

METABOLIC RATES OF FREELY DIVING WEDDELL SEALS: CORRELATIONS WITH OXYGEN STORES, SWIM VELOCITY AND DIVING DURATION

By MICHAEL A. CASTELLINI*, GERALD L. KOOYMAN
AND PAUL J. PONGANIS

*Scripps Institution of Oceanography, Scholander Hall, University of California
San Diego, La Jolla, CA 92093, USA*

Accepted 30 December 1991

Summary

The metabolic rates of freely diving Weddell seals were measured using modern methods of on-line computer analysis coupled to oxygen consumption instrumentation. Oxygen consumption values were collected during sleep, resting periods while awake and during diving periods with the seals breathing at the surface of the water in an experimental sea-ice hole in Antarctica. Oxygen consumption during diving was not elevated over resting values but was statistically about 1.5 times greater than sleeping values. The metabolic rate of diving declined with increasing dive duration, but there was no significant difference between resting rates and rates in dives lasting up to 82 min. Swimming speed, measured with a microprocessor velocity recorder, was constant in each animal. Calculations of the aerobic dive limit of these seals were made from the oxygen consumption values and demonstrated that most dives were within this theoretical limit. The results indicate that the cost of diving is remarkably low in Weddell seals relative to other diving mammals and birds.

Introduction

To construct reasonable models of the metabolism and the physiological constraints on the behavior of freely diving marine mammals, estimates of accessible body oxygen stores are divided by estimates of diving metabolic rate; the resulting time is defined as the approximate aerobic diving limit (ADL) and the results compared with dive duration/lactate appearance curves (Kooyman *et al.* 1980, 1983). The calculation of body oxygen stores available for diving involves summing the oxygen capacity of various tissues and estimating the level of oxygen extraction from these stores during the dive. While body oxygen stores are relatively straightforward estimates, determining to what level the oxygen stores

* Present address for correspondence and for reprint requests: Institute of Marine Science, University of Alaska, Fairbanks, AK 99775, USA.

Key words: marine mammals, diving metabolism, seals, *Leptonychotes weddellii*, Antarctica.

are utilized during diving is complex and has only been achieved under artificial conditions of forced submersion in elephant seals (Elsner, 1969). It is even more difficult to estimate the metabolic rate in a freely diving seal and this value is usually extrapolated from exercise studies under non-field conditions or is taken from general relationships of mass vs metabolic rate.

Only one previous study has measured the oxygen consumption rates of seals diving under natural conditions. Kooyman *et al.* (1973) published oxygen consumption (\dot{V}_{O_2}) values for freely diving Weddell seals (*Leptonychotes weddellii*) in Antarctica. They built a large respirometry system over a hole in the sea-ice into which the seals could breathe after returning from dives. They concluded that diving \dot{V}_{O_2} was only about twice that at rest, much lower than the foraging metabolic rates estimated using different methods for fur seals and sea lions (Costa *et al.* 1989; Ponganis *et al.* 1990; Costa, 1991). However, because of the cumbersome methods used by Kooyman *et al.* (1973), the system could not be used to monitor the seals continuously over long periods or during periods of rapid change. Therefore, the range of behavior studied was limited.

The purpose of this project was to utilize modern methods of on-line computer-based monitoring to collect values of \dot{V}_{O_2} continuously from Weddell seals during a range of activities and over long periods in order to test and to expand the earlier findings of Kooyman *et al.* (1973). Using the same basic animal handling methods of the earlier study, patterns of oxygen consumption were monitored during recovery periods from long and short dives, during bouts of sleep-associated apnea and during awake, rest periods.

Materials and methods

Animal handling

Procedures for working with Weddell seals under free-diving conditions have been well documented and this study followed those general techniques (Kooyman, 1968; Kooyman *et al.* 1973). Five adult Weddell seals (average mass = 355 ± 59 kg; 3 females, 2 males) were captured on the sea-ice near McMurdo Station, Antarctica. The animals were weighed on a strain gauge cattle platform, accurate to ± 1 kg, and then allowed to enter the sea water through a hole cut in the ice under a small portable heated laboratory.

Because the seals were confined to the study site, which was located several kilometers from any other breathing hole, they always came back to the 'laboratory'. There were no other restrictions on the seals' behavior and, over several days, they routinely made many short dives, some long dives, exhibited long bouts of sleep apnea, rested quietly and, in some cases, reamed at the hole to build an exit.

Oxygen consumption

The methods used here were modeled on previous laboratory studies of

computer-analyzed open-circuit oxygen consumption rates of seals in water (Davis *et al.* 1985; Fedak, 1986). Basically, once the animal was in the water, a large acrylic dome was placed over the hole and sealed against the water surface. Room air was moved through the dome at a rate of about 600 l min^{-1} using a vacuum motor. Exact flow rates for each experiment were determined by passing a known flow of 100% nitrogen into the dome intake and measuring the change in oxygen content of the outflow air. A subsample of the outflow air was continuously drawn through water vapor and carbon dioxide extraction columns and then analyzed for oxygen content with an Ametek S3-A oxygen analyzer. The analog output of the oxygen analyzer was sent to a digital converter and then to an Apple computer. A BASIC program, modified from Davis *et al.* (1985) to provide more rapid sampling, collected the data and calculated the percentage of oxygen in the expired air and the oxygen consumption of the seal every 10 s. These data were reduced and analyzed using QUATTRO (Borland) and STATISTIX (Analytical Software) computer packages.

Event recording

Resting oxygen consumption values were summed and averaged for seals that were quiet, awake and breathing regularly. For both dive and sleep apnea 'events', the oxygen consumption was summed for the time that the seal was breathing until the next event. During bouts of these activities, the recovery breathing period is short (less than 5 min; Castellini *et al.* 1988) and easily defined as the time until the next dive or breath-hold. For isolated dives interspersed with long periods at the surface, recovery was defined as the time at which oxygen consumption returned to resting values or when a period of sleep apnea began. The total amount of oxygen consumed during the recovery period was divided by the time of breath-holding plus the time of recovery. For example, for a 15 min dive with a 4 min recovery, the oxygen used during the 4 min at the surface was divided by the total dive plus recovery time of 19 min to arrive at an oxygen consumption rate for the entire event. This oxygen consumption value was then plotted against the time of the breath-hold in order to relate oxygen consumption rates to dive or sleep apnea time.

Swimming velocity

On two of the five seals, swimming velocity was measured with a self-contained microprocessor-based paddlewheel assembly, as described in detail by Ponganis *et al.* (1990). The instrument was glued to the fur of the seals over the shoulder area. The microprocessor sampled swimming velocity every 7.5 s and logged the average velocity every 15 s. The minimum velocity that could be measured was 0.25 m s^{-1} . When the experiment was finished, the instrument was removed from the seal and the data were transferred to a portable computer for analysis. Two additional animals were added to the study group for determination of swimming velocity only, providing a total of four seals in this section of the project.

Results

Dive and sleep apnea profiles

During this study, 87 dives and 119 sleep apnea events were recorded for the five seals. Fig. 1 shows the frequency of dive and apnea events as a function of apnea time. Most dives (77%) lasted less than 20 min with a modal diving time of 4.5 min and a maximum diving time of 82 min. All sleep-associated apnea events lasted less than 14 min (max=13.5 min) and had a modal time of 6 min.

Resting metabolic rate

The resting rate of oxygen consumption (RMR) for five seals was 4.1 ± 0.3 ml O_2 min^{-1} kg^{-1} (\pm s.d.; Table 1) over a total recorded time of 8.8 h. In one seal that reamed at the ice hole, the metabolic rate was 5.6 ml O_2 min^{-1} kg^{-1} .

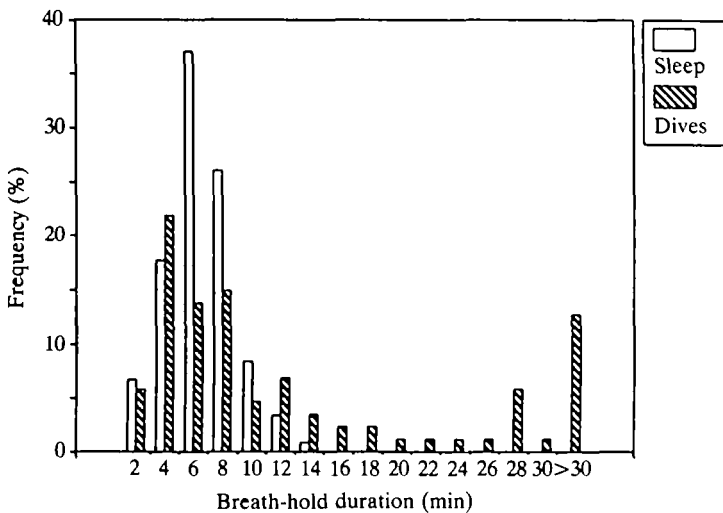


Fig. 1. Histogram of frequency of diving and sleep apnea duration for five Weddell seals. The plot separates events of less than 30 min into 2-min blocks and sums all events over 30 min duration into a single bar.

Table 1. *Average rates of oxygen consumption in Weddell seals*

Seal number	Resting	Sleeping	All dives	Short dives	Long dives
1	4.4	3.1	3.8	4.4	2.7
2	3.9	3.1	5.8	6.4	4.3
3	4.3	4.4	4.4	5.0	3.2
4	3.7	3.2	3.7	4.0	3.2
5	4.3	—	4.9	5.3	3.6
Mean \pm s.d.	4.1 ± 0.3	3.5 ± 0.6	4.5 ± 0.9	5.0 ± 0.9	3.4 ± 0.6

Values are given in ml O_2 min^{-1} kg^{-1} .

Short dives last less than 14 min.

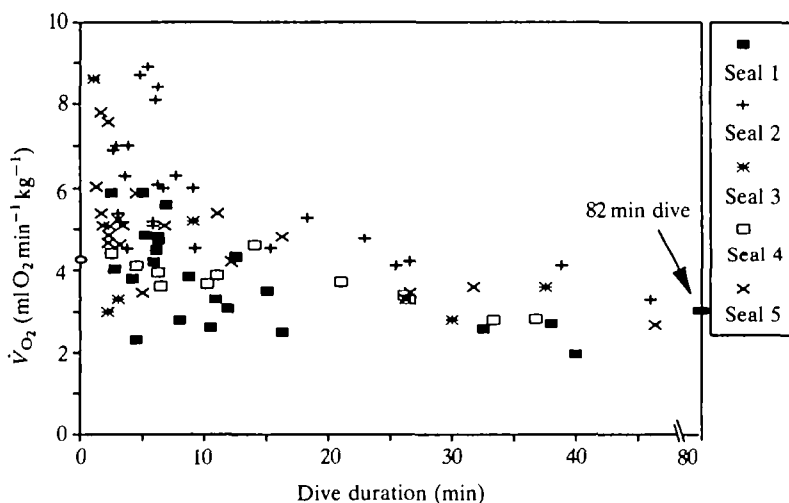


Fig. 2. Rate of oxygen consumption for all dive events for five Weddell seals *versus* diving duration. The longest diving duration recorded (82 min) is noted on the right-hand axis while the average resting value of oxygen consumption ($4.1 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) is marked on the left-hand axis.

Metabolic rate for diving events

The metabolic rates for all dive 'events' (diving time plus recovery time) are averaged for each seal in Table 1. The individual rates of oxygen uptake for all 87 dives are plotted against diving time in Fig. 2. The average resting value of $4.1 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ is marked on the left-hand axis. There was a statistically significant decline in metabolic rate with diving time (unweighted least-squares linear regression test; $P < 0.005$), but diving time accounted for only a small fraction of the variance ($r^2 = 0.27$) in oxygen consumption (see Discussion). Because the theoretical ADL for adult Weddell seals of this mass is in the range of 14–15 min (Kooyman *et al.* 1980, 1983; Qvist *et al.* 1986), and because the maximum sleep apnea time was 13.5 min, the data were subsampled to include only those dive events that would be both clearly aerobic and comparable to sleep apnea durations. The average diving time of this 'short dive' (less than 14.0 min) subgroup was 5.5 ± 3.1 min ($N = 61$) with an average oxygen consumption of $5.0 \pm 0.9 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$. As with the preceding analysis, there was a significant negative correlation ($P = 0.009$) between short diving times and metabolic rate, but high variance ($r^2 = 0.11$). The average diving time of the 'long dives' (greater than 14.0 min) was 31.0 ± 14.1 min with an average oxygen consumption of $3.4 \pm 0.6 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$. As for short dives, there was a weak but significant decline in metabolic rate with longer diving time ($r^2 = 0.19$; $P = 0.03$).

Metabolic rate during sleep-associated apnea

For the 119 sleep apnea events monitored, the relationship of oxygen consump-

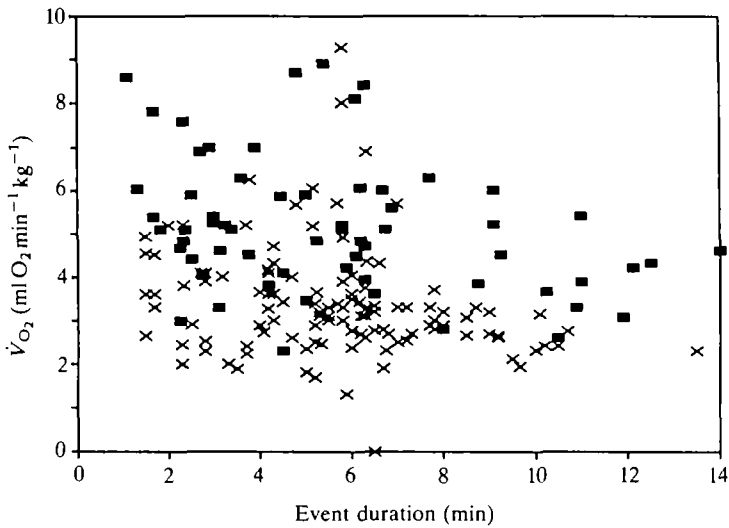


Fig. 3. Rate of oxygen consumption for dive (■) and sleep (×) events of less than 14 min duration.

tion to apnea time is shown in Fig. 3. Average metabolic rates during sleep for each seal are contained in Table 1. For this group of sleep apnea events, the average apnea time was 5.6 ± 2.3 min with an average oxygen consumption rate of 3.5 ± 0.6 ml O₂ min⁻¹ kg⁻¹. There was a very weak relationship between oxygen consumption rate and sleep apnea duration ($r^2=0.05$; $P=0.01$).

Comparison of resting, sleeping and diving oxygen consumption

The mean oxygen consumption values (\pm standard deviation) for all conditions are given in Table 1. Kruskal–Wallis one-way nonparametric analysis of variance of resting, sleeping and all dive metabolic rates indicated that the three means were not different from one another (KW value=6.8; $P=0.08$). However, this comparison included the long dives that may have had a significant anaerobic component. Therefore, tests for differences in mean oxygen consumption rate were carried out on the same resting, sleeping and diving data set using only short dives and excluding those dives longer than 14 min. When the long dives were excluded, the mean values for oxygen consumption during resting, sleeping and short diving were not equal (ANOVA nonparametric; $P=0.03$). To elucidate which of the means was different, a Tukey (HSD) pairwise comparison of means was conducted. This analysis indicated that the resting oxygen consumption value was not different from short diving or from sleeping values but that the sleeping and short-diving values were significantly different from one another. The oxygen consumption values for sleeping and short diving (Fig. 3) were further compared using a Student's *t*-test; this confirmed the Tukey analysis, indicating that the means were different ($P<0.001$). Therefore, it was concluded that oxygen

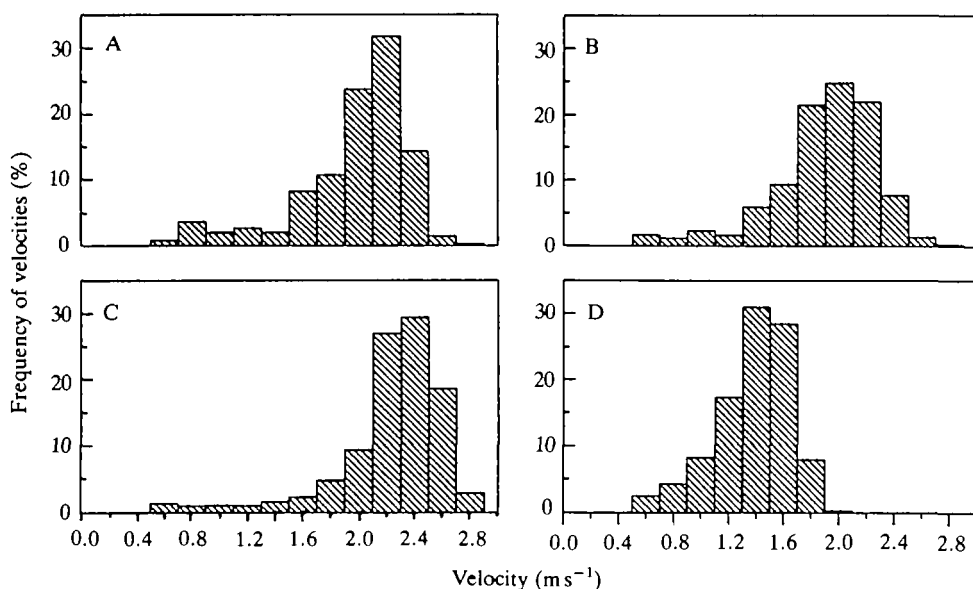


Fig. 4. Histogram of frequency of measured swimming speeds in four Weddell seals. Sample (N) sizes for each plot: A, 2298; B, 1113; C, 1723; D, 3223. Body mass (kg) for each seal: A, 125; B, 333; C, 403; D, 450.

consumption during short dives was not elevated over resting values but was statistically about 1.5 times elevated over sleeping apneas of similar duration.

Swimming velocity

8357 determinations of swimming velocity were made for four seals (Fig. 4). The modal velocity for three of the seals was about 2.0–2.1 m s^{-1} , while the fourth seal had a modal velocity of about 1.5 m s^{-1} . All the seals showed very little variation around the modal speed (72% of all velocities were within $\pm 0.2 \text{ m s}^{-1}$ of the mode).

Discussion

Past studies

The cost of diving in marine mammals is a difficult value to derive given the problems of assessing metabolic rate for an animal at sea. This problem has been approached in the past by extrapolating metabolic rate data from animals in swim flumes or small open-water pens (Ashwell-Erickson and Elsner, 1981; Davis *et al.* 1985; Fedak, 1986; Worthy *et al.* 1987; Feldkamp *et al.* 1989), but it is difficult in these approaches to model the free-ranging and varied behavior of unrestrained animals. Overall metabolic rates for free-ranging otariids have been estimated using the doubly labelled water technique (Costa and Gentry, 1986; Costa *et al.* 1989) but, although this technique is valuable for assessing energy balance

equations, it is not detailed enough to separate the components of energy cost into periods of diving, sleep and rest. Generally, isotope turnover studies have estimated metabolic rate in otariids to be about 5–6 times higher than predicted standard metabolic rates (SMR) at swimming speeds that are equal to or less than those of Weddell seals (Costa and Gentry, 1986; Costa *et al.* 1989; Feldkamp *et al.* 1989; Ponganis *et al.* 1990). Thus, sea lions seem to swim more slowly than Weddell seals but to have a higher metabolic rate. Recent field metabolic rate studies of harbor seals also showed a metabolic rate about 5–6 times higher than predicted (Reilly and Fedak, 1991).

Resting metabolic rate

The average value for resting metabolic rate of the five seals in this study ($4.1 \pm 0.3 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) was less than the value reported by Kooyman *et al.* (1973) for their five seals ($5.1 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) despite the larger average size of the seals in the earlier study (425 kg vs 355 kg). Furthermore, the early study also included periods of sleep apnea in its average, which should have lowered the overall value for rest. The reason for the differences between the two studies is not known; however, both resting values exceeded the estimated metabolic rate for seals weighing about 350 kg based on the Kleiber 'mouse to elephant curve' ($2.5 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$; Kleiber, 1961). This was probably because the basic requirements for measuring SMR could not be obtained in either study. That is, since these rest periods followed soon after dives that were probably for feeding, the seals were probably in a post-prandial state. If so, a food-induced thermogenesis component would have raised the metabolic rate. For example, sea otter RMR is over 50% higher after they have eaten (Costa and Kooyman, 1984). Thus, the oxygen consumption values for both studies are higher than those that Lavigne *et al.* (1986a,b) have shown to occur under controlled laboratory conditions, where the metabolic rate of marine mammals can approach values of resting metabolic rate predicted from mass. However, the results of the current study tend to confirm the hypothesis of Bartholomew (1977) that 'resting' metabolic rates under field conditions are elevated and probably never reach predicted minimum values.

Metabolic rate during diving

The relationship between the duration of all dives and oxygen consumption is statistically significant, but accounts for only 27% of the variation in metabolic rate with dive duration. Much of the remaining variability is probably due to the behavioral requirements of short dives in which the cost of diving varies greatly (Fig. 2). In fact, when the short, aerobic dives are analyzed separately, the correlation between diving time and oxygen consumption is even weaker and dive duration accounts for only 10% of the relationship. This is not surprising because short dives can involve hunting, local exploration and social or antagonistic activities involving differing levels of physical activity (Kooyman, 1968). The average value of oxygen consumption during these short dives ($5.0 \pm 0.9 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) was not significantly different from oxygen consumption during

rest ($4.1 \pm 0.3 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$). Kooyman *et al.* (1973) arrived at the same conclusion using different analytical techniques.

The rate of oxygen consumption during long dives ($3.4 \pm 0.6 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) was also no different from the resting rate (*t*-test; $P=0.06$), but was significantly lower than the rate of oxygen consumption during short dives (*t*-test; $P=0.01$). However, because short dives are usually feeding dives (Kooyman, 1968), they may have an additional heat increment of feeding that would increase the metabolic rate. Also, the difference between long and short dives may be influenced by the fact that it can take a up to an hour for all the lactate produced during long dives to be processed (Kooyman *et al.* 1980). Thus, the actual oxygen consumption of long-term events may be spread over an extended recovery period or hidden in the cost of subsequent dives during which the lactate would continue to be processed (Castellini *et al.* 1988). In general, the recovery time between dives is short and constant in Weddell seals for dives below the ADL and increases rapidly for dives beyond the ADL (Kooyman *et al.* 1980; Castellini *et al.* 1988). Thus, the variation in metabolic rate for short dives is probably not closely related to patterns of surface recovery time.

The significant decline in metabolic rate with diving time indicates that diving metabolism is not constant in Weddell seals and tends to be lower with longer dives. It is intriguing, however, that the metabolic rate of the 82-min dive ($3.0 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) in seal no. 1 was within the standard deviation of the average metabolic rate for dives longer than 14 min in this animal (seal no. 1, Table 1; Fig. 2; average metabolic rate for dives longer than 14 min and shorter than 82 min is $2.6 \pm 0.6 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$). In other words, for dives beyond about 14 min, in this seal, all the oxygen-conserving responses appear to have been invoked. It could also be that such fine detail of differences in oxygen consumption cannot be discerned by the methods utilized.

It is clear that diving, whether short or long, is not energetically costly in this species, and that the cost is much lower than the 4–6 times resting values measured in other diving species (Nagy *et al.* 1984; Costa *et al.* 1989; Davis *et al.* 1989; Costa, 1991; Kooyman *et al.* 1992; Reilly and Fedak, 1991).

Swimming velocities

The swimming velocities show that the seals swam at nearly constant speed. Thus, the histograms in Fig. 4 do not show a wide range of speeds but instead cluster about the mode. It is not known why three of the seals swam at about 2 m s^{-1} and the fourth swam at about 1.5 m s^{-1} . Because no seals were monitored simultaneously for both velocity and oxygen consumption, direct correlations of these two data sets are not possible. However, the tight velocity distribution and the variable oxygen consumption pattern suggest that the two are not closely related in Weddell seals.

Aerobic diving limit

By dividing total body oxygen stores by the diving metabolic rate, a theoretical

Table 2. Calculation of aerobic diving limit range in Weddell seals

Seal number	Mass (kg)	DMR (ml O ₂ min ⁻¹ kg ⁻¹)	RMR (ml O ₂ min ⁻¹ kg ⁻¹)	ADL (min)	
				DMR	RMR
1	377	4.4	4.4	13.4	13.4
2	403	6.4	3.8	9.2	15.5
3	328	5.0	4.3	11.8	13.7
4	310	4.0	3.7	14.7	15.9
5	333	5.3	4.3	11.1	13.7
Mean±s.d.	355±59	5.0±0.9	4.1±0.3	12.0±2.1	14.4±1.2

The range in the aerobic diving limit (ADL) is calculated by dividing the total oxygen stores (59 ml O₂ min⁻¹ kg⁻¹; Kooyman, 1989) by the short-diving (DMR) and resting (RMR) metabolic rates.

The detailed assumptions involved in the calculation of total body oxygen stores are given in the Appendix. Using the DMR, 68% of all dives were shorter than the ADL. Using the RMR, 71% of all dives were shorter than the ADL.

value for the aerobic diving limit can be derived. Available oxygen stores in the five seals were calculated to be 59 ml O₂ kg⁻¹ based on known relationships of respiratory and tissue oxygen capacities to body mass in Weddell seals (Appendix). Because the diving and resting metabolic rates were statistically similar, dividing the oxygen store by both metabolic rate values provides a range for the ADL from 9 to about 16 min (Table 2). Fig. 1 shows that most (70%) dives for Weddell seals in this study were within this calculated aerobic dive limit. By monitoring blood lactate values during free dives of various durations, Kooyman *et al.* (1980, 1983) have shown that the actual aerobic diving limit of adult and immature Weddell seals (140–450 kg) ranges from 10 to 19 min. In the free-ranging situation, approximately 3–8% of all dives are beyond the calculated ADL (Kooyman *et al.* 1980, 1983). However, because no blood lactate values were collected from the seals in this study, the theoretical ADL could not be verified.

Metabolic rate during sleep apnea

Periodic breathing during periods of sleep in phocid seals is common (Bartholomew, 1954; Kooyman, 1968; Ridgway *et al.* 1975; Huntley, 1984; Castellini, 1991). In Weddell seals, it is known that long-duration sleep apnea appears to be aerobic with no significant build-up of lactate during or after the apnea (Kooyman *et al.* 1980). It is also known that several major physiological changes that occur during diving breath-holds also occur during sleep apnea: for example, significant and rapid cessation of ventilatory tachycardia and progressive hypoxia (for a review, see Castellini, 1991). The primary physiological differences between the two events are that the diving seal is exercising and its level of alertness is much greater. Thus, although both diving and sleeping conditions may have the same

length of apnea, the sleeping seal is quiet while the diving seal is exercising. It is not surprising then that the metabolic rate during sleeping was less than that during diving events of the same duration. What is surprising is the relatively minor distinction: \dot{V}_{O_2} during diving was only 1.5 times that during sleeping. If it is assumed that the main difference between the two states is exercise, then some predictions can be made as to the cost of swimming, at the muscle level, in these seals.

Cost of exercise

Anatomical studies of phocids have shown that about 9–12% of the body mass is propulsive muscle (Bryden and Felts, 1974; Fujise *et al.* 1985). Using this assumption, the average locomotory muscle mass of the Weddell seals in this study would maximally be about 42 kg (0.12×355 kg). The difference in metabolic rate between the sleeping and diving seals is $1.5 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ or $532 \text{ ml O}_2 \text{ min}^{-1}$ for a 355 kg seal. Assuming that all of this difference is due to locomotory muscle activity, then an increase of $532 \text{ ml O}_2 \text{ min}^{-1}$ during diving divided by 42 kg of muscle yields an addition in muscle metabolic rate over the sleeping rate due to exercise of about $12.7 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$. Using estimates of resting muscle metabolic rates of about $1.5\text{--}2.0 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ (Friedman and Selkurt, 1966; McGilvery, 1979), then exercising muscle would minimally consume about $14 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ ($12.7 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1} + 1.5 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$). Assuming that there is an oxygen store in the muscle of 60 ml kg^{-1} [$(45 \text{ g myoglobin kg}^{-1}) \times (1.34 \text{ ml O}_2 \text{ g}^{-1} \text{ myoglobin})$; see Appendix], then the oxygen supply would last about 4–5 min [$(60 \text{ ml O}_2 \text{ kg}^{-1}) / (14 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1})$] unless the circulation supplemented the oxygen stores or anaerobic muscle metabolism made a significant contribution during aerobic dives. Because anaerobic metabolism is not important during short dives (Kooyman *et al.* 1980, 1983; Guppy *et al.* 1986; Castellini *et al.* 1988), the circulation must either be open continuously or must pulse periodically to provide additional oxygen to the depleted tissue stores, as hypothesized by Kooyman (1987, 1989) for skeletal muscle and Elsner *et al.* (1985) for cardiac muscle.

The relationship between dive duration and ADL in Weddell seals may not be directly applicable to other species of divers. Several species of otariids, and king and emperor penguins, appear to dive routinely beyond their theoretical ADL (Kooyman and Ponganis, 1990; Kooyman *et al.* 1992; Ponganis *et al.* 1992). In each of these cases, however, data on the diving metabolic rate or the blood chemistry necessary to confirm the ADL do not exist.

In conclusion, the data in this study show that there is a weak but significant inverse relationship in the Weddell seal between dive duration and metabolic rate, with the shortest dives having the highest metabolic cost. However, the cost of diving is not very great in freely diving Weddell seals and cannot be distinguished from resting values. Oxygen consumption during periods of sleep apnea is also no different from consumption at rest, but is about 1.5 times lower than exercise values. These low metabolic demands of diving help to explain the ability of this

species both to dive for 15–20 min without shifting from aerobic-based metabolism and to dive for extremely long periods of up to 82 min.

Appendix

Calculation of the available oxygen stores during diving are based on the following assumptions from Kooyman (1989): total blood volume is 14.8% of body mass, diving hematocrit is 58.0%, hemoglobin is 23.7 gm% and oxygen capacity is 32.5 vol%. Available blood oxygen is from arterial blood assumed to be 95% oxygen-saturated and extracted to 20% during the dive. Venous blood is 5 vol% less than arterial blood and extracted to zero oxygen content. Venous fraction of total blood volume is 0.66. Myoglobin concentration is 45 gm kg⁻¹ muscle and myoglobin oxygen affinity is 1.34 ml O₂ g⁻¹ myoglobin. Muscle mass is 33% of total body mass. Diving lung volume is 50% of total lung capacity and oxygen concentration in the lung is assumed to be 15%. Based on these values, the calculated total oxygen store available for an adult Weddell seal during a dive is about 59 ml O₂ kg⁻¹.

Field work was supported by NSF, Division of Polar Programs funding (NSF DPP 86–13729) to G.L.K. and additional analysis with NIH funding (R29 HL38765) to M.A.C. We would like to thank S. Eckert, E. Ponganis, K. Ponganis and P. Thorson for their help in instrument development and computer programming and for field assistance in the Antarctic.

References

- ASHWELL-ERICKSON, S. AND ELSNER, R. (1981). The energy cost of free existence for Bering Sea harbor and spotted seals. In *The Eastern Bering Sea Shelf: Oceanography and Resources* (ed. D. W. Hood and J. A. Calder), pp. 869–899. University of Washington Press: US Department of Commerce.
- BARTHOLOMEW, G. A. (1954). Body temperature and respiratory and heart rates in the northern elephant seal. *J. Mammal.* **35**, 221–218.
- BARTHOLOMEW, G. A. (1977). Energy metabolism. In *Animal Physiology: Principles and adaptations* (ed. M. S. Gordon), pp. 57–110. New York: Macmillan Press.
- BRYDEN, M. M. AND FELTS, W. J. L. (1974). Quantitative anatomical observations on the skeletal and muscular systems of four species of Antarctic seals. *J. Anat.* **118**, 589–600.
- CASTELLINI, M. A. (1991). The biology of diving: Behavioral, physiological and biochemical limits. In *Advances in Comparative and Environmental Physiology* (ed. R. Gilles), pp. 105–132. Berlin: Springer-Verlag.
- CASTELLINI, M. A., DAVIS, R. W. AND KOOYMAN, G. L. (1988). Blood chemistry regulation during repetitive diving in Weddell seals. *Physiol. Zool.* **61**, 379–386.
- COSTA, D. P. (1991). Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds: Implications for list history patterns. *Am. Zool.* **31**, 111–130.
- COSTA, D. P., CROXALL, J. P. AND DUCK, C. D. (1989). Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology* **70**, 596–606.
- COSTA, D. P. AND GENTRY, R. L. (1986). Free ranging energetics of Northern Fur seals. In *Fur Seals: Maternal Strategies on Land and Sea* (ed. R. L. Gentry and G. L. Kooyman), pp. 79–101. Princeton: Princeton University Press.
- COSTA, D. P. AND KOOYMAN, G. L. (1984). Contribution of specific dynamic action to heat balance and thermoregulation in the sea otter, *Enhydra lutris*. *Physiol. Zool.* **57**, 199–202.

- DAVIS, R. W., CROXALL, J. P. AND O'CONNELL, M. J. (1989). The reproductive energetics of gentoo and macaroni penguins at South Georgia. *J. Anim. Ecol.* **58**, 59–74.
- DAVIS, R. W., WILLIAMS, T. W. AND KOOYMAN, G. L. (1985). Swimming metabolism of yearling and adult harbor seals *Phoca vitulina*. *Physiol. Zool.* **58**, 590–596.
- ELSNER, R. E. (1969). Cardiovascular adjustments to diving. In *The Biology of Marine Mammals* (ed. H. T. Andersen), pp. 117–146. New York: Academic Press.
- ELSNER, R. E., MILLARD, R. W., KJEKSHUS, J. K., WHITE, F., BLIX, A. S. AND KEMPER, W. S. (1985). Coronary blood flow and myocardial segment dimensions during simulated dives in seals. *Am. J. Physiol.* **249**, H1119–H1126.
- FEDAK, M. A. (1986). Diving and exercise in seals: a benthic perspective. In *Diving in Animals and Men*, Kongsvald Symposium, Norwegian Society of Sciences and Letters (ed. J. W. Brubakk, J. W. Kanwisher and G. Sundnes), pp. 11–32. Trondheim: Tapir Publishers.
- FELDKAMP, S. D., DE LONG, R. L. AND ANTONELIS, G. A. (1989). Foraging behavior of California sea lions, *Zalophus californianus*. *Can. J. Zool.* **67**, 872–883.
- FRIEDMAN, J. J. AND SELKURT, E. E. (1966). *Physiology*. Boston: Little, Brown and Co.
- FUJISE, Y., HIDAKA, H., TATSUKAWA, R. AND MIYAZAKI, N. (1985). External measurements and organ weights of five Weddell seals (*Leptonychotes weddelli*) caught near Syowa station. *Jap. Fish. Bull.* **85**, 96–99.
- GUPPY, M., HILL, R. D., SCHNEIDER, R. C., QVIST, J., LIGGINS, G. C., ZAPOL, W. M. AND HOCHACHKA, P. W. (1986). Micro-computer assisted metabolic studies of voluntary diving of Weddell seals. *Am. J. Physiol.* **250**, R175–R187.
- HUNTLEY, A. C. (1984). Relationships between metabolism, respiration, heart rate and arousal states in the northern elephant seal. PhD thesis, University of California, Santa Cruz.
- KLEIBER, M. (1961). *The Fire of Life. An Introduction to Animal Energetics*. New York: Wiley.
- KOOYMAN, G. L. (1968). An analysis of some behavioral and physiological characteristics related to diving in the Weddell seal. *Antarct. Biol. Series.* **11**, 227–261.
- KOOYMAN, G. L. (1987). A reappraisal of diving physiology: Seals and penguins. In *Comparative Physiology: Life in Water and on Land*, vol. 9 (ed. P. Dejours, L. Bolis, C. R. Taylor and E. R. Weibel), pp. 459–469. Berlin: Springer-Verlag.
- KOOYMAN, G. L. (1989). *Diverse Divers. Physiology and Behavior*. Zoophysiology Series 23. Berlin: Springer-Verlag.
- KOOYMAN, G. L., CASTELLINI, M. A., DAVIS, R. W. AND MAUE, R. A. (1983). Aerobic diving limits of immature Weddell seals. *J. comp. Physiol.* **151**, 171–174.
- KOOYMAN, G. L., CHEREL, Y., LE MAHO, Y., CROXALL, J. P., THORSON, P. H., RADOUX, V. AND KOOYMAN, C. A. (1992). Diving behavior and energetics during foraging cycles in king penguins. *Ecol. Monograph* (in press).
- KOOYMAN, G. L., KEREM, D. H., CAMPBELL, W. B. AND WRIGHT, J. J. (1973). Pulmonary gas exchange in freely diving Weddell seals. *Respir. Physiol.* **17**, 283–290.
- KOOYMAN, G. L. AND PONGANIS, P. J. (1990). Behavior and physiology of diving emperor and king penguins. In *Penguin Biology* (ed. L. S. Davis and J. T. Darby), pp. 231–244. New York: Academic Press.
- KOOYMAN, G. L., WAHRENBRÖCK, E. A., CASTELLINI, M. A., DAVIS, R. W. AND SINNETT, E. E. (1980). Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: evidence for preferred pathways from blood chemistry and behavior. *J. comp. Physiol.* **138**, 335–346.
- LAVIGNE, D. M., INNES, S., WORTHY, G. A. J. AND KOVACS, K. M. (1986a). Metabolic rate–body size relations in marine mammals. *J. theor. Biol.* **122**, 123–124.
- LAVIGNE, D. M., INNES, S., WORTHY, G. A. J., KOVACS, K. M., SCHMITZ, O. J. AND HICKIE, J. P. (1986b). Metabolic rates of seals and whales. *Can. J. Zool.* **64**, 279–284.
- MCGILVER, R. W. (1979). *Biochemistry: A Functional Approach*. Philadelphia: W. B. Saunders.
- NAGY, K. A., SIEGFRIED, W. R. AND WILSON, R. P. (1984). Energy utilization by free-ranging jackass penguins, *Spheniscus demersus*. *Ecology* **65**, 1648–1655.
- PONGANIS, P. J., GENTRY, R. L., PONGANIS, E. P. AND PONGANIS, K. V. (1992). Analysis of swim velocities during deep and shallow dives of two northern fur seals, *Callorhinus ursinus*. *Mar. mamm. Sci.* (in press).
- PONGANIS, P. J., PONGANIS, E. P., PONGANIS, K., KOOYMAN, G. L., GENTRY, R. L. AND TRILLMICH, F. (1990). Swimming velocities in otariids. *Can. J. Zool.* **68**, 2105–2112.

- QVIST, J., HILL, R. D., SCHNEIDER, R. C., FALKE, K. J., LIGGINS, G. C., GUPPY, M., ELLIOT, R. L., HOCHACHKA, P. W. AND ZAPOL, W. M. (1986). Hemoglobin concentrations and blood gas tensions of free-diving Weddell seals. *J. appl. Physiol.* **61**, 1560–1569.
- REILLY, J. J. AND FEDAK, M. A. (1991). Rates of water turnover and energy expenditure of free-living male common seals (*Phoca vitulina*). *J. Zool., Lond.* **223**, 461–468.
- RIDGWAY, S. H., HARRISON, R. J. AND JOYCE, P. L. (1975). Sleep and cardiac rhythm in the gray seal. *Science* **187**, 553–555.
- WORTHY, G. A. J., INNES, S., BRAUNE, B. M. AND STEWARD, R. E. A. (1987). Rapid acclimation of cetaceans to an open-circuit respirometer. In *Approaches to Marine Mammal Energetics* (ed. A. C. Huntley, D. P. Costa, G. A. J. Worthy and M. A. Castellini), pp. 115–126. Society for Marine Mammalogy Special Publication No. 1.