygen consumption rates generally increasing over time for F00BO and decreasing for F97SI (Fig. 3).

### *ADL Estimates*

Estimated theoretical ADL ranged from 3.7 to 11.6 min for F00BO and from 3.6 to 12.2 min for F97SI. The ranges reflect the variation observed in diving oxygen consumption during the trials. Mean theoretical ADL was 7.1 ( $\pm 2.4$ ) and 7.6 ( $\pm 2.3$ ) min for F00BO and F97SI, respectively.

## DISCUSSION

Our study provides the first estimates of diving oxygen consumption for Steller sea lions and shows that this species can exhibit a marked decrease in oxygen consumption while submerged. Furthermore, it is the first study to demonstrate such metabolic depression in an otariid while freely diving in the open ocean.

There are potential limitations with using captive animals to understand physiological processes of wild animals. For example, there may be differences in the physical condition of captive and wild animals. However, these differences are likely to be reduced in our study by the fact that the sea lions were diving in the open ocean for about a year before experimental trials were initiated. Another possible disparity is the potential for wild animals to predict their dive duration and depth before diving, and to adjust their metabolism accordingly (Wilson and Peters 1999). However, our animals were not naïve to the required dive parameters during individual trials because of the focused training they had on the specific parameters of experimental dives for a 7–10-d period before each new depth or duration. Furthermore, we did not observe any clear relationship between diving oxygen consumption and relative experience in dive duration.

It might be predicted that, during the pre-dive baseline period in the metabolic chamber, the sea lions anticipated the timing of dives and consequently prepared

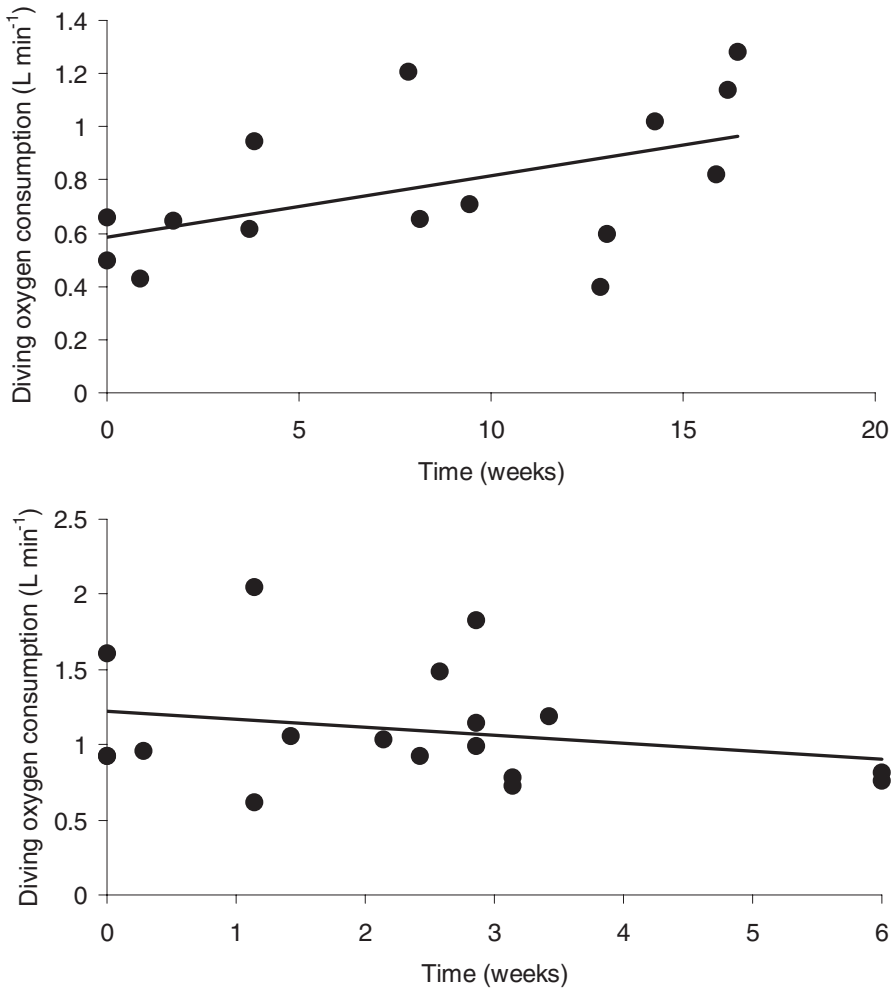


Figure 3. Relationships between diving oxygen consumption and relative experience in dive duration for each sea lion. No significant variation in oxygen consumption occurred over the course of trials at a particular dive duration for either F00BO (top:  $r^2 = 0.27$ ,  $P = 0.16$ ) or F97SI (bottom:  $r^2 = 0.13$ ,  $P = 0.3$ ).

themselves physiologically for the submergence (*e.g.*, Wilson *et al.* 2003). This may have manifested itself by an increase in metabolism in an effort to saturate tissues with oxygen and remove excess carbon dioxide, prior to the dive. However, our estimates of oxygen consumption during the pre-dive period were very similar to measurements of the two experimental animals resting under standard conditions on land (Fig. 2) and were similar to those measured during the final 3 min of the trial.

Despite these experimental caveats, our results clearly show that while submerged, Steller sea lions can reduce their rates of oxygen consumption relative to surface rates. Although this key feature of the classic “dive response” has been discussed for many

years, it is only relatively recently that researchers have been able to quantify it in freely diving animals (*e.g.*, Kooyman *et al.* 1973, Gallivan 1981, Castellini *et al.* 1992, Hurley and Costa 2001, Sparling and Fedak 2004, Williams *et al.* 2004). Although differing methods of data analyses can make direct comparisons of diving oxygen consumption between studies problematic, dive-by-dive measurements for other species generally support our findings. For example, mean diving oxygen consumption rates of 5.68 and 6.05 mL kg/min, and the mean percentage reductions of 45% and 41% we measured, are similar to the lower estimates of between 6 and 12 mL kg/min and 47%–65% in submerged California sea lions (Hurley and Costa 2001). Furthermore, when expressed as a multiplier of Kleiber, our mean estimates of 1.97 and 2.09 are also similar to submerged California sea lions (Hurley and Costa 2001) and are within the ranges of the estimates for diving phocids (*e.g.*, gray seals, *Halichoerus grypus*, [Sparling and Fedak 2004] and diving Weddell seals [Castellini *et al.* 1992]). However, as described theoretically (Davis and Kanatous 1999) and as observed in the wild (Castellini *et al.* 1992, Williams *et al.* 2004), during the majority of dives, Weddell seals do not appear to exhibit marked decreases in oxygen consumption, with rates being highly variable and mean values being similar to resting rates. Potential metabolic suppression only appears to be observed consistently during extended duration dives. This is similar to the patterns observed in California sea lions; oxygen consumption rates during short duration dives appeared similar to resting rates and only during long dives were potential metabolic changes observed (Hurley and Costa 2001). Despite small sample sizes, it is possible that our experimental animals exhibited this pattern of high variability in diving oxygen consumption rates during short dives and a more focused response during longer dives (Fig. 2).

Previous at-sea measures of FMR have suggested that otariids generally exhibit markedly higher foraging metabolic rates than phocids (up to around seven times the predicted basal rate of a terrestrial animal of equal size [Costa and Gales 2000]). This is markedly different from the results obtained in our study and suggests that otariids in the wild do not exhibit reductions in oxygen consumption during dives. However, such disparity potentially results from differences in diving characteristics of wild and trained animals, or from extended periods of surface activity (such as surface swimming) in wild animals. The latter is important when making direct comparisons between our study and previous otariid studies; it is possible that by using the long-term metabolic measure of FMR (estimated over periods of days rather than on a dive-by-dive basis), potential reductions in oxygen consumption are masked by elevated rates of oxygen consumption during extended periods of swimming at the surface. Conversely, otariids are highly mobile and, given that our animals were stationary at depth, potentially significant energy activities such as locomotion and capture and assimilation of prey (Williams *et al.* 2004) have not been accounted for in our study. Nevertheless, our study does illustrate that Steller sea lions appear to possess a degree of control in their metabolism that would potentially allow them to extend foraging durations underwater. In this respect, it seems reasonable to assume that Steller sea lions in the wild would also endeavor to prolong their time foraging by exhibiting such reductions in oxygen consumption.

Information on diving oxygen consumption rate allows the physiological limitations of diving to be better estimated. Specifically, direct measures of diving oxygen consumption, in combination with estimates of oxygen storage capacity (Lenfant *et al.* 1970), allowed us to estimate mean theoretical ADLs for each sea lion. Many studies of diving behavior have compared dive profiles of wild animals (specifically dive

duration) with estimated ADLs. In many such studies (for review, see Butler 2001) a substantial proportion of the recorded dives appear to exceed the ADLs. Using FMR to estimate metabolism, many recent studies of otariid metabolism have calculated ADLs (e.g., Costa *et al.* 2001, 2004). For example, ADLs of New Zealand sea lions (*Phocarctos hookeri*) were estimated to be between 1.7 and 2.8 min, and with mean dive durations of between 2.6 and 4.3 min, it was suggested that a large proportion of dives were beyond their aerobic limits (Costa and Gales 2000). Furthermore, Australian sea lions (*Neophoca cinerea*) appear to typically dive 1.4 times their calculated ADLs (Costa *et al.* 2001). In contrast, however, Antarctic fur seals (*Arctocephalus gazella*) appeared to rarely exceed their ADLs, with the mean dive durations being around 0.8 times their calculated aerobic limits (Costa *et al.* 2001).

Although some of this discrepancy might originate from anaerobic metabolism, it is more likely that either total oxygen stores are underestimated or diving metabolism is overestimated. For example, a recent study measured oxygen stores of 58.6 mL/kg for mesopelagic California sea lions (Costa *et al.* 2004), significantly higher than the 38 mL/kg measured by Lenfant *et al.* (1970). However, the latter is equally plausible, given that oxygen stores are likely to be over estimated because they assume that all potential oxygen stores are available during dives. As highlighted above, FMR is a measure that is averaged over periods of days rather than on a dive-by-dive basis. Therefore, potential reductions in oxygen consumption during dives may be masked by elevated rates of oxygen consumption during extended periods at the surface.

Although many studies have investigated the relationships between ADLs and diving strategies (e.g., Kooyman *et al.* 1983; Burns and Castellini 1996; Costa and Gales 2000; Costa *et al.* 2001, 2004), there remains the difficulty that the precise definitions and calculations of ADLs are often disparate among studies making direct comparisons difficult and potentially leading to incorrect conclusions. As highlighted by Hurley and Costa (2001), estimates of ADLs such as those in our study should perhaps be described as "maximum aerobic limits," as the animals are essentially stationary at depth. Our results suggest that only a small proportion of dives carried out by wild Steller sea lions are beyond their estimated maximum aerobic limits. However, as animals diving and foraging at sea potentially exhibit a far more active metabolic condition than those in our study, they are likely to have shorter ADLs. For example, if our experimental animals exhibited diving oxygen consumption rates similar to those at the surface, ADLs for each sea lion would have been estimated as 3.5 ( $\pm 0.4$ ) and 3.9 ( $\pm 0.4$ ) min for F00BO and F97SI, respectively. Given that the majority of dives by wild sea lions are still within these durations (Merrick and Loughlin 1997, Loughlin *et al.* 2003), it is conceivable that, like other species in the wild (e.g., Williams *et al.* 2004), little or no reduction in oxygen consumption is required during the majority of dives, and reductions occur only after they exceed a certain duration threshold.

Recent work suggests that there is a concise link between foraging ecology and the tendency to approach physiological limitations during dives; otariid species that forage epipelagically appear to dive within their ADLs and those that forage benthically or mesopelagically appear to consistently operate well beyond their ADLs (Costa *et al.* 2004). Given that Steller sea lions generally feed at or near the seabed, we might expect that they regularly approach or exceed their aerobic limitations in the wild. Such a foraging strategy is likely to benefit from increased aerobic efficiency and may be a factor in explaining why we observed decreases in oxygen consumption during dives (even during short duration dives). Furthermore, it highlights the fundamental links between foraging strategies and aerobic limitations in diving pinnipeds, and

illustrates that the physiology of each species is likely to consist of a unique suite of mechanisms that facilitate their different foraging strategies.

Although our study provides important insights into metabolic processes during a sea lion dive, further work is required to assess how diving behavior influences diving metabolism, and how the energy costs of diving by wild animals vary under a range of realistic diving scenarios. Unlike previous studies (*e.g.*, Castellini *et al.* 1992, Costa and Gales 2000, Sparling and Fedak 2004), we did not find any significant variation in diving oxygen consumption with either dive depth or duration. This may partly be a result of insufficient sample sizes and small effects sizes, and further research is clearly required to fully understand diving energy and the underlying determinants of variation observed in diving oxygen consumption rates.

In conclusion, our study has provided estimates of diving oxygen consumption rates for Steller sea lions and shows that this species can exhibit marked decreases in oxygen consumption while submerged. This has important consequences in the evaluation of physiological limitations such as ADLs and subsequent interpretations of diving behavior in the wild.

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