Metabolic rates of captive grey seals during voluntary diving

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Summary

The energetic cost of diving in marine mammals is a difficult value to derive given the problems of assessing metabolic rate for an animal at sea. Nevertheless, it is fundamental to our understanding of the foraging strategies of air-breathers exploiting underwater food sources. We measured the metabolic rates of eight captive grey seals, voluntarily diving in a quasi-natural setting. Oxygen consumption during post-dive surface periods was measured using open-flow respirometry, and dive behaviour of the seals was recorded using time depth recorders (TDRs). Mean diving metabolic rate (DMR) for both adults and juveniles was 1.7 times the predicted standard metabolic rate of terrestrial animals of equal size. For all animals, DMR was lower than the rate of metabolism measured whilst they were resting at the water's surface. On a dive-by-dive basis, DMR decreased with dive duration but increased with mean swim speed.

Regressing the maximum 5% of DMRs against dive duration resulted in a significant negative relationship that was not significantly different from the relationship between the calculated maximum rate of aerobic metabolism and dive duration, suggesting that these seals were diving within, and up to, their aerobic limits. We developed a model that allows the prediction of DMR from information on dive behaviour of the type routinely collected in telemetry studies of wild seals. The model accurately predicts DMR using behavioural data from periods of diving with known metabolism data. This model can be used to predict the at-sea metabolic rate of wild grey seals, an important input into ecosystem models.

Key words: grey seal, *Halichoerus grypus*, diving metabolic rate, aerobic dive limit, hypometabolism.

Introduction

Despite technological advances that have given us an insight into the behaviour of phocid seals at sea, measurements of energy expenditure during active diving and foraging in this group are extremely difficult to make. The energetics of diving has received attention from ecologists and physiologists for both practical and theoretical reasons. Firstly, the rate of energy use during diving is important in understanding the complex balance of behaviour and physiology that shapes the foraging strategies of air-breathing animals exploiting an underwater prey resource. Pinnipeds provide a unique system for studying the relative importance of physiology in determining foraging behaviour (Costa et al., 2001). In order to determine how physiology constraints affect dive behaviour, we need to know how behaviour during the dive affects the rate of utilisation of the animals' stored oxygen. Central to this is the concept of the aerobic dive limit (ADL). The ADL is the dive duration beyond which animals start to rely on anaerobic metabolism and is often used to place dive behaviour within a physiological context. The concept of the ADL has received much attention in the literature over the past few decades (e.g. Kooyman et al., 1983; Ponganis et al., 1993, 1997; Boyd and Croxall, 1996; Burns and Castellini, 1996; Moss and Castellini,

1996; Butler and Jones, 1997; Burns, 1999; Davis and Kanatous, 1999; Cabanac, 2000; Costa et al., 2001; Croll et al., 2001; MacArthur et al., 2001; McIntyre et al., 2002). However, ADL is difficult to measure experimentally, especially in free-living animals. It is more commonly estimated by dividing total body oxygen stores by metabolic rate during diving (DMR). However, this presents a problem in that actual DMR is difficult to measure under field conditions. It has only been measured in animals in captivity, or diving in unique situations. DMR of freely diving pinnipeds has only been directly measured to date in Weddell seals (*Leptonychotes weddelli*) diving under ice (Kooyman et al., 1973, 1980, 1983; Castellini et al., 1992; Ponganis et al., 1993, Williams et al., 1999) and in captivity in northern elephant seals (*Mirounga angustirostris*; Webb et al., 1998a), grey seals (*Halichoerus grypus*; Fedak, 1986; Reed et al., 1994), Baikal seals (*Phoca sibirica*; Ponganis et al., 1997) and California sea lions (*Zalophus californianus*; Hurley and Costa, 2001). In all of these studies, diving metabolism varied with dive type and duration. There is currently little information on how DMR relates to the range of behaviour exhibited in free-living animals. While Castellini et al. (1992) measured DMR and

swimming speed in free-living Weddell seals, the two were never measured simultaneously. Williams et al. (1999) examined the relationship between propulsion mode and post-dive oxygen consumption in free-living Weddell seals and found that stroking dives were energetically more costly than gliding dives.

The present study examines the relationships between diving behaviour and oxygen consumption in grey seals diving voluntarily in a quasi-natural setting.

A second reason for an interest in the metabolic rates of diving seals is that the energetic costs of diving are incorporated, explicitly or implicitly, in various models of seal prey consumption that are used to predict the impacts of seal populations on prey species (e.g. Øritsland and Markussen, 1990; Markussen and Øritsland, 1991; Olesiuk, 1993; Mohn and Bowen, 1996; Stenson et al., 1997; Nilssen et al., 2000; Winship et al., 2002). Metabolism while at sea makes up a large component of a seal's annual energy budget, yet it is this component we know least about. For example, in the Steller sea lion (*Eumetopias jubatus*) bioenergetic model developed by Winship et al. (2002), uncertainty in metabolism parameters, particularly activity cost parameters, had the largest effect on the error in estimates of food consumption.

The doubly labelled water (DLW) technique has been used to measure at-sea field metabolic rates (FMR) of many otariid species, e.g. New Zealand sea lions (*Phocartos hookeri*; Costa and Gales, 2000), northern fur seals (*Callorhinus ursinus*; Costa and Gentry, 1986), Australian sea lions (*Neophoca cinerea*; Costa et al., 1989; Costa and Gales, 2003) and Antarctic fur seals (*Arctocephalus gazella*; Costa et al., 1989; Arnould et al., 1996). To date, at-sea metabolic rate has only been measured using this method in two phocid species, the harbour seal (*Phoca vitulina*; Reilly and Fedak, 1991) and the northern elephant seal (Andrews, 1999). The need for timely recapture and the cost involved in dosing large animals with isotopes makes it difficult to apply this technique to phocids such as the grey seal. Grey seals go out to sea on foraging trips that can last several days and move between haul-out sites in an unpredictable manner (McConnell et al., 1999). They can be captured at haul-outs but the chances of recapturing the same animal are small. Furthermore, DLW can only give measures of the average energy expenditure over a time period of several days, and individual metabolic rates cannot be assigned to individual dive types. At-sea FMR integrates the energy expended during all activities, including resting periods, so FMR measured in this way has limited utility for examining the relationships between energy expended and dive variables such as depth, duration and swimming speed over periods shorter than an entire foraging trip.

Other approaches to estimate at-sea energy requirements include predicting basal metabolic rate (BMR) based on empirically derived equations relating body mass to metabolic rate (Kleiber, 1975), then using a multiplier of BMR to account for activity at sea. This multiplier is generally extrapolated from metabolic rate data from animals swimming in flumes or in small tanks (e.g. Davis et al., 1985; Fedak et al., 1988; Williams et al., 1991); however, these are not likely to provide realistic models of the varied behaviour of free-ranging, unrestrained animals. Flume studies require seals to swim continuously against a current, on or near the surface, something that phocid seals do not do in the wild. Similarly, animals restricted to small tanks cannot exhibit the same range of behaviour as their wild counterparts. Free-ranging animals need to manage their O_2 stores to maximise foraging time and energy intake (Fedak and Thompson, 1993; Thompson et al., 1993). How an animal manages O_2 use in a situation of forced exercise or while diving in small tanks may be very different. A complete understanding of the energetic requirements of the time spent at sea by phocid seals will require an approach that combines laboratory-based measurements with data on freely living animals.

This paper presents estimates of dive-by-dive metabolic rates in grey seals with simultaneous measurement of behaviour in an experimental set-up that mimics the natural dive behaviour of grey seals more closely than in any previous captive studies. Because of the difficulties in directly measuring DMR in wild seals, we present a general model that can be used to predict the energy expenditure of diving grey seals from behavioural parameters. It is proposed that this model be used in conjunction with telemetry-derived behavioural information from field-based studies to estimate the metabolic cost of foraging in free-living animals.

Materials and methods

Animals

Eight female grey seals (*Halichoerus grypus* Fabricius), three juveniles and five adults, were used in this study. All seals were caught in the wild from local haul-out sites and taken by boat to the captive facility of the Sea Mammal Research Unit (SMRU) in St Andrews. Seals were released back into the wild after a maximum period of one year. While at SMRU, the animals were housed in outdoor seawater pools at ambient temperature and fed a diet of herring supplemented with vitamins (aquavits).

Measurement of oxygen consumption during diving

Oxygen consumption was measured during voluntary diving in a large pool measuring 42 m×6 m×2.5 m. All seals used in this study were fasted overnight before measurements were made. Oxygen consumption was measured by open-flow respirometry. A schematic of the system used is shown in Fig. 1. A Perspex breathing chamber was set into a modified mesh panel at one corner of the pool; an airtight seal was formed by submerging the edges of the box under 6 cm of water. Aluminium mesh panels covered the entire pool, preventing the seals from surfacing anywhere apart from the breathing chamber during experiments. The pool was divided into four lanes to increase the distance that seals could travel in any one dive (Fig. 2). For several weeks before the diving trials were carried out, the seals were trained to dive away from

the breathing box by receiving food rewards at feeding holes. The breathing chamber had an inlet, which opened to the outside, and an outlet, which was connected by 3.8 cm-diameter flexible hosing to a pump situated inside the laboratory (~6 m away). Another section of this flexible hose, 1.5 m long, was attached to the inlet, acting as 'dead space', so that none of the seals' expirations were lost through the inlet. Ambient air was drawn through the box at a rate depending on the animals' requirements (200–400 l min^{-1}), sufficient to make the change in O_2 concentration during breathing around 1%. Flow was maintained and monitored using Sable Systems Flow Kit 500H (Sable Systems International, Las Vegas, NV, USA). A 500 ml min^{-1} subsample was pumped at positive pressure through a drying column, a CO_2 absorber and another drying column before entering a 'Servomex' paramagnetic oxygen analyser (model OA570; Sybron Taylor; Servomex, Crowborough, UK), which measured the oxygen concentration in the sample gas. The oxygen analyser was connected to a laptop computer using a PCMIA16-bit analogue-to-digital converter (PC-CARD DAS16/16; Amplicon Liveline, Brighton, UK). The O_2 analyser output was sampled 10 times per second using a program designed and written for this application in Hewlett Packard Virtual Engineering Environment (HPVEE). The program calculated and stored a moving average of the fractional O_2 concentration every 10 s. The system had a lag of approximately 110 s from when the seals began breathing until the first deflection on the O_2 analyser, and a 95% response time of 2.5–3 min.

The respirometry system was calibrated at the beginning of every run using the nitrogen dilution technique described by Fedak et al. (1981). This calibration technique has relatively small errors as long as the flow through the system remains constant between measurement and calibration. Flow rates of nitrogen were regulated to arbitrary values using a glass tube flow-meter (Brooks Instruments, Emerson Process Management, Stockport, UK). This flow-meter was calibrated weekly using a Brooks Vol-U-Meter gas calibrator. All volumes of gas were converted to STPD. Calibration curves relating flow-meter reading to measured flow in $l\,s^{-1}$ were constructed and equations produced using least-squares regression.

Oxygen consumption ($\dot{V}_{O_2}$) of the seal was calculated using the following equation from Fedak et al. (1981):

$$\dot{V}_{O_2} = (0.2094V_{N_2}/0.8)(\Delta C/\Delta C^*)\,, \qquad (1)$$

where ΔC and ΔC^* refer to the deflection of the analyser during measurement and calibration, respectively, and V_{N_2} is the
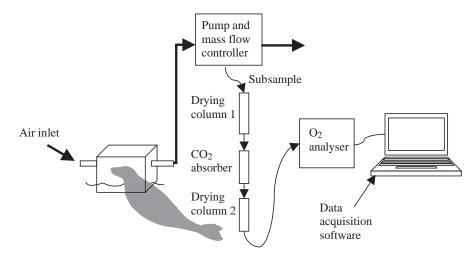

Fig. 1. Schematic diagram of the open-flow respirometry system. The arrows show the direction of air-flow through the system.
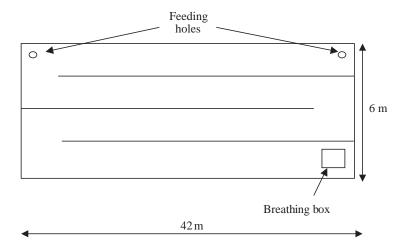

Fig. 2. Schematic of the pool used in the measurement of diving metabolic rate. The entire surface of the pool is covered by aluminium mesh so that the seal can only surface and breathe in the box situated in one corner. The pool is divided into lanes using nets, so that during measurement the seals can travel a maximum of 168 m away from the breathing box. The depth of the pool is 2.5 m.

volume of nitrogen used in the calibration. The output from the oxygen analyser was monitored continuously in a laboratory inside the building so that seals were not aware of any human presence throughout experimental trials. The metabolic rate of each dive cycle was calculated by summing the oxygen consumed during the post-dive surface recovery period and dividing it by the duration of the entire dive plus surface period. For most dive 'events', the recovery breathing time is short (normally 0.5–2 min) and easily defined as the time until the next dive. Where animals spent extended periods at the surface after a dive, oxygen consumption tended to return to resting values after an initial recovery period. Only dives where the recovery breathing period was short and immediately followed by another dive were included in the analysis of DMR. Resting metabolic rate (RMR) was estimated

from oxygen consumption during periods where animals spent extended periods at the surface, showing no activity (>10 min); periods of apnoea were excluded from the data. In the analysis comparing DMR with RMR, to minimise variation caused by other factors we only included data where both RMR and DMR were measured on the same day for a given individual. This way we controlled for differences between individuals (and within individuals over time) and differences due to environmental conditions by carrying out a paired *t*-test on the difference between DMR and RMR. We obtained DMR and RMR measurements on the same day for seven out of eight animals.

Measurement of behaviour

The seals' behaviour was measured using a time depth recorder (Mk 8 TDR; Wildlife Computers, Redmond, WA, USA) attached to the head of the animal. The turbine housed in the tag rotated as the animal swam and the tag counted and logged the number of revolutions of the paddle wheel per second (measured TDR speed or MTS). MTS was converted to estimated true speed (ETS) using a calibration, where actual speed measured by observers timing a seal swimming over known distances was compared with the measured TDR speed (Jones, 2001). The equation relating measured speed to true speed using least-squares regression (r^2=0.96) was:

$$ETS = 1.403 \times MTS . \qquad (2)$$

A wet/dry sensor measured surface and dive durations. A digital watch was synchronised with the TDR clock, and the time the seal entered and left the water was noted for each individual trial. This enabled the experimental period to be isolated from the TDR record when it was downloaded. Data from the TDR were downloaded at the end of a set of measurement trials (typically 1 week), and the following parameters were calculated for each dive: dive duration, surface duration, total length of dive cycle, proportion of dive cycle spent submerged, overall mean speed during the dive (in m s^{-1}; average of per second ETS), total distance travelled over dive (ETS in m s^{-1} × duration in s), percentage of dive spent swimming and the mean active swim speed (average of per second ETS readings where ETS >0.02).

So that we could compare the behaviour of the seals in captivity with the dive behaviour of wild seals, information on the dive behaviour of free-living grey seals was obtained using Argos satellite relay data loggers (SRDLs) deployed on 108 grey seals at various locations around the UK between 1990 and 1999. The process by which dive data were collected and processed by the SDRLs is detailed by Fedak et al. (2002).

Model predicting DMR from behaviour

We constructed a generalised linear model that could be used to predict the DMRs of free-ranging seals given the sorts of information about their diving behaviour available from SRDL records from studies of wild grey seals. Post-dive oxygen consumption (in litres) was the response variable

whilst only behavioural variables that were likely to be measured in telemetry studies of the dive behaviour of wild seals were included as predictors. The generalised linear model assumes that the response variable comes from a gamma distribution, i.e. it is a continuous variable with non-normal errors; the variance is proportional to the mean in this case (Venables and Ripley, 1999). The best model was chosen by minimising the Akaike Information Criterion or AIC (Akaike, 1974). The fit of the model was also assessed by examining residual plots and plots of fitted *versus* observed values.

The predictive power of the model was assessed by removing all dives from one individual from the full data set, then re-fitting the model using this reduced data set, and using the new model to calculate the predicted oxygen consumption of the excluded 'novel' animal over all their dives. These could then be compared with the observed oxygen consumption. This was done with each animal in turn.

Results
Dive characteristics

A total of 770 dives was recorded with concurrent measures of dive-by-dive metabolic rate. Table 1 shows a summary of the dive characteristics for each seal. Across all dives, the mean dive duration was 5.3±1.8 min (mean ± S.D.), and the maximum dive duration was 12.5 min. The seals spent, on average, 83% of the dive cycle submerged. Frequency distributions of dive and surface durations are shown in Fig. 3. The mean dive duration of 5.3±1.8 min was similar to the mean dive duration of 3.98±1.82 min calculated from satellite-tagged free-living grey seals (Fig. 4). Mean swim speed from over 3000 dives from five grey seals tagged in Orkney and Shetland was 0.42±0.24 m s^{-1} (Sparling, 2003) compared with the average swim speed of dives in the present study of 0.32±0.25 m s^{-1}.

Diving metabolic rates

Mean rates of oxygen consumption during diving ranged from 0.25 l min^{-1} in a juvenile under one year of age to 0.69 l min^{-1} in the largest adult. Regressing the log$_{10}$ of mean

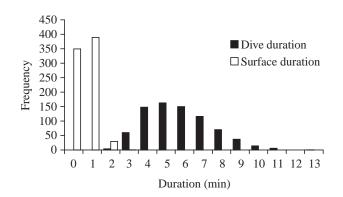Fig. 3. The distribution of dive and surface times for all dives from all eight seals (767 dives in total).

Table 1. *Summary of diving characteristics for all eight seals*

Seal	Mass (kg)	Dive duration (min)	Surface duration (min)	Proportion of dive cycle spent submerged	Mean swim speed during dive (m s^{-1})	DMR (l min^{-1})	DMR (Kleiber)
Bonnie*	45.9	3.86±0.97	0.57±0.26	0.86±0.05	0.31±0.33	0.28±0.09	1.57±0.48
Cassie	130.3	4.39±1.64	1.61±0.73	0.74±0.08	0.22±0.22	0.55±0.13	1.41±0.33
Deirdre	92.9	4.89±1.71	1.08±0.50	0.81±0.08	0.29±0.31	0.50±0.19	1.67±0.62
Feefee	140.3	5.20±1.29	1.23±0.40	0.81±0.05	0.08±0.13	0.67±0.13	1.65±0.32
Heidi	148.7	6.91±0.38	1.10±0.31	0.86±0.05	0.13±0.12	0.69±0.19	1.61±0.45
Jay*	45.2	4.23±2.08	0.88±0.45	0.83±0.05	0.26±0.25	0.25±0.07	1.44±0.41
Kylie*	32.2	3.97±0.62	0.43±0.14	0.90±0.02	0.73±0.13	0.30±0.04	2.20±0.29
Lola	128.2	5.86±1.60	1.26±0.43	0.82±0.06	0.26±0.19	0.68±0.17	2.18±1.51

All values are means ± S.D. *Denotes the seal was a juvenile of <14 months. Diving metabolic rate (DMR; l min^{-1}) is the mean oxygen consumption over a dive cycle. DMR (Kleiber) is the multiple of the basal metabolism predicted by Kleiber's allometric equation (Kleiber, 1975).

DMR (l min^{-1}) against the log$_{10}$ mass (kg) of each animal resulted in the following equations (Fig. 5):

$$\log_{10} \text{DMR} = 0.76 \log_{10} M_b - 1.79 \qquad (3)$$

or

$$\text{DMR} = 0.016 \times M_b^{0.76}, \qquad (4)$$

where M_b is body mass (kg) and DMR is O$_2$ consumption (l min^{-1}); r^2=0.97, d.f.=7, P<0.0001.

The slope of the relationship is not significantly different from Kleiber's equation (Kleiber, 1975) relating basal metabolism to body mass using Bailey's computation for the comparison of two regression coefficients (Bailey, 1959). (Although the number of animals is low and thus may give an unreliable measure of the scaling exponent, within the animals studied here at least, which exhibited a sixfold size range, DMR did seem to scale to mass$^{0.76}$.) All subsequent metabolism measurements, where data are combined from more than one animal, are expressed as a multiple of Kleiber's prediction of BMR for a similarly sized animal, hereafter symbolised by K. Expressing metabolism in this way allows us to effectively control for the effect of mass when investigating variation in metabolic rates related to variables other than mass within this sample. When expressed this way, DMR in this study ranged from 1.4(K) to 2.2(K). Rates of oxygen consumptio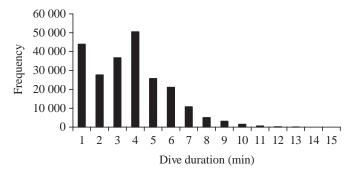n for the seven seals for which we managed to measure both states were lower during diving than when they were resting at the surface (Fig. 6). Across individuals, there was a mean reduction in metabolic rate of 10–33%. This difference was significant (paired t=3.86, P=0.003).

DMR and dive behaviour

Fig. 7 shows a 3-D plot of the relationship between swim speed, dive duration and DMR. From this we can see that the longest dives are also those with the lowest mean swim speeds and the lowest metabolic rates. Conversely, the shortest dives tend to have higher mean speeds and higher metabolic rates. Fig. 8 shows DMR in relation to dive duration. It shows a cloud of points with a curvilinear upper edge. We hypothesised that this edge was suggestive of a physiological limit imposed by available O$_2$ stores, which would operate as a constraint on behaviour during the dive. We examined the hypothesis that this upper edge was related to oxygen stores and the rate of their use by fitting a line through the 95th percentile of DMR. A theoretical limit to aerobic metabolism was modelled by
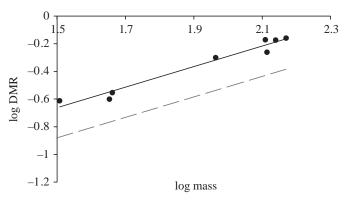
Fig. 4. Frequency distribution of dive durations from satellite-tagged UK grey seals (total number of dives was >219 000 from 108 seals).

Fig. 5. Diving metabolic rates (DMR) in relation to mass. Each point is the mean DMR of an individual seal (*N*=8 seals). The solid line is the line fitted by least-squares regression, weighted by the number of dives from each individual. The equation for this line is: log DMR = log mass (0.76–1.79) (r^2=0.92, *P*<0.0001). The broken line represents Kleiber's prediction of BMR in terrestrial mammals.
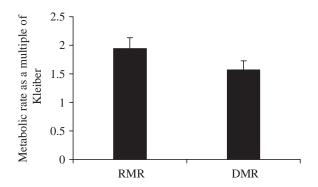
Fig. 6. Mean (+S.D.) metabolic rates (the multiple of the basal metabolism predicted by Kleiber's allometric equation; Kleiber, 1975) of seven grey seals during diving (DMR) or during rest (RMR) at the water surface. Resting values are for alert, inactive animals breathing continuously. These data are compared with values for the same individuals, on the same day, during diving. The difference is significant (paired t-test, $t=3.86$, $P=0.003$).
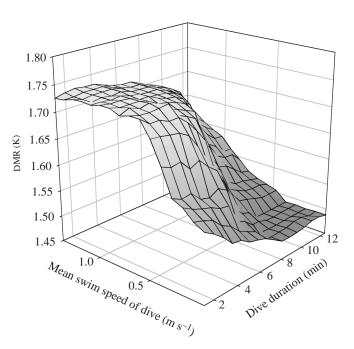

Fig. 7. 3-D surface plot of the relationship between diving metabolic rate (DMR), dive duration and mean speed during a dive (from all dives from all animals). Surface fitted to data using running median smoothing of the values at neighbouring points.

calculating the mass-specific maximum rate of metabolism during a dive of a given duration, given the total body oxygen stores available to the animal. For example, the oxygen store available to a diving grey seal of 50 kg can be estimated as 3 litres (60 ml O_2 kg^{-1}; Kooyman, 1989). Therefore, for a dive lasting 5 min, the maximum possible rate of oxygen utilisation during that dive is 0.6 l min^{-1} or 12 ml min^{-1} kg^{-1}. Likewise, a seal of 100 kg has an estimated oxygen store of 6 litres, corresponding to a maximum rate of 1.2 l min^{-1} or, similarly, 12 ml min^{-1} kg^{-1} for a 5-min dive. The slopes of the two lines could then be compared. Because of the curvilinear appearance of this edge, and the curvilinear nature of the relationship between maximum possible aerobic DMR and dive duration, the y-axis was $\log_{10}$ transformed.

This regression yielded a significant negative relationship between maximum $\log_{10}$ DMR and dive duration for seven out of eight seals. When dives from all animals were pooled, this regression was significant ($P<0.05$). Dives from all animals were pooled, and the edge predicted by regression of the 95th percentile was compared to the maximum predicted aerobic DMR. The line depicting maximum theoretical metabolic rate lies within the confidence limits of the fitted 95th quantile regression line (Fig. 9).

Predictive model

The full model predicting post-dive oxygen consumption ($\dot{D}_{O_2}$; litres) from dive behaviour is as follows:

$$\dot{D}_{O_2} = B_0 + B_1 M_b^{0.75} + B_2 t_d + B_3 t_s + B_3 \overline{U} + B_4 M_b^{0.75} t_d + \\ B_5 M_b^{0.75} t_s + B_6 \overline{U} t_d + B_7 t_d t_s , \quad (5)$$

where B_0–B_7 are coefficients, t_d and t_s are dive and surface duration, respectively, in seconds, M_b is mass in kg and $\overline{U}$ is mean speed in m s^{-1}. Removing dives from each animal in turn from the data set and refitting the model resulted in a set of slightly different models; however, the same explanatory variables were significant in each one. Actual $\dot{D}_{O_2}$ is plotted

against predicted $\dot{D}_{O_2}$ for each dive in Fig. 10. Predicted oxygen consumption was not significantly different from actual oxygen consumption (paired t-test, d.f.=769, $t=1.86$, $P=0.064$). Over individual dives, the mean difference between predicted and actual metabolic rates was 3.7% (95% C.I. 1.9–5.5%).

Discussion

The complete cycle of a dive and the subsequent breathing bout can be considered as the basic physiological unit in diving seals (Fedak et al., 1988). Metabolic rate measured as an average over this period is estimated easily from gas exchange at the surface. This rate is likely to exhibit variations directly attributable to variations in behaviour and physiological state on a dive-by-dive basis.

Relevance to free-living animals

The range of dive behaviour exhibited by the seals in this study, in terms of dive durations, swimming speed and distance travelled, is similar to that recorded in wild grey seals using satellite telemetry. Although there may be differences in behavioural motivation for performing dives between the seals in this study and freely diving seals in the wild, the physiological processes and consequences are likely to be similar. However, there are some obvious differences in diving behaviour between the animals in our study and free-living seals. Depth was simulated in our experiments by the distance that seals could swim away from the breathing box, i.e. depth was transformed from a vertical to a horizontal distance. Thus,
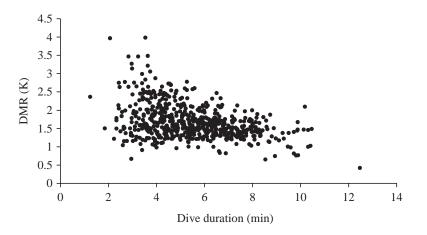
Fig. 8. Variation in metabolic rate as a function of dive duration. Metabolic rates are oxygen consumption over the whole dive plus surface period expressed as a multiple of Kleiber's (1975) predicted basal metabolic rate. Dives from all eight seals are shown.

all portions of the dive were 0.5–2.5 m below the surface and there was no true ascent or descent phase. There may be problems, therefore, in making direct extrapolations from the seals in our study to seals diving in the wild. The energetic consequences of the interactions between buoyancy, pressure, drag and swimming mode are not clear. Phocid seals generally exhale before diving so the relative contribution of lung compression to buoyancy changes is likely to be less than in other marine mammal species. Although Williams et al. (1999) did demonstrate that Weddell seals consumed more oxygen during the post-dive surface recovery period following gliding dives than stroking dives that covered the same distance, the authors only present total oxygen consumed and do not control for the length of the dive or for the length of the surface recovery period. For a negatively buoyant animal during
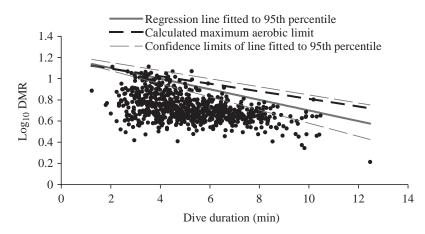

Fig. 9. Log-transformed diving metabolic rate (DMR) plotted against dive duration for all dives. Also indicated is the boundary defined by quantile regression of the 95th percentile plus upper and lower 95% confidence limits to this line. The regression is significant at *P*<0.05. The thick, broken line represents the relationship between maximum possible aerobic log DMR and dive duration, based on maximum utilisation of body oxygen stores during the dive.

descent, the negatively buoyant force will exceed the magnitude of drag, so the animal will be aided in descent by a net downward force. During ascent, the animal has to overcome the effects of negative buoyancy and drag and therefore it has to work harder (Webb et al., 1998b; Beck et al., 2000). Any energetic savings made on descent will therefore presumably be balanced by these additional costs during ascent. Conversely, a positively buoyant animal may expend more energy descending but savings may be made on ascent. Although the exact balance of costs during ascent and descent remains to be addressed, there may be no net difference in terms of energetic cost between horizontal dives and vertical dives. There are also other aspects of behaviour exhibited by wild seals that were not represented in our diving trials, such as prey pursuit and capture. However, grey seals may adopt a 'sit and wait' tactic during foraging rather than actively pursuing prey (Thompson and Fedak, 1993), which may not add to the energetic cost of the dive. How different modes of locomotion and different foraging strategies affect diving metabolism are avenues of exploration that we are currently addressing with further experimental work. Despite these limitations, we believe that our experimental set-up approximates the behaviour of free-living animals more closely than any previous work on the diving metabolism of captive phocids.

Diving metabolic rate – evidence of hypometabolism?

Mean DMR of all 770 dives in this study was 1.7±0.45(K). This is comparable to 1.6(K) in free-living Weddell seals diving under ice (Castellini et al., 1992). Eighty percent of all DMRs, even when seals were active and swimming an average of 100 m during dives, were lower than resting levels measured under standard conditions in the same seals. Kooyman (1989) defined hypometabolism as a rate of metabolism lower than the rate that occurs under the standard conditions of resting in the post-absorptive and normally quiet period of the 24-h cycle. In the present study, DMRs were lower than those measured under standard resting conditions by 10–30%, suggesting hypometabolism during diving in grey seals. This is further reinforced if we consider that we have potentially overestimated the rate of oxygen utilisation over the submerged part of the dive cycle, since 'excess' oxygen is consumed during the surface period and is not utilised during the dive. The reduction between standard RMR and submerged metabolic rate is lower than the 47–65% reduction reported by Hurley and Costa (2001) in trained California sea lions and the 60–70% reduction of metabolic rate in grey seals found by Scholander (1940) during forced dive experiments with grey and hooded seals. This
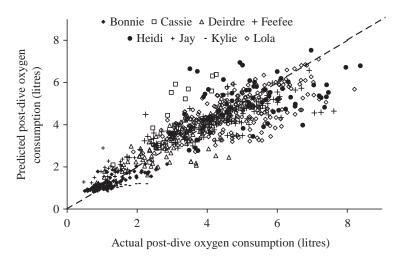
Fig. 10. Test of the model's predictions of post-dive oxygen consumption ($\dot{D}_{O_2}$). Each point is an individual dive, with a different symbol for each animal. The predicted post-dive O_2 is the $\dot{D}_{O_2}$ predicted by the model for that dive using the model that was fitted excluding all the dives from that animal. The broken line represents a 1:1 relationship between predicted and observed oxygen consumption.

difference in the extent of the hypometabolism demonstrated between these studies and ours is probably a result of the higher levels of activity of the animals in our study and the fact that our animals were diving voluntarily and were therefore not exhibiting the extreme response typical of forced dives.

Our findings have implications for estimates of food consumption by seal populations. Bioenergetic models of phocid seal populations generally use a multiplier of 2–3 times the Kleiber predicted metabolic rate to estimate the energy requirements associated with at-sea activity in free-living phocid seals (Olesiuk, 1993; Mohn and Bowen, 1996; Nilssen et al., 2000). If free-living seals spend a significant portion of their time at the lower rates demonstrated in the present study, current estimates of energy requirements might be higher than they are in reality. More information is therefore required on the activity budgets and foraging energy requirements of wild seals.

Mass and DMR

Mass had a large effect on absolute diving metabolic rate (l min^{-1}). This is not surprising since, on an individual level, energy associated with maintaining body tissues probably represents the biggest single portion of expenditure and this is obviously higher in absolute terms for larger animals. On a per kg basis, pups had a higher DMR than adults but, when DMR was expressed as a multiple of Kleiber, pups had identical rates to adults, suggesting that DMR scales intra-specifically with mass$^{0.75}$. This result emphasises the premium of large size to diving ability. Furthermore, bioenergetic models generally use a higher multiplier of Kleiber's predicted metabolic rate for juveniles than the one used for adults to predict average requirements. This may be a source of error in such models, especially for populations

that are skewed towards juvenile age classes (e.g. Olesiuk, 1993).

Dive duration and swim speed

Both the duration and mean swim speed of a dive influenced DMR. Our results indicate that DMR decreases with increasing dive duration. Several other studies have reported a similar relationship between DMR and submersion duration. Thorson (1993) reported that elephant seals showed decreasing MR with increasing submersion duration. Hurley and Costa (2001) reported a similar finding for California sea lions. The plot of DMR as a function of dive duration shows points scattered below a maximum boundary that decreases curvilinearly with dive duration and above a minimum boundary that is largely independent of dive duration. A similar pattern has also been demonstrated in free-ranging Weddell seals (Castellini et al., 1992) and in previous laboratory studies of grey seals (Reed et al., 1994). The points that form the upper boundary are likely to represent the maximum possible aerobic metabolic rate, a value that is determined by a combination of the dive duration and the size of the oxygen store available to the animal during that dive. Our data suggest that there is close agreement between the maximum DMRs exhibited by our seals and the limit imposed by body oxygen stores. Only 2% of all dives measured exceeded the theoretical capacity of the animal to provide all the energy for the dive aerobically. We could not directly address the possible contribution of anaerobic metabolism to DMR in this study, since we did not measure blood lactate levels. However, we consistently observed a high proportion (80–90%) of time spent submerged during diving periods, suggesting that animals were not using anaerobic metabolism to extend dive duration.

When submerged, diving mammals must balance the energetic demands of locomotion with the conservation of a limited oxygen store (Castellini et al., 1992; Skrovan et al., 1999). Swimming activity during a dive influences the rate of oxygen consumption of the actively exercising muscles, which in turn affects the aerobic limit to dive duration. Williams et al. (1999) found that Weddell seal dives that consisted of prolonged gliding resulted in lower post-dive oxygen consumption than dives that consisted of continuous swimming, although the duration of the dives or surface periods was not reported so a direct comparison in terms of metabolic rate is not possible. In the present study, mean swim speed during the dive had a significant effect on the metabolic rate of a dive, and the dives with the highest swim speeds also tended to be the shortest. Hindell et al. (2000) examined the influence of swimming speed on dive duration in free-living southern elephant seals (Mirounga leonina). They showed that maximum dive duration is dependent on swimming speed; consequently, a seal has a range of different ADLs depending on its activity during the dive, as well as possibly the extent of metabolic suppression. It is clear that exercise performed when

submerged requires energy for the working muscles, and this rate of energy usage has implications for the amount of time a seal can remain submerged before having to return to the surface to replenish oxygen stores. This idea is by no means novel and has been discussed by many authors (e.g. Kooyman, 1989; Fedak 1986; Thompson et al., 1993; Hindell et al., 2000) but there have been few empirical studies describing how whole-body metabolism varies as a function of variation in pinniped diving activity of the type performed routinely by free-living animals.

Metabolic rate of grey seals measured in a swim flume displayed a fivefold range, with activity ranging from sleep to swimming at 1.6 m s^{-1} (Fedak et al., 1988). Furthermore, the fraction of time spent submerged decreased as speed increased (Fedak, 1986). This pattern was also seen in harbour seals swimming in a flume at speeds over 1.2 m s^{-1} (Williams et al., 1991). Our seals had metabolic rates that ranged between 1 and 4 times predicted basal rates as speeds increased up to a maximum of 1.4 m s^{-1}. We did not observe a similar increase in the proportion of time spent at the surface when seals were swimming at higher speeds during dives. The present study differs from those involving seals swimming in flumes in that any swimming activity is voluntary and occurs as part of a dive. The mean swim speed of our seals rarely reached these higher speeds; although the speed reported for each dive is the mean for the whole dive, some dives consist of bursts of fast swimming at speeds over 2 m s^{-1}. Similarly, in nature, grey seals spend a significant fraction of their time during dives motionless or swimming at low speeds (Thompson and Fedak, 1993). Furthermore, seals in a flume are forced to swim just below the surface where drag is much higher than a few metres below, a behaviour that phocid seals do not display in the wild. This will add to the energetic costs for animals in flumes, costs that are not likely to be an issue for free-living, foraging grey seals.

The diving patterns exhibited by wild seals are likely to be a product of a complex interplay of many interrelated variables. On an individual dive level, the outcome will be particular to a set of circumstances such as prey type, distribution and size. Unravelling these relationships further will require approaches that combine laboratory studies of physiology and behaviour, such as this one, with field studies on diving behaviour and observations and further lab studies of a more manipulative nature testing behavioural and physiological responses to differences in prey type and distribution.

Predictive model

Across the range of mass in this study (from juvenile seals of 32 kg to adults of 150 kg), the relationship between predicted and actual metabolic rate had a slope close to 1. On average, over all dives tested, our model overestimated actual metabolic rates by 4%. To put these errors into context, predicting diving metabolic rates for the animals in this study by applying a Kleiber multiplier of 2 resulted in overestimates of 14–18%. Our model predicted the metabolic rate of seals in captivity,

with relatively little error, based on their behaviour as monitored by telemetry. Therefore, we can conclude that applying the model to telemetry-derived behavioural data from wild seals would allow us to predict the metabolic costs of dives of different types exhibited in the wild with increased accuracy over the use of a simple multiplier applied over all at-sea behaviour. We can then use these predictions as an input into models that predict the energy requirements of the population.

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