Field Metabolic Rates of Walrus (*Odobenus rosmarus*) Measured by the Doubly Labeled Water Method

Mario Acquarone,[1] Erik W. Born,[2] and John R. Speakman[3]

[1]*National Environmental Research Institute, Frederiksborgvej 399, DK-4000 Roskilde, Denmark*
[2]*Greenland Institute of Natural Resources, P.O. Box 570, DK-3900 Nuuk, Greenland*
[3]*Aberdeen Centre for Energy Regulation and Obesity (ACERO), School of Biological Sciences,
University of Aberdeen, Aberdeen AB3 2TZ, United Kingdom*

Current Address: Frue Kirkestræde 5, DK-5000 Odense, Denmark (MA)

Abstract

The energy and food requirements of free-ranging pinniped species are difficult to measure and, as a consequence, are unknown for most species. They can be inferred from measures of Field Metabolic Rate (FMR) made by the Doubly Labeled Water (DLW) method, however. In this work, we confirmed our hypothesis that the FMR of pinnipeds measured by DLW can be described by an allometric relationship as a function of body weight. Although costly and difficult to apply, the DLW method is one of the few possible methods generating estimates of energy demands for unrestrained, free-living animals. The results of its application on two adult, male, free-living Atlantic Walruses (*Odobenus rosmarus rosmarus*), weighing 1,370 kg and 1,250 kg, respectively, estimated from length and girth measures, are presented here. These data extend the size range of the seven pinniped species for which the DLW method has been applied by a factor of 10. The animals were measured at a site in northeast Greenland (76° N) during the summer. FMR was dependent on the pool model for estimating metabolic rate and was approximately 13% higher when using the single-pool compared with the two-pool model. The estimates using the two-pool model were 328.1 (SE 8.7) MJ•day -1 and 365.4 (SE 15.4) MJ•day -1 for each of the two walruses. These figures were combined with estimated FMR using the same method in seven other pinniped species to derive a new, refined predictive equation for pinniped FMR (Ln-FMR [MJ•day -1] = 0.173 + 0.816 Ln-Total Body Mass [kg]). This equation suggests that pinniped food requirements might sometimes be twice as high as that assumed in some fisheries models, which are based on multiples of the theoretical basal metabolism.

Key Words: Walrus, *Odobenus rosmarus*, field metabolic rate, feeding rates, pinnipeds, Doubly Labeled Water, Greenland

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 (Innes et al., 1987; Bowen, 1997; Trites et al., 1997; Bjorge et al., 2002; Winship et al., 2002). 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 (Innes et al., 1987). While heart rate monitoring is a valuable method for estimating metabolic rates (Butler et al., 2004), 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—for example, bradycardia (Elsner, 1999)—may complicate its interpretation. On the other hand, the use of BMR to estimate food consumption of marine mammals is problematic because the conditions required for the measurement of BMR were established for terrestrial animals (White & Seymour, 2003) and may be inappropriate for marine mammals. Moreover, individual estimates for species around an allometric prediction of BMR are often substantially discrepant, and the multiplication factor used to convert basal to field metabolism generates its own uncertainty in the final result. In consequence, the resultant estimates using this BMR-factorial approach may easily be in error by a factor of 2.

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 Labeled Water (DLW) technique (Lifson & McClintock, 1966; 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 enormously with body mass (Butler et al., 2004). Because of the high costs of working on larger species, the seven pinniped species for which DLW estimates of FMR have been published are far lighter than the largest species (Reeves et al., 1992) and ranged only between 27 and 114 kg (Nagy et al., 1999; Costa & Gales, 2003). 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 modelers to include DLW measurements into fisheries model calculations. Our hypothesis for this work was that FMR of pinnipeds measured by DLW can be described by an allometric relationship as a function of body weight, which is valid for a large part of the spectrum of pinniped body sizes.

In this study, we used the DLW method to estimate the FMR of two free-ranging male walruses. The BM of the two animals in this study extends by ten-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 ranges 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 northeast Greenland at 76° 52.8' N, 19° 37.9' W (Born et al., 1995). In August 2001, two walruses were enriched with DLW. Before handling, they were completely immobilized (Born & Knutsen, 1992a). During immobilization, the animals' axillary girth and standard body length (American Society of Mammalogists, 1967) were measured for estimation of Total Body Mass (TBM) (Knutsen & Born, 1994; Born et al., 2003); a satellite radio and a time-depth recorder (TDR) were attached, one on each tusk; and venous access was gained by catheterization of the epidural vein in the lumbar region for isotope enrichment and

blood sampling. Upon recapture, a similar immobilization procedure was used, the size measures were repeated, and blood sampling and instrument data were retrieved.

For comparison, in August 2000, three other walruses and an additional walrus in 2001 were also instrumented with satellite radios and TDRs to obtain behavioral data, but they were not enriched with DLW. By monitoring the activity patterns of a control group of animals not using DLW, we could confirm that the behavioral patterns of the animals that were measured were not adversely affected by the DLW protocols and are, hence, relevant more widely than the small sample we could afford to inject with isotopes.

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 then taken at approximately 30-min intervals for 4 h for determination of the isotope equilibration curve and isotope dilution spaces. Animal A was enriched on 16 August 2001 at 1642 h (all times reported are Universal Time [UT]) and recaptured on the 21 August 2001 at 1752 h. Animal B was enriched on 7 August 2001 at 2108 h and recaptured on 16 August 2001 at 1530 h. Immediately after sampling, whole blood was flame sealed into 100-ml precalibrated glass pipettes (Modulholm A/S, Vasekaer 6-8, DK-2730 Herlev, Denmark, VITREX model 1272). Seawater background samples were collected and flame 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 (max. 20 d) and were subsequently kept refrigerated 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 ^2H concentration. For ^2H-analysis H_2 gas was produced by reduction with excess $LiAlH_2$ as described in Ward et al. (2000). For ^{18}O-analysis, 10 ml 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 to 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 analyzer. All isotope enrichments were measured in d-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 TDRs 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 TDR with 500-m range (Wildlife Computers, 16150 NE 85th Street, Suite 226, Redmond, WA 98052, USA) were each attached to a tusk of six adult male walruses, using the method in Born & Knutsen (1992b). The TDRs were programmed to sample depth, temperature, and light level at intervals of 5, 300 and 300 or 15, and 600 and 120 s, respectively. The GIS software *ArcView*, *Version 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*, *Version 5.0* (D. Douglas USGS, Alaska Science Center, 100 Savikko Road, P.O. Box 240009, Douglas, AK 99824, USA, unpub. method).

The TDR data were analyzed 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 analyzed 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 analyzing the temperature record of the TDR, where only temperatures below 2.5° C were considered as coming from a submerged sensor. Numbers of dives, dive duration, and surface times were also determined for each individual.

Results

All six animals spent on average 33.0% of their time hauled out (Table 1), which is typical of walruses during summer (Born et al., 1997). Diving activity accounted for 50.8% of the time spent at sea, with an average rate of 165 dives per day, each lasting 3.5 to 5.5 min (Figure 1; Table 1). Although the time spent hauled out by the two DLW animals was similar, Animal B was diving more actively than Animal A as indicated by the number of dives per day, the mean dive duration and dive depth, and the maximum depth reached (Table 1). The data for the two DLW animals did not differ from the other four controls in any parameter studied.

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

Body water (BW) percentage of BM from dilution of the oxygen isotope was 45.0% in Animal A and 49.5% in Animal B. The lower BW content of the larger Animal A suggested that it had relatively more body fat. The estimated FMRs were 345.0 (SE 7.5) MJ•day -1 for Animal A and

Table 1. Activity of six adult male walruses in northeast Greenland during August 2000 and 2001; the energy expenditure of Animals A and B was determined using DLW in 2001. Animals D, E, and F were studied in 2000; and A, B, and C were studied in 2001.

| ID	Condition	Mass kg	Days monitored *n*	Time hauled out %	Dives/day *n*	Mean dive duration min (sd)	Mean depth m (sd)	Max depth m
A	DLW	1,370	5.0	27.2	108	3.5 (2.1)	12.6 (5.5)	55
B	DLW	1,250	8.7	27.2	133	4.4 (2.1)	15.8 (10.5)	145
C	Control	1,546	14.9	41.1	208	4.8 (1.8)	14.9 (12.9)	192
D	Control	1,115	12.0	47.8	170	5.1 (1.4)	12.1 (5.1)	84
E	Control	1,086	7.2	34.5	200	4.9 (1.1)	11.3 (4.2)	51
F	Control	1,284	12.0	20.0	170	5.5 (2.2)	12.3 (7.6)	189
Average	Control	1,275	10.0	33.0	165	4.7	13.2	119
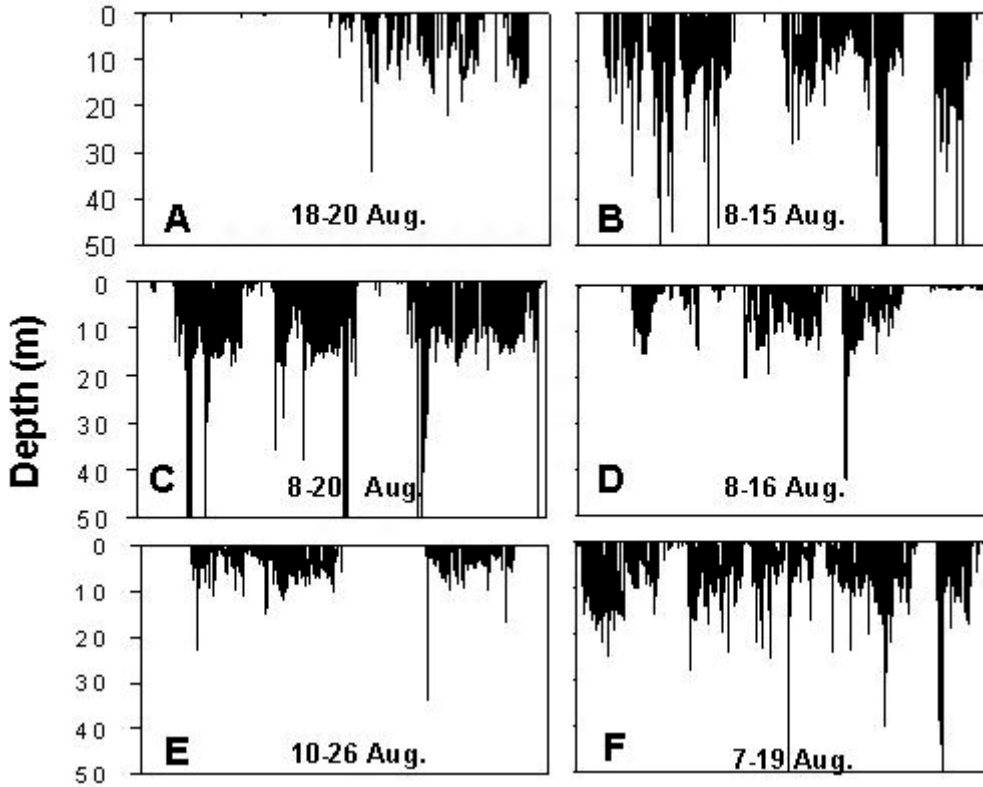
Figure 1. Dive profiles measured by use of time-depth recorders in six adult male walruses in northeast Greenland in August 2000 and 2001 (see also Table 1)

417.4 (SE 6.2) MJ•day -1 for Animal B, using the single-pool model for calculation (Lifson & McClintock, 1966) (mean = 381.2 MJ•day -1). Using the two-pool model (Speakman, 1997) and the mean observed dilution space ratio of 1.09 (Schoeller et al., 1986), the corresponding estimates were 328.1 (SE 8.7) MJ•day -1 and 365.4 (SE 15.4) MJ•day -1, respectively (mean = 346.8 MJ•day -1). A best-fit relationship between FMR and BM, including only the previous DLW studies of pinnipeds (Table 2; Lifson & McClintock's [1966] single-pool calculation) explained 88.3% of the variation in FMR. For a pinniped weighing 1,300 kg, this equation would predict an FMR of 665 MJ. The direct estimate of FMR in the present study was 43.0% lower than this prediction, highlighting the difficulties of extrapolation beyond the original data from which the equation was generated. This discrepancy clearly indicated the need for a more precise equation for larger pinnipeds. We derived such an equation using the estimated FMR for the walrus measured here based on the single-pool model. The new allometric equation (Ln-FMR [MJ•day -1] = 0.173 + 0.816 Ln-Total Body Mass [kg]) for

Table 2. Average body mass and Field Metabolic Rate by the Doubly Labeled Water method in eight species of pinnipeds

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

[1]Costa & Gales, 2003; [2]Nagy et al., 1999; [3]this study

Ln FMR (MJ/d) = 0.173 + 0.816 * Ln TBM (kg)
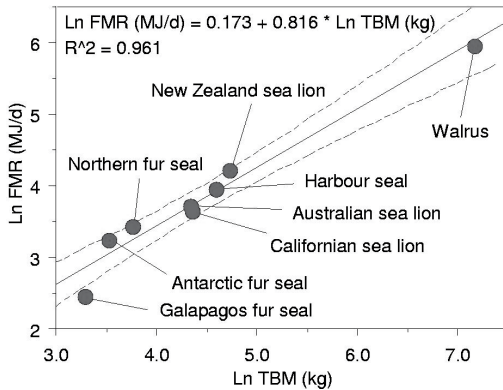R^2 = 0.961

Figure 2. Field Metabolic Rate (FMR) in relation to body mass (BM) in eight different pinniped species based on measurements using the Doubly Labeled Water method (actual data and references in Table 2); 95% confidence intervals of the regression are shown as dashed lines.

pinniped FMR explained 96.1% of the variation (*n* = 8 species) (Figure 2). Including data on diving behavior and activity (where available) did not improve the relationship.

Discussion

An FMR of 381 MJ•day -1 for a 1,300 kg walrus as measured in this study corresponds to the consumption of about 95 kg food per day (fresh matter) calculated from the mean energy composition of the walrus prey items from East Greenland (Born et al., 2003) and assuming the average digestive coefficient for energy for a clam diet (92.7%) (Fisher et al., 1992). This value is within and at the upper end of the previously estimated range of 42 to 92 kg food intake for free-ranging walruses weighing 1,100 to 1,200 kg (Fay, 1982).

The greater FMR value of Animal B may have been due to its higher diving activity (Table 1). The mean haulout time for all six animals measured by TDR in this study was similar to previous estimates from this and other areas: 30% from this area (Born & Knutsen, 1997), 26% from Alaska (Hills, 1992), and 26% from Svalbard (Gjertz et al., 2001). Variability in haulout time between individuals at all sites is considerable (Born & Knutsen, 1997; Gjertz et al., 2001) as was also observed in the present study.

For consistency with the previous studies, the single-pool equation of Lifson & McClintock (1966) to derive FMR was used here but this equation overestimates energy demands for animals that are larger than 5 to 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. Our estimates, and those of Costa & Gales (2003), indicated that the overestimate using the single-pool method (Lifson & McClintock, 1966) might only be 9 to 17% (averaging 13%). Since we had to derive a predictive equation based only on the single-pool model, this overestimate of food requirements should be borne in mind if the equation is utilized in a predictive manner.

Current fisheries models that have utilized estimated daily food consumption predicted from multiples of BMR (predicted from BM using the Kleiber equation [Kleiber, 1932, 1961]) have routinely assumed that the FMR of pinnipeds is around 3x BMR (Trites et al., 1997; Nilssen et al., 2000; Bjorge et al., 2002; Winship et al., 2002). Our study, along with the other DLW studies contributing to the derived equation, however, suggested that this is a serious underestimate of pinniped food intake even if the overestimate from using the single-pool model is taken into account. FMRs derived from the equation in this study averaged between 5.5 (for a 100-kg seal) and 6.5 (for a 1,300-kg seal) times the Kleiber BMR prediction (4.8x to 5.7x if the 13% lower estimate from the two-pool model is used). 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 utilized 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 the DLW method preclude its routine use in studies of the energetics of larger pinniped species such as the walrus. Nevertheless, the current study 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.

Commission for Scientific Research in Greenland, the Greenland Institute of Natural Resources, the Danish National Environmental Research Institute, and the University of Aberdeen) and the European Commission's MCTS.

Literature Cited

American Society of Mammalogists. (1967). Standard measurement of seals. *Journal of Mammalogy*, *48*(3), 459-462.

Bjorge, A., Bekkby, T., Bakkestuen, V., & Framstad, E. (2002). Interactions between harbour seals, *Phoca vitulina*, and fisheries in complex coastal waters explored by combined Geographic Information System (GIS) and energetics modelling. *ICES Journal of Marine Science*, *59*(1), 29-42.

Born, E. W., & Knutsen, L. Ø. (1992a). *Immobilization of Atlantic walrus (*Odobenus rosmarus rosmarus*) by use of etorphine hydrochloride reversed by diprenorphine hydrochloride* (Technical Report No. 14). Copenhagen, Denmark: Greenland Home Rule, Department for Wildlife Management. 15 pp.

Born, E. W., & Knutsen, L. Ø. (1992b). Satellite-linked radio tracking of Atlantic walruses (*Odobenus rosmarus rosmarus*) in northeastern Greenland, 1989-1991. *Zeitschrift fur Saugetierkunde – International Journal of Mammalian Biology*, *57*(5), 275-287.

Born, E. W., & Knutsen, L. Ø. (1997). Haul-out and diving activity of male Atlantic walruses (*Odobenus rosmarus rosmarus*) in NE Greenland. *Journal of Zoology (London)*, *243*, 381-396.

Born, E. W., Gjertz, I., & Reeves, R. R. (1995). Population assessment of Atlantic walrus (*Odobenus rosmarus rosmarus L.*). *Norsk Polarinstiutt*, *Meddelelser*, *138*. 100 pp.

Born, E. W., Dietz, R., Heide-Jorgensen, M. P., & Knutsen, L. Ø. (1997). Historical and present distribution, abundance and exploitation of Atlantic walruses (*Odobenus rosmarus rosmarus L.*) in eastern Greenland. *Meddelelser om Grønland – Bioscience*, *46*. 73 pp.

Born, E. W., Rysgaard, S., Ehlmé, G., Sejr, M. K., Acquarone, M., & Levermann, N. (2003). Underwater observations of foraging free-living Atlantic walruses (*Odobenus rosmarus rosmarus*) and estimates of their food consumption. *Polar Biology*, *26*, 348-357.

Bowen, W. D. (1997). Role of marine mammals in aquatic ecosystems. *Marine Ecology – Progress Series*, *158*, 267-274.

Boyd, I. L., Bevan, R. M., Woakes, A. J., & Butler, P. J. (1999). Heart rate and behavior of fur seals: Implications for measurement of field energetics. *American Journal of Physiology – Heart and Circulatory Physiology*, *276*(3), H844-H857.

Butler, P. J., Green, J. A., Boyd, I. L., & Speakman, J. R. (2004). Measuring metabolic rate in the field: The pros and cons of the doubly labeled water and heart rate methods. *Functional Ecology*, *18*(2), 168-183.

Costa, D. P., & Gales, N. J. (2003). Energetics of a benthic diver: Seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecological Monographs*, *73*(1), 27-43.

DeMaster, D. P., Fowler, C. W., Perry, S. L., & Richlen, M. E. (2001). Predation and competition: The impact of fisheries on marine-mammal populations over the next one hundred years. *Journal of Mammalogy*, *82*(3), 641-651.

Elsner, R. (1999). Living in water. In J. E. Reynolds & S. A. Rommel (Eds.), *Biology of marine mammals* (pp. 73-116). Washington, DC: Smithsonian Institution Press.

Fay, F. H. (1982). Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. *U.S. Department of the Interior, Fish and Wildlife Services*, *North American Fauna*, *74*. 279 pp.

Fisher, K. I., Stewart, R. E. A., Kastelein, R. A., & Campbell, L. D. (1992). Apparent digestive efficiency in walruses (*Odobenus rosmarus*) fed herring (*Clupea harengus*) and clams (*Spisula* sp.). *Canadian Journal of Zoology*, *70*(1), 30-36.

Gjertz, I., Griffiths, D., Krafft, B. A., Lydersen, C., & Wiig, Ø. (2001). Diving and haul-out patterns of walruses *Odobenus rosmarus* on Svalbard. *Polar Biology*, *24*(5), 314-319.

Hills, S. (1992). *The effect of spatial and temporal variability on population assessment of Pacific walruses*. Ph.D. thesis, University of Maine at Orono. 217 pp.

Innes, S., Lavigne, D. M., Earle, W. M., & Kovacs, K. M. (1987). Feeding rates of seals and whales. *Journal of Animal Ecology*, *56*(1), 115-130.

Kleiber, M. (1932). Body size and metabolism. *Hilgardia*, *6*(11), 315-353.

Kleiber, M. (1961). *The fire of life* (1975 ed.). Malabar, FL: Robert E. Krieger Publishing Co., Inc. 453 pp.

Knutsen, L. Ø., & Born, E. W. (1994). Body growth in Atlantic walruses (*Odobenus rosmarus rosmarus*) from Greenland. *Journal of Zoology (London)*, *234*, 371-385.

Lifson, N., & McClintock, R. (1966). Theory of use of turnover rates of body water for measuring energy and material balance. *Journal of Theoretical Biology*, *12*(1), 46-74.

Lydersen, C., Griffiths, D., Gjertz, I., & Wiig, Ø. (1992). A tritiated water experiment on a male Atlantic walrus (*Odobenus rosmarus rosmarus*). *Marine Mammal Science*, *8*(4), 418-420.

McPhee, J. M., Rosen, D. A. S., Andrews, R. D., & Trites, A. W. (2003). Predicting metabolic rate from heart rate in juvenile Steller sea lions *Eumetopias jubatus*. *Journal of Experimental Biology*, *206*(11), 1941-1951.

Nagy, K. A. (1983). *The doubly labelled water ($^3HH^{18}O$) method: A guide to its use* (UCLA Publication No. 12-1417). Los Angeles: University of California Press.

Nagy, K. A., Girard, I. A., & Brown, T. K. (1999). Energetics of free-ranging mammals, reptiles, and birds. *Annual Review of Nutrition*, *19*, 247-277.

Nilssen, K. T., Pedersen, O. P., Folkow, L. P., & Haug, T. (2000). Food consumption estimates of Barents Sea harp seals. In G. A. Vikingsson & F. O. Kapel (Eds.), *Minke whales, harp seals and hooded seals: Major predators in the North Atlantic ecosystem* (pp. 9-27). Tromsø, Norway: The North Atlantic Marine Mammal Commission.

Reeves, R. R., Leatherwood, S., & Brent, S. (1992). *The Sierra Club handbook of seals and sirenians.* San Francisco: The Sierra Club. 256 pp.

Schoeller, D. A., Ravussin, E., Schutz, Y., Acheson, K. J., Baertschi, P., & Jequier, E. (1986). Energy-expenditure by doubly labeled water: Validation in humans and proposed calculation. *American Journal of Physiology*, *250*(5), R823-R830.

Speakman, J. R. (1995). Estimation of precision in DLW studies using the 2-point methodology. *Obesity Research*, *3*, 31-39.

Speakman, J. R. (1997). *Doubly labeled water: Theory and practice.* London: Chapman & Hall. 399 pp.

Speakman, J. R., Nagy, K. A., Masman, D., Mook, W. G., Poppitt, S. D., Strathearn, G. E., et al. (1990). Interlaboratory comparison of different analytical techniques for the determination of O-18 abundance. *Analytical Chemistry*, *62*(7), 703-708.

Trites, A. W., Chrisensen, V., & Pauly, D. (1997). Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. *Journal of North Atlantic Fisheries Science*, *22*, 173-187.

Ward, S., Scantlebury, M., Krol, E., Thomson, P. J., Sparling, C., & Speakman, J. R. (2000). Preparation of hydrogen from water by reduction with lithium aluminium hydride for the analysis of delta H-2 by isotope ratio mass spectrometry. *Rapid Communications in Mass Spectrometry*, *14*(6), 450-453.

White, C. R., & Seymour, R. S. (2003). Mammalian basal metabolic rate is proportional to body mass (2/3). *Proceedings of the National Academy of Sciences of the United States of America*, *100*(7), 4046-4049.

Winship, A. J., Trites, A. W., & Rosen, D. A. S. (2002). A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatu*s in Alaska, USA. *Marine Ecology – Progress Series*, *229*, 291-312.