Direct measures of pinniped field metabolic rate: implications for fisheries models

Mario Acquarone [*], Erik W. Born [§] & John R. Speakman [#]

[*] National Environmental Research Institute of Denmark, P.O. Box 359, DK-4000 Roskilde, Denmark and Royal Veterinary and Agricultural University, DK-1870 Frederiksberg, Denmark

[§] Greenland Institute of Natural Resources, P.O. Box 570, DK-3900 Nuuk, Greenland

[#] Aberdeen Centre for Energy Regulation and Obesity (ACERO), School of Biological Sciences, University of Aberdeen, Aberdeen AB3 2TZ, United Kingdom and ACERO, Division of Energy Balance and Obesity, Rowett Research Institute, Aberdeen, AB21 9SB

Abstract

The food requirements of free-ranging pinniped species can be derived from measures of Field Metabolic Rate (FMR) by the Doubly Labelled Water (DLW) method. However, fisheries models typically rely on indirect estimates of pinniped food requirements based on their theoretical basal metabolism multiplied by 3-4. Reluctance to employ direct measures of metabolism might be due to the limited body-size range of the seven pinniped species for which DLW studies are available to date. The measure of FMR of walruses in this study extends this range by a factor of 10. It also allows the derivation of a predictive equation for pinniped FMR [Ln-FMR (MJ/day) = 0.173 + 0.816 Ln-Total Body Mass (kg)] and it suggests that pinniped food requirements might be double as high as assumed in fisheries models.

Keywords: food requirements, metabolic rate, feeding rates, pinnipeds, marine mammals, doubly labelled water; *Odobenus rosmarus*

Introduction

Conflicts between fisheries and marine mammals have escalated and are likely to increase during the next century (DeMaster *et al.* 2001). Fisheries models for evaluating the impact of marine mammal predators on fish stocks require accurate estimates of food intake rates (Trites *et al.* 1997; Winship *et al.* 2002; Bjorge *et al.* 2002; Innes *et al.* 1987; Bowen 1997). Field energy demands (generally called Field Metabolic Rate or FMR) and thus food consumption rates of free-ranging marine mammals have been estimated from their heart rate (Boyd *et al.* 1999) or by multiplying their inferred basal metabolic rate (BMR) by some factor (BMR x 2-3) (Innes *et al.* 1987; Lavigne *et al.* 1986). However, heart rate monitoring is a valuable method for estimating metabolic rates, but it requires species-specific validation of the relationship between heart rate and metabolic rate and it may not accurately reflect metabolic rates during digestive events (McPhee *et al.* 2003). Furthermore the adaptations of marine mammals to diving, e.g. bradycardia (Elsner 1999), may complicate its interpretation. Finally, the use of BMR to estimate food consumption of marine mammals is problematic, as the conditions required for the measurement of BMR were established for terrestrial animals (White & Seymour 2003) and may be inappropriate for marine mammals.

An alternative approach is to calculate the energy demands from CO_2 production, measured from the differential elimination of two isotopic tracers in body water – known as the Doubly Labelled Water (DLW) technique (Speakman 1997; Costa & Gales 2003). This technique avoids some of the problems associated with the other methods, and the resultant FMR measurement can be incorporated directly into fisheries and other ecological models. A problem with the DLW technique is the high cost of the isotopic labels, which increases exponentially with body mass. For this reason the 7 pinniped species for which DLW estimates of FMR have been derived are far lighter than the largest species (Reeves *et al.* 1992) and ranged only between 27 and 114 kg (Costa & Gales 2003; Nagy *et al.* 1999). A reliable allometric equation for FMR versus body mass (BM) can be generated for animals within this BM range (Nagy *et al.* 1999), but the predicted estimates for larger animals are potentially inaccurate due to extreme extrapolation, which has perhaps contributed to the reluctance of modellers to include DLW measurements into fisheries model calculations.

In this study we used the DLW method to estimate the FMR of two free-ranging male walruses. The body mass of the two animals in this study extends by 11 fold the mass of the previous largest pinniped measured by the DLW method (and they are by far the largest animals studied using this methodology). These estimates extend the validity of the allometric equation for pinniped FMR across most of the body size range of pinnipeds.

Materials and Methods

Study site and animals

The study animals, all adult male Atlantic walruses (*O.r.rosmarus*) (Table 1), were chosen from an all-male group on a terrestrial haulout site in NE Greenland at 76°52.8'N, 19°37.9'W (Born *et al.* 1995).

In August 2001, two animals were enriched with DLW. Before handling, they were completely immobilised (Born & Knutsen 1992a). During immobilisation the animals' axillary girth and standard body length (Committee on Marine Mammals 1967) were measured for estimation of TBM (Knutsen & Born 1994; Born *et al.* 2003), a satellite radio and a dive recorder were attached to the tusks and venous access was gained by catetherization of the epidural vein in the lumbar region for isotope enrichment and blood sampling. Upon recapture a similar immobilisation procedure was used, the size measures were repeated along with blood sampling and instrument data retrieval.

For comparison in August 2000 (3) and 2001 (1) four other animals were also instrumented with a satellite radio and a dive recorder to obtain behavioural data.

Energy expenditure

At initial capture, the two designated animals' venous blood was sampled through the catheter for determination of background isotope concentration. Each animal was subsequently administered an intravenous dose of 97.75 g of deuterated water, 43.9 % ^2H_2O (Merck 1.13366, E.Merck, D-6100 Darmstadt, Germany), and 157.62 g of ^{18}Oxygen enriched water, 41.5 % $H_2{}^{18}O$ (Rotem Industries Ltd., P.O.Box 9046, Beer-Sheva 84190, Israel). A series of blood samples was taken at approximately 30-

minute intervals for 4 hours for determination of the isotope equilibration curve, and isotope dilution spaces. Animal A was enriched on the 16 August 2001 at 16:42 and recaptured on the 21 August 2001 at 17:52. Animal B was enriched on the 7 August 2001 at 21:08 and recaptured on the 16 August 2001 at 15:30. Immediately after sampling whole blood was stored in 2.0 ml standard glass vials and flame sealed into 100 µl precalibrated glass pipettes (Modulholm A/S, Vasekaer 6-8, DK-2730 Herlev, Denmark, VITREX model 1272). Seawater background samples were collected and sealed in 2.0-ml glass vials throughout the experimental period to investigate variation in environmental isotope enrichment. All samples were stored at ambient temperature (max. 3 °C) while in the field and were subsequently kept at 5 °C prior to analysis.

All blood samples were vacuum distilled into Pasteur pipettes (Nagy 1983) and the distillate was used for determination of both ^{18}O and ^{2}H concentration. For ^{2}H-analysis H_2 gas was produced by reduction with excess $LiAlH_2$ as described in Ward et al. (2000) For ^{18}O-analysis 10 µl of distillate was measured using the small sample equilibration method (Speakman *et al.* 1990). The isotopic composition of the injectate was measured by diluting a weighed quantity of the injectate (0.1-0.2 ml) into a weighed quantity of tap water (60 ml). This mixture was then treated in exactly the same manner as the distillate from the blood samples. In each batch of samples for analysis, laboratory standards were included to account for day-to-day variation in the analyser. All isotope enrichments were measured in δ-units and converted to ppm using the established ratios for reference materials. We evaluated precision of the derived estimate of CO_2 production using the iterative procedures in Speakman (1995), and converted the mean estimate to metabolic rate assuming an RQ of 0.85. Calculations were made using the DLW program (version 1.0, Speakman and Lemen, Naturware, 1999).

Activity of the animals

The two study animals and four other walruses were instrumented with satellite linked radio transmitters and dive recorders to obtain data on movement, haulout and dive activity (Table 1).

An ARGOS System SPOT2 satellite-linked radio transmitter with “time at temperature” histograms and a MK7 Time Depth Recorder (TDR) with 500 m range (Wildlife Computers, 16150 NE

85th Street - Suite 226, Redmond, Washington 98052 USA) were attached to each of the tusks of six adult male walruses using the method in Born and Knutsen (1992b). The TDR's were programmed to sample depth, temperature, and light level at intervals of 5, 300 and 300 or 15, 600 and 120 seconds respectively. The GIS software ArcView 3.2a was used for calculation of the horizontal movement of the walruses after satellite-telemetered locations of all quality classes had been run through a PC-SAS®ARGOS-filter (V.5.0, D.Douglas USGS, Alaska Science Center, 100 Savikko Road, PO Box 240009, Douglas, AK 99824, USA, unpublished method).

The TDR data were analysed using the software provided by the manufacturer (the Zero-Offset-Correction and Dive-Analysis). Periods when the walruses were hauled out on land or ice were excluded from the analysis of dive activity. Minimum depth for dives to be analysed and maximum depth to be considered at surface were set to 6 m. The time spent at sea or out of the water was determined by analysing the temperature record of the TDR, where only temperatures below 2.5 °C were considered as coming from a submerged sensor. Number of dives, dive duration, surface times were also determined for each individual.

Results

Animals spent on average 33.0 % of their time hauled out which is typical of walruses during summer (Born & Knutsen 1997). Diving activity accounted for 50.8 % of the time spent at sea, with an average rate of 165 dives per day with a duration of 3.5-5.5 min (Figure 1 and Table 1). Although the time spent hauled out by the two DLW animals was similar, B was diving more actively than A as indicated by the number of dives per day, the mean dive duration and dive depth and the maximum depth reached (Table 1).

A previous study (Lydersen *et al.* 1992) had suggested that isotopes (tritium) in walruses might equilibrate within 1 hour. We found however that equilibration time of the isotopes took approximately 2.5-3.0 h. We therefore used these estimates of the initial isotope enrichment combined with the recapture samples to estimate field metabolic rate.

Body water (BW) percentage of body mass from dilution of the oxygen isotope was 45.0 % in A, and 49.5 % in B. The lower BW content of the larger A suggested that it had relatively more blubber. The estimated FMR's were 345.0 (SE 7.5) MJ/day for A and 417.4 (SE 6.2) MJ/day for B, using the single-pool model for calculation (Lifson & McClintock 1966) (mean = 381.2 MJ/day). Using the two-pool model (Speakman 1997) and the mean observed dilution space ratio (Schoeller *et al.* 1986) (1.09), the corresponding estimates were 328.1 (SE 8.7) MJ/day and 365.4 (SE 15.4) MJ/day, respectively (mean = 346.8 MJ/day). A best fit relationship between FMR and BM including only all previous DLW-studies of pinnipeds (Table 2; Lifson and McClintock (1966) single-pool calculation) explained 88.3 % of the variation in FMR. The direct estimate of FMR in the present study was about 43 % lower than that predicted by this relationship clearly indicating the need for a more precise equation for larger pinnipeds. The new allometric equation [Ln-FMR (MJ/day) = 0.173 + 0.816 Ln-Total Body Mass (kg)] for pinniped FMR in this study explained 96.1 % of the variation (n=8 species) (Figure 2). Including data on diving behaviour and activity did not improve this relationship.

Environmental background isotope enrichments measured in sea water did not fluctuate significantly during the study period and did not differ significantly from the background enrichments in the animals' blood collected prior to injection.

Discussion

A FMR of 381 MJ/day for a 1300 kg walrus as measured in this study, corresponds to the consumption of about 83 kg food per day (fresh matter) calculated from the mean energy composition of the walrus prey items from East Greenland (Born *et al.* 2003). This value is well within previously estimated range of 42-92 kg food intake for free-ranging walruses weighing 1100-1200 kg (Fay 1982).

The greater FMR value of B may have been due to its higher diving activity (Table 1). Haul-out time for all animals measured by TDR in this study was on average 33 % which is higher than 30 % previously reported from this area (Born & Knutsen 1997) 26 % from Alaska (Hills 1992) and 26 % from Svalbard (Gjertz *et al.* 2001). However for the same areas variability in haul-out time between individuals can be considerable (Gjertz *et al.* 2001; Born & Knutsen 1997).

The single pool equation of Lifson and McClintock (1966) to derive FMR was used here for consistency with the previous studies, but this equation over-estimates energy demands for animals that are larger than 5-10 kg (Speakman 1997). A two-pool model calculation is probably more appropriate. Since most papers do not quote the necessary parameters to make recalculations, we were unable to construct a prediction based on the two-pool method. However, our estimates, and those of Costa and Gales (2003), indicate that the overestimate using the single-pool method (Lifson & McClintock 1966) might only be 9-17 % (averaging 13 %).

Current fisheries models that have utilised estimated daily food consumption predicted from multiples of BMR [predicted from body mass using the Kleiber equation (Kleiber 1932; 1961)] have routinely assumed that the FMR of pinnipeds is around 3 x BMR (Trites *et al.* 1997; Winship *et al.* 2002; Bjorge *et al.* 2002; Nilssen *et al.* 2000). Our study, along with the other DLW studies contributing to the derived equation, however, suggests that this is a serious underestimate of pinniped food intake. FMR's derived from the equation in this study average between 5.5 (for a 100-kg seal) and 6.5 (for a 1300-kg seal) times the Kleiber BMR prediction. Using these direct estimates of FMR would more than double the estimated daily food requirements of pinnipeds and their projected impacts on prey species. Consequently, many current fisheries models may seriously underestimate the impacts of marine mammal predators on fish stocks.

The allometric equation for pinniped FMR derived here can be utilised to revise the impact of pinnipeds on fish stocks in fisheries models, since it provides a mass-specific prediction of FMR for most species without the need for extrapolation. Most importantly, it is based on *direct* measurements of FMR rather than inferences from multiples of basal metabolism.

The costs of DLW preclude its routine use in studies of the energetics of larger pinniped species such as the walrus. Nevertheless, the current study has demonstrated that occasional measurements of FMR can improve and refine the assumptions that underpin models being used to assess levels of competition between seals and fisheries.

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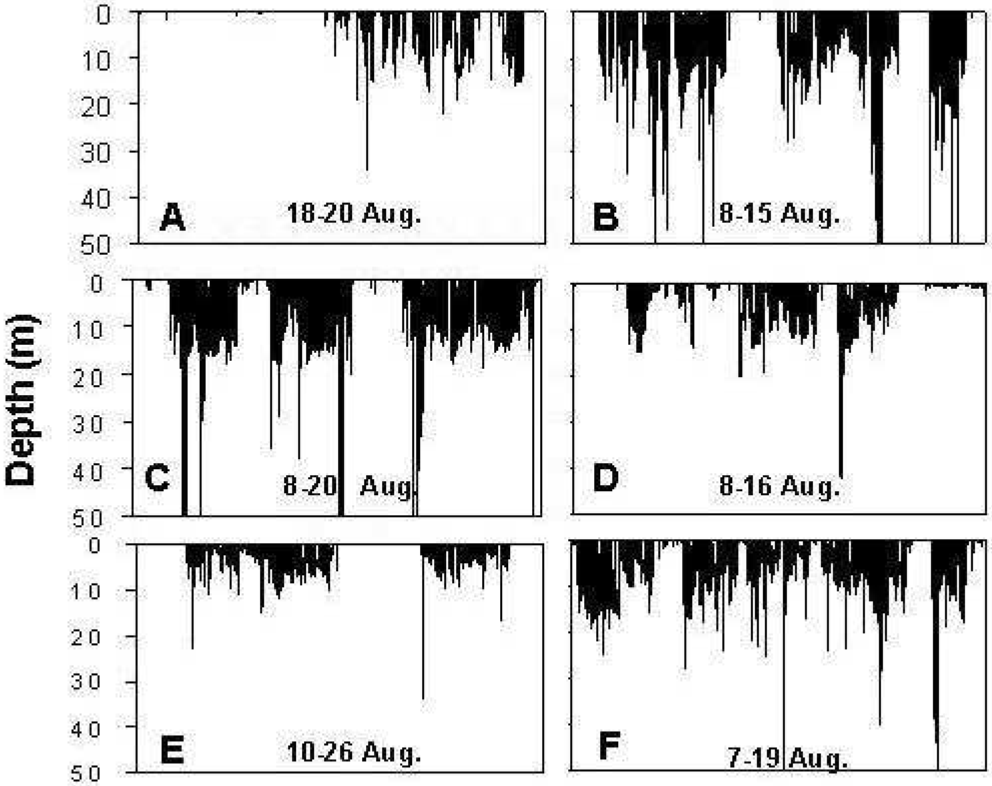

Figure 1: Dive profiles by Time-at-Depth recorders of six adult male walruses in North-east Greenland in August 2000 and 2001 (Table 1).

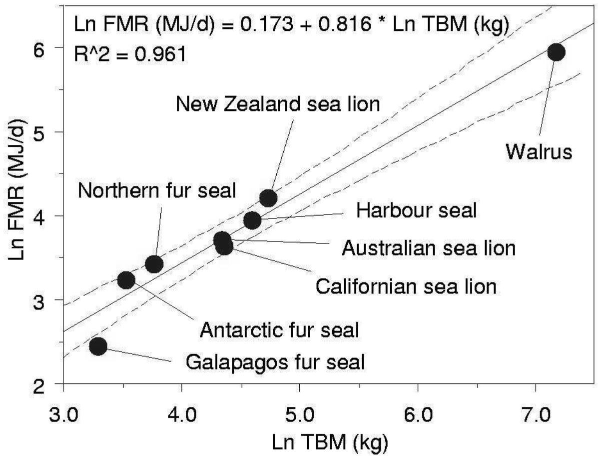

Figure 2: Field metabolic rate (FMR) in relation to body mass (BM) in eight different pinniped species based on measurements using doubly labelled water (actual data in Table 2). 95 % confidence intervals of the regression are shown as dashed lines.

ID	Mass	Days monitored	Time hauled-out	Dives/day	Mean dive duration	Mean depth	Max depth
	kg	n	%	n	min (sd)	m (sd)	m
A	1,370	5.0	27.2	108	3.5 (2.1)	12.6 (5.5)	55
B	1,250	8.7	27.2	133	4.4 (2.1)	15.8 (10.5)	145
C	1,546	14.9	41.1	208	4.8 (1.8)	14.9 (12.9)	192
D	1,115	12.0	47.8	170	5.1 (1.4)	12.1 (5.1)	84
E	1,086	7.2	34.5	200	4.9 (1.1)	11.3 (4.2)	51
F	1,284	12.0	20.0	170	5.5 (2.2)	12.3 (7.6)	189

Table 1: Activity of six adult male walruses in North-east Greenland during August 2000 and 2001.

Species	**Scientific name**	**BM (kg)**	**FMR (MJ/d)**
Galapagos fur seal[1]	*Arctocephalus galapagoensis*	27.0	11.7
Antarctic fur seal[1,2]	*Arctocephalus gazella*	34.2	25.7
Northern fur seal[1,2]	*Callorhinus ursinus*	43.4	30.6
Australian sea lion[1,2]	*Neophoca cinerea*	76.4	40.9
Californian sea lion[2]	*Zalophus californianus*	78.0	38.6
Harbour seal[2]	*Phoca vitulina*	99.0	52.5
New Zealand sea lion[1,2]	*Phocarctos hookeri*	114.1	68.0
Walrus[3]	*Odobenus rosmarus*	1,310.0	381.2

Table 2: Average body mass and field metabolic rate by doubly labelled water in eight species of pinnipeds. References: 1-Costa & Gales 2003, 2-Nagy *et al.* 1999, 3-this study.