ENERGY, NITROGEN, AND ELECTROLYTE FLUX AND SEA WATER DRINKING IN THE SEA OTTER ENHYDRA LUTRIS[1]

DANIEL P. COSTA[2]

Center for Coastal Marine Studies, University of California, Santa Cruz, Santa Cruz, California 95064

(Accepted 6/16/81)

An elevated metabolism requires the sea otter, *Enhydra lutris,* to include large quantities of invertebrate prey in its diet. This necessitates processing large quantities of energy, nitrogen, electrolytes, and water. Feeding studies were conducted to document these high material and energy fluxes and the dilution of tritiated water through time was used to measure total water flux. Total energy influx on a diet of clam and squid was 234 ± 19 ($\bar{X}$ ± SE) kcal/kg-day with an assimilation efficiency of 82% and an estimated metabolic efficiency of 72%. Material influx from food was 5.22 ± 0.41 ($\bar{X}$ ± SE) g/kg-day nitrogen and 166 meq/kg-day electrolytes (Cl, Na, K, Mg). The presence of large lobulate kidneys may allow for the production of large volumes of urine at elevated concentrations. Urine samples from wild and captive animals had a mean osmotic pressure of 1,627 ± 91 mOsm/kg (range, 910–2,130), which was composed of 647 meq/L Na, K, Cl and 698 ± 67 mmol/L urea. Total water flux was 269 ± 25 mL/kg-day. Mean seawater ingested was estimated to be 62 mL/kg-day (range, 0–124), and it may aid in the urea elimination by increasing the urinary osmotic space.

INTRODUCTION

The sea otter (*Enhydra lutris*) is the smallest marine mammal and inhabits the cool to temperate littoral waters of the North Pacific Ocean. Thermoregulation in this environment requires an elevated metabolism necessitating a food consumption greater than 20% of the otter's body mass per day (Kenyon 1969; Costa and Kooyman, unpublished manuscript). Throughout its range, *E. lutris* eats both fish and invertebrates; however, California populations of this species feed primarily on invertebrates (Miller 1974). Consumption of sufficient invertebrate prey to fuel a high metabolic rate may require the processing of large quantities of nitrogen, electrolytes, and water.

Because invertebrates possess higher electrolyte concentrations than teleost fish it may be necessary for otters to drink seawater in order to supplement water intake and maintain positive water balance. It has been shown that some marine mammals are capable of maintaining water homeostasis on a diet of marine teleost fish without ingesting seawater

[1] This project was supported by a joint contract from the U.S. Fish and Wildlife Service and the Marine Mammal Commission, contract no. 14-16-008-2047. Sea otters were captured under U.S. Fish and Wildlife permit PRT # 9-22-C, and abalone were collected under a research collector's permit from the California Department of Fish and Game. This research was conducted as partial fulfillment of the Doctor of Philosophy degree at the University of California at Santa Cruz, and I received support from teaching assistantships and independent research funds from the University. I would like to thank B. Kruse; P. Silver; J. Vandervere; Dr. T. Williams; T. Loughlin; A. Williams; and the California Department of Fish and Game and its employees, J. Ames, H. Hardwick, and D. Miller for their support and assistance. I thank my major advisor, Dr. K. S. Norris and Drs. J. S. Pearse, K. A. Nagy, C. L. Ortiz, and R. Pierce for their guidance through all stages of this project. Drs. J. Graham, G. Kooyman, and R. Rubin, as well as anonymous reviewers, provided invaluable comments on the final manuscript. Sea World, San Diego, provided facilities and the use of otters 1 and 2; Hopkins Marine Station, Pacific Grove, California, supplied space and running sea water for the holding tank.

[2] Present address: Physiological Research Laboratory A-004, Scripps Institution of Oceanography, La Jolla, California 92093.

Physiol. Zool. 55(1):35–44. 1982.

 0031-935X/82/5501-8060$02.00

(Harrison and Kooyman 1968; Pilson 1970; Depocas, Hart, and Fisher 1971; Tarasoff and Toews 1972). Whereas, others have been observed to ingest seawater while fasting (Tefler, Cornell, and Prescott 1970; Gentry 1981; Hui, in press), and for some terrestrial mammals which eat marine organisms it is obligatory (Carpenter 1968). To date no study has directly examined water balance and seawater drinking in a marine mammal consuming an invertebrate diet.

The purpose of this study was to quantify the rate of energy, nitrogen, electrolyte, and water flux on a diet of squid, clam, and abalone and to determine if sea otters drink seawater. This was accomplished by measuring the food requirements, the composition of the diet, and the water turnover of captive sea otters.

MATERIAL AND METHODS

FEEDING EXPERIMENTS

Five sea otters were used in experiments conducted in San Diego and Pacific Grove, California, over a 2-yr period. Otters 1 and 2 had been in captivity for 2 yr and were studied at Sea World, San Diego, California. Otters 3, 4, and 5 were collected off Pacific Grove, California, and held in a holding tank (Costa 1978) at the Hopkins Marine Station, Monterey, California. Otter 3 was maintained in the tank May 20–26, 1976, concurrently with otter 4, who was in captivity May 16–26, 1976. Otter 5 was kept alone February 9–14, 1977.

Simultaneous food consumption and water flux determinations were made for 9 days with one otter (no. 4), and 4 days with the others. Otters 1 and 2 were fed fresh frozen clam, *Spissula solidissima;* otters 3 and 4 were fed fresh frozen squid, *Loligo opalescens* (both obtained commercially); and otter 5, fresh frozen red abalone, *Haliotus rufescens* (collected by diving). All otters were fed their experimental diet for at least 24 h prior to the start of the experiment. Otters 1 and 2 had been maintained on a similar diet since their capture in 1972. At least four times daily, animals were fed by hand with weighed amounts of food. Alliquots of the food from each feeding were frozen for later determination of electrolyte, water, caloric, and nitrogen content.

Otter 5 would not eat while observed. However, whole abalone left in its tank were usually eaten within 2 h. Food remaining in the tank after 4 h was weighed to determine net consumption in order to estimate food energy and nitrogen influx. Since it was not possible to measure assimilation efficiency and changes in the food while it remained in the seawater tank, otter 5 was only used in estimates of food energy and nitrogen influx.

Fecal production of otters 1 and 2 on the clam diet was measured 1 wk prior to these experiments (Fausett 1976) and that of otters 3 and 4 was monitored during the feeding tests. All feces excreted by otters 3 and 4 during a 48-h period of constant observation were quickly (within 30 s) collected with a pool skimmer net which was then emptied and rinsed with distilled water into a plastic pan. Feces were compact and there was no significant loss of a liquid fraction. Collected feces were dried in a forced-air ventilation oven to constant weight at 80 C. They were weighed and later analyzed for electrolyte, nitrogen, and caloric content. Fecal samples collected from the pool deck were analyzed and had similar composition to those collected in water. The body mass (table 2) of otters 1 and 2 was determined by Sea World personnel at the beginning of the experiment. Otters 3, 4, and 5 were weighed at the beginning and end of the experimental period, and they lost 0.5% ± 0.3 SD of their initial mass per day.

WATER FLUX

Total water flux was determined by the dilution of tritiated water through time (Nagy and Costa 1980). At the beginning of the feeding study, an intraperitoneal injection of tritiated water (0.8–1.0 mCi/mL) was made. After a 3-h equilibration period, and at the end of the study, blood

was sampled for determination of tritium-specific activity and electrolyte concentrations. Two additional blood samples were taken from otter 4 during the test period to verify that water flux was constant through time. Total body water was determined by the dilution technique (Foy and Schnieden 1960). Total water influx and efflux were determined with the steady-state water flux equation for otters 1, 2, and 4 and the exponentially changing body weight equation for otter 3 (Lifson and McClintock 1966; Nagy and Costa 1980).

Urine samples were collected by urethral catheterization once each from otters 3, 4, and 5, 4 h after feeding. Additional urine samples were collected from five wild sea otters that had died either shortly before (within 20 min, otters 7 and 8) or at some unknown time (otters 6, 9, and 13) prior to urine collection. Samples were also obtained from five otters that urinated during handling (otters 10, 11, 12, 14, and 15). These animals had been maintained for other studies at the Scripps Institution of Oceanography on a diet similar to the study otters.

Blood samples obtained from eight wild sea otters captured for other studies were analyzed for calcium, sodium, potassium, urea-nitrogen, and glucose concentrations by commercial laboratories (Veterinary Reference Laboratory, San Jose, California, and Santa Cruz Medical Clinic, Santa Cruz, California).

SAMPLE ANALYSIS

Food and feces water content were measured by the wet weight/dry weight difference after drying to a constant weight at 80 C. Nitrogen content was measured by Kjeldahl digestion to ammonia. Ammonia concentration was then measured using an ammonia electrode. For electrolyte analysis, 0.10 g of finely ground material was soaked overnight in 1.0 mL of distilled water. Concentrations of sodium and potassium were analyzed by flame photometry and chloride by potentiometric silver titration in the supernatant fluid. After digestion with concentrated nitric acid, magnesium was analyzed by atomic absorption spectrometry and calcium by atomic emission spectrometry. Urine osmotic concentrations were measured with a freezing-point depression osmometer. Urine urea-nitrogen was assayed by the fearon condensation of urea with diacetyl monoxime using Harleco reagents. Caloric content of food and feces was measured with a nonadiabatic bomb calorimeter (Lieth 1975) using duplicate determinations on 1-g pellets prepared from dried samples ground in a ball mill. Tritium-specific activity was determined by scintillation spectrometry of pure water distilled from the serum samples (Ortiz, Costa, and LeBoeuf 1978).

RESULTS

Energy, nitrogen, electrolyte, and water flux were calculated from the measurements of material flux and the composition of the food and feces shown in table 1. Sodium and chloride concentrations in the experimental diets were less than seawater (table 1). The average food consumption of the five otters was 21.6% ± 1.3 SE of their body mass per day, which is equivalent to 234 kcal/kg-day of food energy. Otters 1–4 assimilated 82% of the energy ingested. Nitrogen intake was 5.22 g/kg-day of which 85% was assimilated (table 2).

Food electrolyte influx was 166 meq/kg-day. Assimilation of electrolytes was calculated from fecal efflux. Monovalent ions were assimilated equally and to a greater degree than bivalent ions. Magnesium efflux was greater than influx (table 3).

Urine electrolyte concentrations were hypertonic to plasma. Mean urine osmolality was 1,627 mOsm/kg with a maximum of 2,130 mOsm/kg (table 4). Mean plasma concentrations of captive and wild sea otters were: calcium 1.2 ± 0.06 (X ± SE) meq/L (no. = 11); chloride, 105 meq/L (no. = 2); urea, 21 ± 1.5 (X ± SE) mM (no. = 11); glucose 5.8 + 0.07 (X ± SE) mM (no. = 8).

Total body water (TBW) was 72.2%

TABLE 1

THE ELECTROLYTE WATER, ENERGY AND NITROGEN CONTENT OF THE FOOD AND FECES OF OTTERS 1–4 EXPRESSED AS PER GRAM DRY WEIGHT

Item	Na		K		Mg		Ca		Cl		H_2O (ml/gr)	ENERGY (kcal/gr)	N (gr/100gr)
	ueq/gr	meq/L	ueq/gr	meq/L	ueq/gr	meq/L	ueq/gr	meq/L	ueq/gr	meq/L			
Spissula solidissima:	1,045	343	183	61	192	63.5	86	28	1,293	428	3.02	4.78	10.5
Feces	696	153	90	18	1,750	384	90	20	783	225	4.56	3.48	6.75
Loligo opalescens:	1,680	348	175	38	358	77.4	74	16	2,001	433	4.62	4.83	11.1
Feces	453	106	60	14	1,246	292	282	66	469	170	4.26	4.73	8.2
Haliotus rufescens:	...	...	...	...	...	...	...	...	...	...	3.65	4.57	11.7
Seawater*	...	470	...	10	...	108	20	...	548	...	...	...	...

NOTE.—Otters 1 and 2 ate *Spissula solidissima,* Otters 3 and 4 ate *Loligo opalescens*. Electrolyte concentrations were determined from the dry weight electrolyte content and water content of the food and feces. Seawater concentrations are included for comparison (Svedrup, Johnson, and Flemming 1942).

* Svedrup, Johnson, and Flemming (1942).

TABLE 2

BODY MASS, ENERGY AND NITROGEN INFLUX AND ASSIMILATION RATES OF SEA OTTERS IN THIS STUDY

Otter	Mass (kg)	Sex	Energy Influx (kcal/kg-day)	Energy Assimilation (%)	Nitrogen Influx (gr/kg-day)	Nitrogen Assimilation (%)
1	18.6	F	280	82.6*	6.21	84.7
2	25.0	M	279	84.1*	6.19	85.9
3	25.4	M	218	77.8	4.34	81.8
4	24.8	M	202	84.0	4.50	86.7
5	27.6	M	191	...	4.88	...
$\bar{X}$	24.3	...	234	82.1	5.22	84.8
SE	1.5		19	1.5	.41	1.1

NOTE.—Calculations are based on caloric and nitrogen contents of the experimental diets (see table 1).
* Assimilation efficiencies of otters 1 and 2 were derived from Fausett (1976).

(table 5). Total water influx (table 5) was 269 mL/kg-day. Food accounted for 68% of this influx (182 mL/kg-day). Equivalent flux estimates were obtained over different sampling periods with otter 4.

DISCUSSION

ENERGY METABOLISM

The energy consumption (234 kcal/kg-day) of these sea otters is quite high. However, it is in agreement with earlier estimates of this species' energy requirements (189 kcal/kg-day, Kenyon [1969]; 307 kcal/kg-day, Fausett [1976]). The energy ingested by these sea otters during routine activity in their enclosure is 2.4 times their standard metabolic rate (SMR) (Morrison, Rosenmann, and Estes 1974; Costa and Kooyman, unpublished manuscript) and 8 times the SMR of a terrestrial mammal of equal size (Kleiber 1975). Even compared to other marine mammals, such as similar-size harbor seals (25–35 kg, Depocas et al. [1971]), sea otters consumed 2.6 times as much food energy. As a group marine mammals appear to have higher weight-specific metabolic rates than terrestrial mammals (Hart and Irving 1959; Morrison, Rosenmann, and Estes 1974; Ashwell-Erickson and Elsner, in press) and the high metabolic rate of sea otters is consistent with this trend (Morrison et al. 1974). One hypothesis for this high metabolism is that surface area to volume relationships have a greater influence on heat loss in aquatic endotherms due to the higher thermal conductivity of water. Harbor porpoise, the smallest cetacean (Kanwisher and Sundnes 1966), and sea otters possess higher weight-specific metabolic rates than larger marine mammals. The higher metabolism of these small marine mammals may be explained by the increased heat loss resulting from their small body size.

A higher food consumption can partially be explained by the otter's low assimilation efficiency (82%), which is the lowest yet reported for a carnivore. The lowest previously reported value (90%) was for the least weasel on a diet of voles and starlings (Moors 1977). Other marine mammals have assimilation efficiencies comparable to terrestrial carnivores. For example, northern fur seals assimilate 91% and 92% of the fish and squid they ingest (Miller 1978), and spotted seals assimilate 95% and 92% of the ingested pollock and herring, respectively (Ashwell-Erickson et al. in press). The low assimilation in sea otters may result from their rapid (3h) food passage rate (Stulken and Kirkpatrick 1955). To meet their energy demands otters must forage frequently (every 5.5 h, Loughlin [1979]) rapidly processing their food and in so doing they may

lose some of the ingested energy. This, in turn, may be partially compensated for by using heat liberated from specific dynamic action (SDA) for thermoregulation during rest (Costa and Kooyman, unpublished manuscript).

In order to estimate net energy utilization, a correction for nitrogenous energy loss must be made. Assuming steady-state conditions, nitrogen influx minus fecal nitrogen efflux equals urinary nitrogen excretion. If all of the excess nitrogen is excreted as urea, the chemical energy lost in the urine is calculated to be 25 ± 5 kcal/kg-day or 10% of the total ingested energy. Net metabolizable energy is the difference between total energy ingested and the sum of fecal (18%) and urinary energy (10%) loss; it is equal to 168 kcal/kg-day or 72% of the ingested food energy.

ELECTROLYTE FLUX

Chloride is fairly representative of the major electrolytes in the diet and can be used for comparisons. Chloride flux in sea otters was 30 and 39 times greater than fluxes reported for harbor seals and a sea lion on fish diets (Depocas et al. 1971; Pilson 1970). This is due to the higher chloride content of their predominately invertebrate diet (1,293, 2,001 meq/g, table 1; fish 61 meq/g, Pilson [1970]) and their large food intake. Most of the electrolytes (82%, table 3) were assimilated leaving a large electrolyte load to be excreted by the kidney. Furthermore, evaporative water loss, in this aquatic environment, is likely to be low, so that most of the water not lost as feces (221 mL/kg-day, table 5) will be excreted by the kidney.

What adaptations to process these large quantities of electrolytes and water exist? Sea otters do not produce a urine that is more concentrated than other marine mammals (sea otter 2,130 mOsm/kg, table 4; sea lion 2,400 mOsm/kg, Pilson [1970]; fur seal 2,364 mOsm/kg, Bester [1975]; ringed seal 2,412 mOsm/kg, Portier [1910]). However, their kidney is lobulate and is larger than other marine mammals: Sea otter kidney mass in 2% of the body weight compared with 1.1% for bottlenose porpoise; 0.25%–0.4% in harbor seal; and 0.33%–0.71% in northern fur seal (Harrison and Kooyman 1968). A large kidney would allow for an increased glomerular filtration rate, allowing elimination of larger urine volumes. Furthermore, sea otters excrete a moderately concentrated urine at large urine volumes, whereas many terrestrial mammals produce concentrated urine at small urine volumes.

WATER FLUX AND THE ROLE OF SEAWATER INGESTION

Errors inherent in measurement of water flux with tritiated water have been extensively discussed (Lifson and McClintock 1966; Nagy and Costa 1980). In the present studies, the principal source of error is the exchange of inspired water vapor for HTO along the respiratory surfaces. This error can be calculated from an estimate of the air ventilated to supply metabolism (Lifson and McClintock 1966) and was calculated to be no greater than 3.6% of the total water flux measured (assuming a 4% oxygen extraction efficiency and 4.8 kcal/L O_2; ambient temperature was between 12–15 C and relative humidity was 68%–80%; exhaled air was assumed to be saturated with water and was measured in the nostril to be 32 C).

Water flux determined for sea otters in this study, even when corrected for differences in body mass, is the highest yet reported for a marine mammal (harbor seal 51 mL/kg-day, Depocas, et al. [1971]; sea lion 28 mL/kg-day, Pilson [1970]) and is only surpassed by large tropical herbivorous mammals (MacFarlane, Howard, and Good 1974). Inspection of table 5 indicates that only otter 4 had a total water flux which was nearly equivalent to the water influx derived from ingested food. The differences could be accounted for if otters 1–3 ingested seawater. Sea otters have been observed ingesting large quantities of seawater in captivity and in the wild (Kenyon 1969, p. 28; Costa and Ostfelt, personal observation). Seawater

TABLE 3

MEAN ELECTROLYTE FOOD INFLUX AND FECAL EFFLUX MEASURED IN OTTERS 1–4

Electrolyte	Food Influx (meq/kg-day)	Fecal Efflux (meq/kg-day)	Assimilation (%)
Na	64.0	5.4	91.6
	(2)	(1.5)	
K	8.8	.9	89.8
	(1.1)	(.4)	
Ca	4.4	1.8	59.1
	(.6)	(.84)	
Mg	11.5	16.1	...
	(.5)	(3.3)	...
Cl	77.6	6.6	91.5
	(1.4)	(.6)	
Total	166.3	30.8	81.5

NOTE.—One unit of SE is given in parentheses.

TABLE 4

URINE COMPOSITION OF WILD AND CAPTIVE SEA OTTERS

OTTER	Na (meq/L)	K (meq/L)	Cl (meq/L)	Urea (mM/L)	Osmolality (mOsm/kg)
3	203	40	319	704	1,575
4	275	57	372	953	1,825
5	370	70	428	848	2,000
6	212	92	262	857	1,500
7	345	75	369	804	2,130
8	95	85	114	271	910
9	353	117	411	736	1,900
10	130	70	207	884	1,591
11	105	70	120	808	1,395
12	273	30	316	185	956
13	295	95	417	529	1,670
14	505	48	555	900	2,000
15	180	71	263	600	1,700
X	257	71	319	698	1,627
SE	33	4	35	67	104
Plasma	152	4.4	105	21	...
Urine/plasma	1.7	16	3.0	33.2	...
Seawater	470	10	548	...	1,000

NOTE.—Plasma composition U/P ratios and seawater composition (Svedrup, Johnson, and Flemming 1942) are given for comparison.

contains considerable magnesium (table 1), which would account for instances (table 3) where fecal magnesium efflux exceeds magnesium influx derived from ingested food.

It is possible to calculate seawater ingestion from total water influx minus food and metabolic water influx. The latter can be estimated as the sum of oxidative water produced from metabolism of fat, carbohydrate, and protein contained in the food (Schmidt-Nielsen and Schmidt-Nielsen 1952). Composition of the food (squid and clam) is given by Watt and Merrill (1963)

Estimates of seawater ingestion (table 6) range from 0 to 124 mL/kg-day. The discrepancies in magnesium flux can also be accounted for if we include seawater magnesium as part of total magnesium influx (table 6). Ingestion of seawater while swallowing prey is unlikely, since sea otters consume their prey while floating on their backs (Kenyon 1969).

Seawater ingestion has been reported in other marine mammals. Harbor seals ingested small amounts (4.8 mL/kg-day) of seawater incidental to prey consumption (Depocas et al 1971). Common dolphins consumed 12–13 mL/kg-day of seawater while fasting (Hui, in press). Sea lions, fur seals, and porpoises ingest seawater or have been shown to be capable of it (Gentry 1981; Pilson 1970; Bester 1975; Tefler et al. 1970).

To a sea otter already burdened with a

TABLE 5

FOOD/WATER INFLUX AND EFFLUX CALCULATIONS BASED ON WATER CONTENT OF FOOD AND FECES

Otter	TBW (%)	Total Water Influx (mL/kg-day)	Food Water Influx (mL/kg-day)	Fecal Water Efflux (mL/kg-day)
1	72.0	328	176	63.8
2	72.8	290	177	58.3
3	72.3	244	181	36.5
4	71.6	213	193	34.2
X	72.2	269	182	48.2
SE	.3	25	4	7.5

NOTE.—Calculations are based on the figures in table 1 and from the HTO turnover.

TABLE 6

ESTIMATED SEAWATER INGESTION AS DERIVED FROM THE DIFFERENCE BETWEEN TOTAL WATER FLUX AND FOOD AND METABOLIC WATER INFLUX

Otter	Total Water Influx (mL/kg-day)	Food Metabolic Influx (mL/kg-day)	Sea-Water Influx (mL/kg-day)	Food/Mg Influx (meq/kg-day)	Fecal/Mg Efflux (meq/kg-day)	Unknown/Mg Influx (meq/kg-day)	Seawater/Mg Influx (meq/kg-day)
1	328	204	124	11.3	21.7	10.4	13.4
2	290	204	85	11.2	21.7	10.5	9.2
3	244	205	39	12.0	11.7	.3	4.2
4	213	213	0	11.5	9.2	2.3	0
X	269	207	62	11.5	16.1	5.9	6.7
SE	25	2	27	.2	3.3	2.7	2.9

NOTE.—Higher magnesium efflux than food influx can be accounted for by magnesium ingested with seawater.

high water flux, seawater ingestion may increase the urinary osmotic space, aiding in the elimination of urea (Wolf et al. 1959). A high protein diet requires the elimination of large amounts of urea and, if sea otters can excrete urine with an electrolyte concentration equivalent to that of seawater, they can drink seawater, increase the urine volume, cause a reduction in urea concentration, and thereby reduce urine osmotic pressure. This effect is consistent with the lower urine osmolality of otter 3, which drank seawater, compared with otter 4, which did not (table 4).

Fish-eating otters would not derive as much benefit from seawater ingestion due to differences in the osmotic composition of their diets. Seawater ingestion would increase the urinary osmotic space for the excretion of urea. However, it would also substantially increase the electrolyte concentration of the urine, since fish have an electrolyte concentration significantly lower than seawater (84 meq/L Cl, Pilson [1970]; seawater 548 meq/L, Svedrup, Johnson, and Flemming 1942), whereas, invertebrate-eating otters consume prey with a composition closer to seawater (428–433 meq/L, table 1). Therefore, seawater ingestion would not increase the electrolyte composition of their urine as much.

Seawater ingestion may be coupled with urea excretion. Most mammalian kidneys require urea to achieve their maximum urine concentrating ability (Gamble et al, 1934; Plakke and Pfeiffer 1967). Seawater ingestion appeared to correlate with nitrogen excretion in feeding, and fasting water stressed pinnipeds (Gentry 1981). Furthermore, marine mammals given seawater without a urea source were not able to excrete seawater without drawing on stored body water (Fetcher and Fetcher 1942; Tarasoff and Toews 1972). Seawater ingestion may be useful for elimination of nitrogenous wastes during periods of osmotic stress, when rates of evaporative water loss are high or when diet results in high fecal or urinary water losses.

LITERATURE CITED

ASHWELL ERICKSON, S., and R. ELSNER. In press. The energy cost of free existence for Bering Sea Harbor and spotted seals. *In* D. W. HOOD and J. A. CALDER, eds. Eastern Bering Sea shelf: Oceanography and Resources. Vol. **2.**

BESTER, M. N. 1975. The functional morphology of the kidney of the cape fur seal, *Arctocephalus pusillus* (Schreber). *Madoqua,* Ser. 2, **4** (74–80): 69–92.

CARPENTER, R. E. 1968. Salt and water metabolism in the marine fish-eating bat *Pizonyx vivesi.* Comp. Biochem. Physiol. **24:**951–964.

COSTA, D. P. 1978. Ecological energetics, water and electrolyte balance of the California sea otter, *Endydra lutris* Ph.D. diss. University of California, Santa Cruz.

COSTA, D. P., and G. L. KOOYMAN. 1981. Oxygen consumption and thermoregulation in the sea otter, *Enhydra lutris,* during immersion and the effect of fur oiling and washing. Unpublished manuscript.

DEPOCAS, F., J. S. HART, and H. D. FISHER. 1971. Sea water drinking and water flux in starved and in fed harbor seals, *Phoca vitulina.* Can. J. Physiol. Pharmacol. **49:**53–62.

FAUSETT, J. 1976. Assimilation efficiency of captive sea otters, *Enhydra lutris.* M.A. thesis. California State University, Long Beach.

FETCHER, E. S., and G. W. FETCHER. 1942. Experiments on the osmotic regulation of dolphins. J. Cell. Comp. Physiol. **19:**123–130.

FOY, J. M., and H. SCHNIEDEN. 1960. Estimation of total body water in the rat, cat, rabbit, guinea pig and man, and the biological half-life of tritium in man. J. Physiol. **154:**169–176.

GAMBLE, J. L., C. F. MCKHANN, A. M. BUTLER, and E. TUTHILL. 1934. An economy of water in renal function referable to urea. Amer. J. Physiol. **109:**139–154.

GENTRY, R. 1981. Seawater drinking in eared seals. Comp. Biochem. Physiol. **68A:**81–86.

HARRISON, R. J., and G. L. KOOYMAN. 1968. General physiology of the pinnipedia *in* R. J. HARRISON, R. L. HUBBARD, R. S. PETERSON, C. F. RICE, and R. J. SCHUSTERMAN, eds. The behavior and physiology of the pinnipeds. Appleton-Century-Crofts, New York. Pps. 212–285.

HART, J. S., and L. IRVING, 1959. The energetics of the harbor seal in air and in water with special consideration of seasonal changes. Can. J. Zool. **37:**447–457.

HUI, C. In press. Sea water consumption and water flux in the common dolphin, *Delphinus delphis.* Physiol. Zool.

KANWISHER, J. W., and G. SUNDNES. 1965. Physiology of a small cetacean. Hvalradets Skrifter. **48:**45–63.

KENYON, K. 1969. The sea otter in the eastern

Pacific Ocean. U.S. Fish Wildlife Service, North American Fauna Ser. no. 68. Government Printing Office, Washington, D.C. 352 pp.

KLEIBER, M. 1975. The fire of life. Krieger, New York.

LIETH, H. 1975. The measurement of caloric values. Pages 119–129 *in* H. LIETH, and R. WHITTAKER, eds. Primary productivity of the biosphere. Springer-Verlag, New York.

LIFSON, N., and M. MCCLINTOCK. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. J. Theoret. Biol. **12**:46–74.

LOUGHLIN, T. R. 1979. Radio telemetric determination of the 24-hour feeding activities of sea otters, *Enhydra lutris*. Pages 717–724 *in* C. J. AMLANER and D. W. MACDONALD, eds., Handbook on biotelemetry and radio tracking. Pergamon, New York.

MACFARLANE, W. V., B. HOWARD, and B. F. GOOD. 1974. Tracers in field measurements of water, milk and thyroxine metabolism of tropical ruminants. Pages 1–23 *in* Tracer techniques in tropical animal production. International Atomic Energy Agency, Vienna.

MILLER, D. 1974. A review of the taxonomic status, life history and some ecological interactions of the sea otter, *Enhydra lutris*. California Dep. Fish Game, Leafl. no. 7. 13 pp.

MILLER, K. 1978. Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. Marine Mammal Comm. final rep. no. 60. 21 pp.

MOORS, P. J. 1977. Studies of the metabolism, food consumption and assimilation efficiency of a small carnivore, the weasel (*Mustela nivules*). Oceologia **27**:185–202.

MORRISON, P., M. ROSENMANN, and J. ESTES. 1974. Metabolism and thermoregulation in the sea otter. Physiol. Zool. **47**:218–229.

NAGY, K. A., and D. P. COSTA. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. Amer. J. Physiol. **238**:R454–R465.

ORTIZ, C. L., D. P. COSTA, and F. J. LEBOEUF. 1978. Water and energy flux in elephant seal pups fasting under natural conditions. Physiol. Zool. **51**:166–178.

PILSON, M. E. W. 1970. Water balance in California sea lions. Physiol. Zool. **43**:257–269.

PLAKKE, R. K., and E. W. PFEIFFER. 1967. Influence of plasma urea on urine concentration in the opossom (*Didelphis marsupialis Virginiana*) Nature **207**:066–067.

PORTIER, P. 1910. Pression osmotique des liquides des oiseaux et mammiferes marins. J. Physiol. Pathol. **12**:202–208.

SCHMIDT-NIELSEN, K., and B. SCHMIDT-NIELSEN. 1952. Water metabolism of desert mammals. Physiol. Rev. **32**:135–160.

STULKEN, D., and C. KIRKPATRICK. 1955. Physiological investigation of captivity mortality in the sea otter. Trans. 20th North Amer. Wildlife Conf. **20**:476–494.

SVEDRUP, H. V., M. W. JOHNSON, and R. H. FLEMMING. 1942. The Oceans. Prentice-Hall, New York.

TARASOFF, F. J., and D. P. TOEWS. 1972. The osmotic and ionic regulatory capacities of the kidney of the harbor seal, *Phoca vitulina*. J. Comp. Physiol. **81**:121–132.

TEFLER, N., L. H. CORNELL, and J. H. PRESCOTT. 1970. Do dolphins drink water? J. Amer. Veteran Ass. **157**:555–558.

WATT, B. K., and A. L. MERRILL. 1963. Composition of foods. *In* U.S. Dep. Agri., Agricultural Handbook no. 8. Government Printing Office, Washington, D.C.

WOLF, A. V., G. L. PRENTISS, L. G. DOUGLASS, and R. S. SWETT. 1959. Potability of sea water with special reference to the cat. Amer. J. Physiol. **196**:663–641.