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Daily Gross Energy Requirements of a Female Northern Elephant Seal *Mirounga angustirostris* at Sea

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Using an energy components analysis of the 73 day continuous time-depth recording of a female northern elephant seal, we estimated the total daily energy requirement to be between 9.4 Mcal and 10.0 Mcal. Total prey energy consumed was estimated between 15.9 and 16.8 Mcal/day, yielding a diet of approximately 10.7 kg of mackerel or 21.0 kg of squid or hake per day. We estimate that at least 60% of the dives must be successful to account for the mass gained during the period at sea.

Northern elephant seals *Mirounga angustirostris* breed in winter along the west coast of Baja California, Mexico and California.[1-3] After giving birth, a female nurses her pup daily for four weeks, fasting from food and water.[4] During this time she loses about 40% of her mass.[5] At the end of lactation, she copulates, weans her pup and returns to sea to feed. After 10 weeks at sea, she returns to the rookery to molt, a process that takes about one month.

Recent studies using time-depth recorders (TDR) attached to free-ranging seals have revealed a continuous deep diving pattern during the post-lactational period at sea.[6-8] In the present study, the dive pattern of a three-year old female was recorded on pressure sensitive paper during 73 days at sea. The female dived continuously, spending as much as 90% of the time underwater. The mean dive depth was 464 m and the deepest dive recorded was to 934 m.[8]

Although the biological meaning of continuous, deep diving remains to be fully explained, a large part of diving must serve foraging. On average, females gain 0.8 to 1.3 kg per day during the period at sea.[7,9] In this paper, we used the 73-day diving record reported by Le Boeuf *et al.*[8] to estimate the energy requirements and foraging efficiency of the seal during the period at sea.

Methods

Dive Recorders, Instrument Attachment and Dive Analysis

A time-depth recorder (TDR) measuring 5.2 cm × 19.3 cm and weighing 980 g recorded dive duration and depth continuously in real time on pressure sensitive paper.[9] It resolved dive depths to 1000 m and dive duration with less than 2% error. The instrument was calibrated before deployment and after recovery.

A 3-year old female elephant seal at Año Nuevo Point, California (37°06.5′N, 122°20.2′W) was anesthetized, weighed, measured and the TDR was attached to its back a few days before the animal went to sea. The animal was near the end of lactation and ready to wean her pup. She went to sea on February 18 and returned to the rookery on May 10, 1987, at which time the TDR was recovered.

At recovery, the dive record was enlarged, digitized and the data were analysed by computer. For each dive the following was calculated: surface interval, beginning time of the dive, duration underwater, maximum depth attained, and time the animal returned to the surface. These data were used to estimate energy requirements and foraging efficiency.

Energy Requirements and the Parameters Used to Estimate Them

An energy components analysis was used to

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estimate energy requirements. This information coupled with information about the prey consumed allows one to correlate intake with foraging effort. A common assumption is that the energy available for growth and reproduction is simply the difference between energy intake as food and energy expended on maintenance,[10,11)]

$$F=R+B+G+M \qquad (1)$$

where F is total energy intake, M is the energy utilization associated with locomotion, R is energy for reproduction (assumed to be nearly zero during this period at sea), B is maintenance energy, and G is energy associated with growth.

These parameters are estimated in Kcal per day and each is considered below:

Maintenance Energy, B

Maintenance energy, B is proportional to δW^{ϕ} for animals, where W is total weight in kg and δ and ϕ are constants.[12)] In this study, the exponent ϕ was assigned a value of 0.75 and δ was assigned a value of 70. These values are typical for most terrestrial mammals, and recent works showed them to be appropriate for phocid seals.[13,14)] The maintenance energy on any day (j) at sea is equivalent to

$$B(j)=70\times(W_0+DW\times j)^{0.75} \qquad (2)$$

where W_0 is the animal's weight on the day before return to sea, DW is the average daily weight gain assuming a linear growth rate.

Growth Rate, G

The energy required for weight recovery can be estimated as

$$G(j)=DW\times\alpha \qquad (3)$$

where α is the caloric density in Kcal/kg. The caloric density of mass changes with the mass of blubber contained in tissue. During this interval, the percentage of adipose tissue in body mass decreased from 39% to 24% while lean mass increased from 61% to 76%.[5)] The caloric density of elephant seal blubber is 8950 Kcal/kg, and elephant seal lean body tissues are about 2350 Kcal/kg.*[1] The percent adipose tissue at the end of lactation and the beginning of the molt, when the animal returns from sea, is approximately 25%.*[2] Thus, the caloric density of the tissue gained during the at-sea period is 4000 Kcal/kg, that is, 75% lean tissue and 25% adipose tissue.

Rate of Locomotory Energy Utilization

The total daily energy utilized for locomotion during the time at sea is estimated from the dive record as

$$M(j)=\varepsilon\times E(j)/\eta \qquad (4)$$

where $E(j)$ is the total work on the j-th day, ε is, the conversion coefficient from joule to cal and η is, the overall propulsive efficiency during swimming and diving. Values of η for turbulent oceanic conditions are unknown.

We used the estimate of $\eta=0.60$. The daily work (E) is the sum of the work associated with each dive unit. Each dive unit is composed of four components, descent, horizontal swimming, ascent, and a surface interval (Fig. 1). The total work at the i-th time on the j-th day, $E(i,j)$, is the sum of the work associated with each of these components:

$$E(j)=\sum_{i=1}^{t_d} E(i,j) \qquad (5)$$

$$E(i,j)=E_d(i,j)+E_u(i,j)+E_h(i,j)+E_s(i,j) \qquad (6)$$

where the subscript d indicates descent, u indicates ascent, h indicates horizontal swimming, t_d is the total dives per day and s indicates surface interval. Each of these components is equal to:

$$E_d(i,j)=1/2\rho C_d A U_d(i,j)^2 L(i,j) \qquad (7)$$

$$E_u(i,j)=1/2\rho C_d A U_u(i,j)^2 L(i,j) \qquad (8)$$

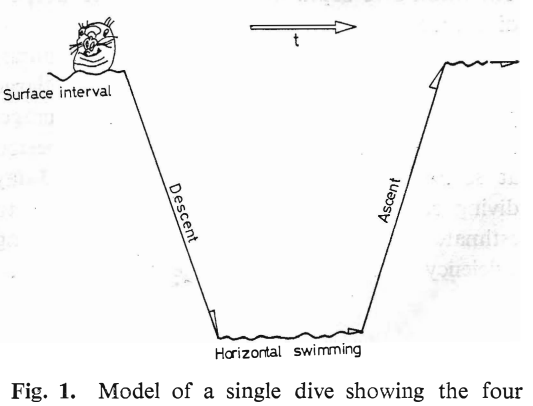

Fig. 1. Model of a single dive showing the four basic components used in the calculation of costs of locomotion: descent, ascent, horizontal swimming and surface interval.

*[1] G. A. Worthy, personal communication.

*[2] D. P. Costa, B. J. Le Boeuf, G. A. Worthy, and A. C. Huntley (unpublished data).

$$E_h(i,j)=1/2\rho C_d A U_h(i,j)^2 H(i,j) \quad (9)$$

$$E_s(i,j)=1/2\rho C_s A S_s(i,j)^2 X(i,j) \quad (10)$$

where ρ is the water density, C_d is the underwater drag coefficient, C_s is the drag coefficient at the surface, A is the cross-sectional area, U is velocity, and L, H and X are distances travelled in the respective components.

A water density (ρ) of 1.024 was assumed.[15] An estimated optimal underwater drag coefficient (C_d) of 0.07 was used.[15] The body drag coefficient at the surface may differ from that underwater, so two estimates were used: a) $C_s=0.09$, $S_s=1.5$ m/s and b) $C_s=0.07$, $S_s=1.0$ m/s.[15] The cross-sectional area was calculated from the average axillary girth measured at the beginning and at the end of the period at sea. Swimming velocity for descent and ascent (U_d and U_u) were calculated directly from the dive record as descent and ascent rate. Horizontal swimming speed (U_h) and surface swimming speed (S_s) cannot be directly measured from the dive record. Since diving occurred virtually continuously at the rate of 2.9 dives per hour during the at-sea period, and only 17% of the time was spent at the surface, the energetic expenditure in these categories is probably small. We estimated horizontal swimming speed (U_h) as 2.0 m/s and surface swimming speed (S_s) in the range of 1.0 to 1.5 m/s based upon the cost of transport and the preferred horizontal swim speed of adult harbor seals.[15] These values were substituted into eqs. (9, 10) with surface interval ($X=S_s$ by Surface interval) and residual underwater duration except descent and ascent intervals.

Total Energy Requirements and Prey Consumption

The total energy requirement for the entire period (Q) at sea is

$$Q=\sum_{j=1}^{N}(B(j)+G(j)+M(j)) \quad (11)$$

where N is the total number of days at sea, $B(j)$ is the daily maintenance energy, $G(j)$ is the daily energy allotted to growth, and $M(j)$ is the daily cost of transport.

The total prey energy consumed must account for that portion of the prey which is indigestible, and the actual assimilation efficiency of the digestible portion. We estimate that 30% of the prey remained undigested, and assimilation efficiency is near 90%.[16] Thus, approximately 60% of the consumed prey energy is available to the seal. Therefore, the total prey energy (P_e) consumed is equal to

$$P_e=1.67\times Q \quad (12)$$

Results

Summary of Diving Behavior

The typical diving behavior throughout the 73 day period at sea was reported by Le Boeuf *et al.*[8] The diving record for the first 20 days at sea is shown in Fig. 2. Except for the first day at sea, the female dived repeatedly to depths averaging between 400 and 500 m. Daytime dive depths exceeded those at night by about 100 m, suggesting that the seal was following the daily vertical migration of prey in the deep scattering layer.[17–18] After the first day, total dives per day ranged from 50 to 76, (t_d=17–76). The dive rate was 2.1 to 3.2 dives per hour with a mean surface interval between dives of less than 3.5 min.

Estimation of Energy Consumption

At departure from the rookery, the female weighed 242 kg (W_0), her standered length was 2.36 m, and her axillary girth was 1.44 m. Upon her return after 81 days at sea, she weighed 288 kg, her standared length was 2.38 m, and her axillary girth was 1.59 m. Her mean cross sectional area, A, was estimated at 1800 cm^2. As this female gained 46 kg during this period, her average daily weight gain, DW, was 0.57 kg. Her dive pattern was recorded for the first 73 days at sea (N=73). The parameters and assumptions used in the calculations are summarized in Table 1.

Using eq. (3), we calculated the energy required for growth (G) as 2280 Kcal/day. The maintenance energy requirement (B) increased from 4300 Kcal/day to 4840 Kcal/day, as a function of the increase in mass, and averaged 4630 Kcal/day. The total energy utilized for locomotion (M), calculated using eq. (4), was 2440 Kcal/day for $C_s=0.07$, and 3140 for $C_s=0.09$.

The total energy utilized for locomotion varied as a function of diving frequency (see Figs. 3 and 4). A marked reduction in dive frequency and estimated energy utilization for locomotion occurred at 15–20 day intervals.

The daily mean energy requirement Q/N from eq. (11) is 9350 Kcal/day for $C_s=0.07$, and 10050 Kcal/day for $C_s=0.09$. Using eq. (12) we estimate the daily mean consumed prey energy P_e/N as 15.9 Mcal/day $C_s=0.07$ and 16.8 Mcal/day for $C_s=0.09$.

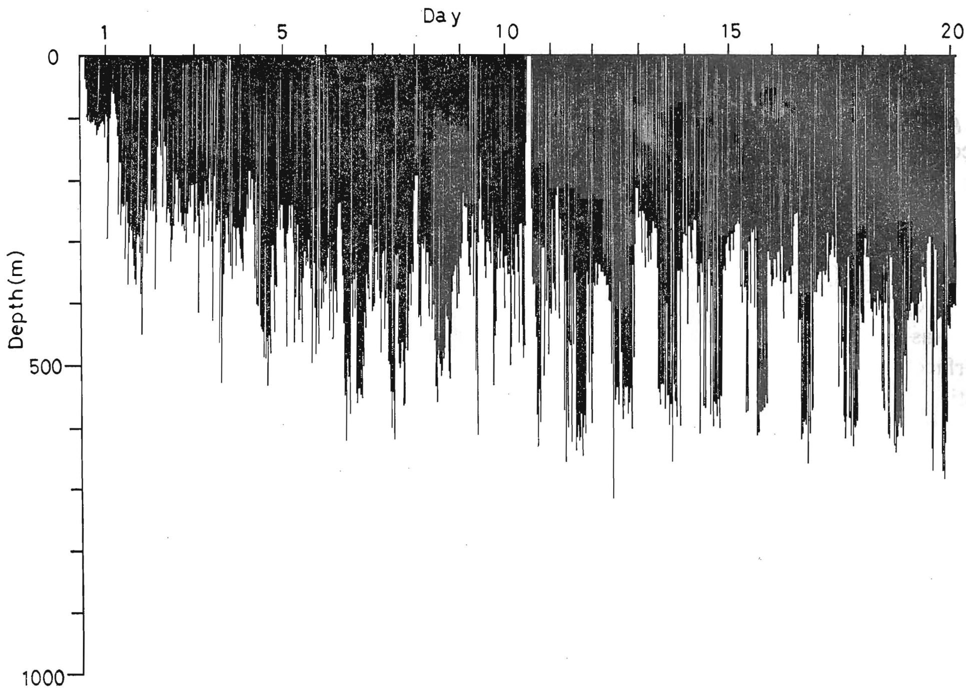

Fig. 2. The pattern of diving for the female northern elephant seal from the start to the 20th. Day is continuous.

Table 1. Parameters and assumptions used in calculations

Symbol	(description, units)	value
α	(caloric density, Kcal/kg)	4000
ε	(conversion coefficient, joule to cal)	0.2389
η	(propulsive efficiency)	0.6
ρ	(sea water density, g/cm^3)	1.024
ϕ	(mass exponent, maintenance)	0.75
A	(mean cross-sectional area, cm^2)	1800
C_d	(drag coefficient, underwater)	0.07
C_s	(drag coefficient, surface)	0.07, 0.09
t_d	(total dives per day)	17–76
N	(number of days)	73
S	(speed, surface, m/s)	1.0, 1.5
U_h	(speed, underwater, m/s)	2.0
W_0	(initial mass, kg)	242
W_{73}	(mass on last day of record, kg)	284*
DW	(mass gain per day, kg/day)	0.57

* estimated from W_{81}.

Estimate of Prey Consumption

We referred to the food consumption of a young captive female northern elephant seal in aquarium to determine the validity of our estimation. The captive female was 2 years old and weighed 205 kg when she was brought to Kamogawa Sea World Aquarium. This animal was maintained on a diet of pacific mackerel. When she was fed mackerel continuously during several days, her mass gradually increased in the direction of the arrows shown in Fig. 5. Then diet was controlled to decrease her mass. The process of mass control is indicated by the symbols in the figure. Interestingly, the captive elephant seal's mass increased whenever the prey mass was over 9.0 kg/day (see Fig. 5).

Feeding habits of elephant seals in the wild show that hake and squid comprise a major portion of the recorded diet. In captivity elephant seals are often maintained on a diet of mackerel, and presumably take this prey in the wild as well.[19] Using the caloric density of mackerel (1587 Kcal/kg)[20] and squid or hake (765 Kcal/kg)[16] we estimated that this free-ranging seal consumed between 9.8 and 10.7 kg of pacific mackerel per day or between 20.4 and 21.9 kg of squid or hake per day.

A total prey consumption of 9.8 kg of mackerel per day seems low when compared with the daily intake of a captive female elephant seal. Since the free-ranging seal must swim to catch prey, and the captive is given the prey, we might expect the total energy requirement of the former to be greater.

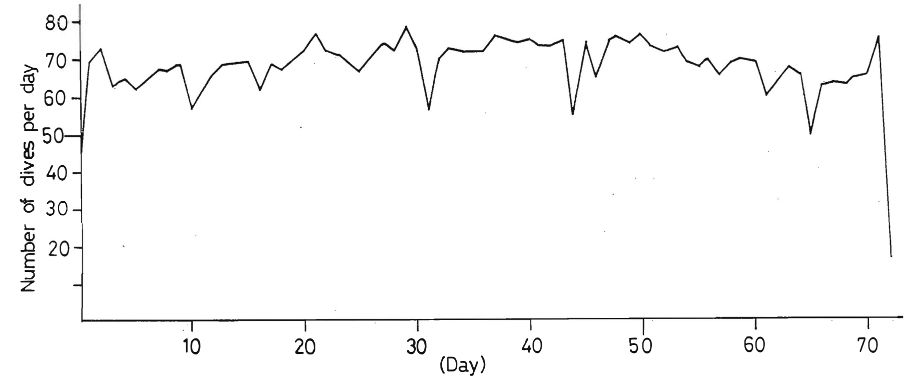

Fig. 3. Number of dives per day for 73 day record.

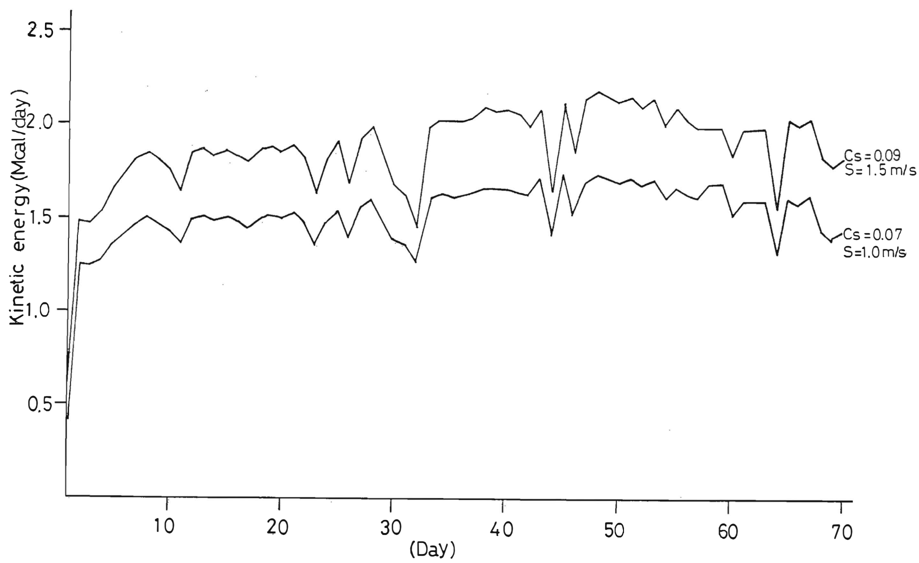

Fig. 4. Total energy utilized for locomotion (Mcal/day) per day for two different swim speeds and surface drag coefficients (C_s).

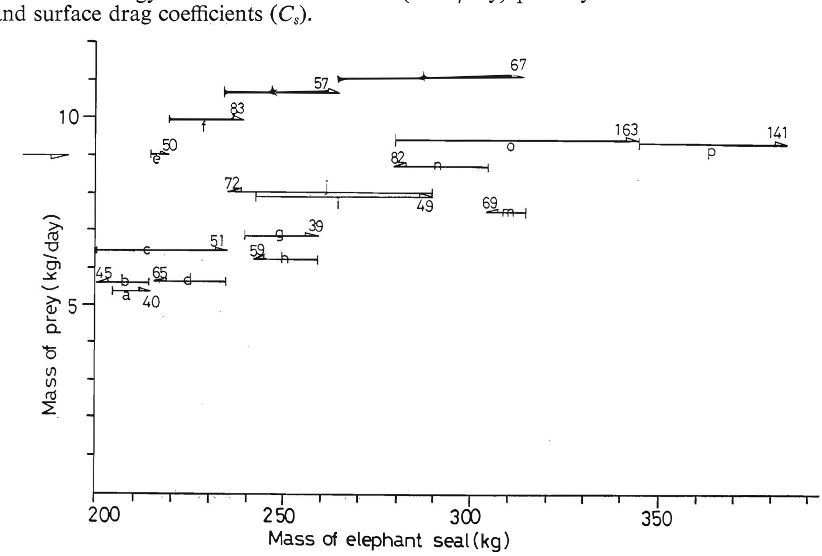

Fig. 5. Relationship between mass condition and mass of prey consumed by a captive female elephant seal in the Kamogawa Sea World Aquarium. Number in the figure means duration the animal was fed continuously the same amount of fish; arrow means trend of elephant seal's mass condition decrease (left) or increase (right); symbol means change in the amount of prey.

Discussion

Prey Consumption

One possible explanation for a lower than expected rate of prey consumption is reduced metabolism during diving. Le Boeuf *et al.*[7] suggest that elephant seals may show metabolic depression during dives and Huntley[21] demonstrated a similar phenomenon during terrestrial apnea in elephant seal weanlings. If metabolism during the dive were lower than the predicted value (eq. 2), resulting in a lower average daily maintenance energy requirement, a larger portion of the consumed prey energy could be devoted to fat deposition.

Foraging Efficiency

The record shown in Fig. 3 includes successful and unsuccessful foraging dives as well as dives that might serve sleeping or transit. If we assume a diet of hake and squid, and that roughly 60% of all dives were successful, that is 40–50 successful dives per day, then 400 to 500 g of prey must have been caught on each dive. At an average weight of 100 g this is equivalent to 4 to 5 individual prey items per dive. This estimate is slightly higher than for other marine mammals consuming similar prey. For example, northern fur seals *Callorhinus ursinus* capture an average of 1.3 pollock per dive, and Galapagos fur seals *Arctocephalus galapagoensis* average 4 squid or 2–3 fish per dives.[22]

Female elephant seals spend 4–8 min at the bottom of dives which may represent foraging.[7] This suggests a capture rate of one prey item every 1–2 min. This, plus the consistency in diving depths over long periods, suggests that the prey patch remains at the same depth and density to allow high encounter rates. Squid and pacific hake *Merluccius productus* are among the best known prey of elephant seals off the California coast.[19] Mature pacific hake migrate along the ocean bottom along the northwestern coast of North America and they spawn near the southern California coast in winter.[23] After spawning, adult fish return to the north during spring and summer to feed. The time of departure and direction of travel of elephant seals may be adapted to the migration course of pacific hake.

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References

1) G. A. Bartholomew: *Univ. Calif. Pub. Zool.*, **47**, 369–472, (1952)
2) M. Nishiwaki: *Bull. Ocean. Res. Inst. Univ. Tokyo*, **1**, 1–64, (1967).
3) B. J. Le Boeuf and M. L. Bonnell: in "Proceedings of a multidisciplinary symposium" (ed. D. M. Powers), Santa Barbara Museum of Natural History, Santa Barbara, 1980, pp. 475–493.
4) B. J. Le Boeuf, R. J. Whiting, and R. F. Gannt: *Behavior*, **43**, 121–156, (1972).
5) D. P. Costa, B. J. Le Boeuf, C. L. Ortiz, and A. C. Huntley: *J. Zool. London.*, **209**, 21–33, (1986).
6) B. J. Le Boeuf, D. P. Costa, A. C. Huntley, G. L. Kooyman, and R. W. Davis: *Can. J. Zool.* **208**, 1–7, (1986).
7) B. J. Le Boeuf, D. P. Costa, A. C. Huntley, and S. D. Feldkamp: *J. Zool.London*, **66**, 446–458, (1988).
8) B. J. Le Boeuf, Y. Naito, A. C. Huntley, and T. Asaga: *Can. J. Zool.*, 67, 2514–2519 (1989).
9) Y. Naito, B. J. Le Boeuf, T. Asaga, and A. C. Huntley: *Antarct.Rec.* **33**, 1–9 (1989).
10) T. Miura, N. Suzuki, M. Nagoshi, and K. Yamamura: *Res. Popul. Ecol.*, **17**, 135–154, (1976).
11) R. Jones and C. Johnston: in "Fisheries mathematics" (ed. J. H. Steel), Academic Press, London, 1977, pp. 37–62.
12) M. Kleiber: in "The fire of life", Robt. Krieger, New York, 1975, pp. 1–453.
13) D. M. Lavigne, S. Innes, G. A. J. Worthy, K. M. Kovacs, O. J. Schmitz, and J. P. Hiakie: *Can. J. Zool.*, **64**, 279–289, (1986).
14) A. C. Huntley: in "Marine mammal energetics", (ed. A. C. Huntley, D. P. Costa, G. A. J. Worthy, and M. A. Castellini), Allen Press, Lawrence KS, 1987, pp. 97–108.
15) T. M. Williams: in "Marine mammal energetics", (ed. A. C. Huntley, D. P. Costa, G. A. J. Worthy, and M. A. Castellini), Allen Press, Lawrence KS, 1987, pp. 128–145.
16) J. H. Prime and P. S. Hammond: in "Marine mammal energetics" (ed. A. C. Huntley, D. P. Costa, G. A. J. Worthy and M. A. Castellini), Allen Press, Lawrence KS, 1987, pp. 165–181.
17) M. O. Nelson and H. A. Larkins: *U. S. Fish. Wildl. Serv. Circ.*, **332**, 23–33, (1970).
18) C. F. Roper and R. E. Young: *Smithson. Contrib. Zool.*, **209**, 1–51, (1973).
19) R. Condit and B. J. Le Boeuf: *J. Mammal*, **56**, 281–290, (1984).
20) Resources Council, Science and Technology

Agency, Japan: Standard table of food Composition in Japan, Fourth revised edition, Printing Bureau Ministry of Finance, Tokyo, 1983, pp. 1-707.

21) A. C. Huntley: Relationships between metabolism, respiration, heart rate and arousal states in the northern elphant seal., Doctoral thesis, University of California, Santa Cruz, 1984, pp. 1–89.

22) D. P. Costa: *Can. J. Zool.*, **66**, 45–52, (1988).

23) D. H. Cushing: in "Climate and fisheries (Trans. Japan. by K. Kawasaki)", Koseisha-Koseikaku, 1986, pp. 1–378.