The Osmotic and Ionic Regulatory Capacities
of the Kidney of the Harbor Seal, *Phoca vitulina*

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Summary. 1. The maximum values obtained for urinary osmotic pressure, and sodium, chloride and potassium ion concentrations are 2050 mOsm/L, 523 mEq Na^+/L, 508 mEq Cl^-/L and 136 mEq K^+/L, respectively. The concentrations of sodium and chloride ions in the urine are about equal to those of sea water and the results show that the harbor seal must draw on body water to eliminate all of the ions introduced by sea water ingestion.

2. Distilled water ingestion results in an increase in urine volume and a decrease in urine osmotic pressure, specific gravity and ion concentrations.

3. Following sea water ingestion, a large increase in urine volume occurs within 2 hours, urine osmolality remains constant or increases, and sodium and chloride ion concentrations increase to maximum values within 3 to 5 hours. Urine specific gravity decreases abruptly 1 to 2 hours after sea water ingestion, followed by a progressive increase for the duration of the tests.

Introduction

The question of osmotic and ionic regulation in marine mammals has been of particular interest because of the apparent lack of "fresh" water available to these animals. In this regard, perhaps the most extensively studied marine mammal is the harbor seal, *Phoca vitulina*. This seal may be found considerable distances up rivers and in estuaries, although most live in an entirely marine environment (Fisher, 1952; Scheffer, 1958). To renew its body water, a seal living in sea water would have to migrate to river mouths periodically to drink fresh water, drink sea water and excrete a hypertonic urine, or obtain water from the metabolic breakdown of its food. Periodic migrations to fresh water seem unlikely, and studies have concentrated on the physiology of the seal's kidney and body fluids in an attempt to answer this question.

Irving *et al.* (1935b) examined the chloride content of urine and fecal matter from seals kept in sea water and determined that the chloride content was comparable to that of terrestrial mammals. They concluded that the seal did not drink sea water and that the kidney was not

unique in its ability to excrete salt. From calculations involving the amount of water available from metabolism of herring and the possible physiological uses of this water, they concluded that the harbor seal could manage adequately on the water derived from ingested fish. Smith (1936) examined the inorganic composition of the urine and salts of rectal washings of one seal and concluded that the seal did not swallow any considerable quantity of sea water. He also assumed that body water and water for urine formation are derived from water in the food and from metabolism. Albrecht (1950) injected sea water into the stomachs of seals and after observing the reactions of vomiting and diarrhoea, concluded that they do not drink sea water. Albrecht dehydrated the animals and observed that the seals could not be induced to drink sea water. Depocas *et al.* (1969) also concluded that these seals do not deliberately drink sea water.

Fresh water drinking has been reported by Irving *et al.* (1935 b) and Albrecht (1950), and has been observed in newly arrived seals in the colony at the University of British Columbia. In all cases, dehydration of the seals had occurred prior to drinking. These seals have never been observed to drink sea water. If it can be assumed that the seal does not drink sea water, the question of internal water conservation should be considered. Although the seal does have sweat glands, Irving *et al.* (1935 b) assumed that evaporated water from perspiration is not necessary for thermal regulation since the animal resides in a cool aquatic habitat. Smith (1936), Hiatt and Hiatt (1942) and Page *et al.* (1954) observed an increase in urine volume in the seal after a meal of herring and a decreased urine flow between feedings. The Hiatts suggested that post-feeding renal vasodilation occurs only when water is available, vasoconstriction and associated reduction in glomerular filtration limiting water excretion at other times. They proposed that it is this reduction of blood flow in the kidneys, and not the change in the number of active glomeruli, that is responsible for the reduced urine output.

Diving and its associated reduction of blood flow to various organs has been shown to play an important role in conserving body water. Initially, Irving *et al.* (1935) demonstrated that during diving there is a decrease in peripheral blood flow in the seal. Furthermore, Bradley and Bing (1942) found that during diving there is marked vasoconstriction of arteries leading to the kidneys with almost complete cessation of glomerular filtration and urine formation. They concluded that the intra-renal vasoconstrictive response to apnea appears to involve both afferent and efferent arterioles in a relatively uniform manner. Bradley *et al.* (1954) observed that sodium, potassium and water excretion decreases greatly with reduction in filtration during apnea. Lowrance *et al.* (1956) compared the effects of anoxia and apnea in the harbor

seal and concluded that they have comparable effects on renal activity. During diving there is no water loss from the lungs.

Several investigators have answered, in part, the question of whether the seal can conserve water from sea water by excreting a hyperosmotic urine. Albrecht (1950) recorded a chloride ion concentration of about 500 mEq/L after introducing sea water by tube. The highest urine sodium and potassium values reported are 480 and 370 mEq/L, respectively (Bradley *et al.*, 1954). These values indicate that the seal cannot excrete sodium and chloride ions in the urine at concentrations higher than those of open sea water: chloride = 548.3 mEq/L; sodium = 470.2 mEq/L; potassium = 9.9 mEq/l (Barnes, 1954).

In the harbor seal, neither the osmotic and ionic regulatory capacities of the kidney, nor the excretory patterns following ingestion of sea water have been fully examined. In this study, the effects of dehydration of the seal and ingestion of distilled water and of sea water in varying volumes and concentrations are examined.

Materials

Two yearling female harbor seals were studied. Over the test period they were kept in running fresh water and fed five pounds of thawed herring daily to maintain their weights at about 45.0 kg.

To ensure that the seals were in a post-absorptive state, they were starved for 36 hours prior to an experiment. The following fluids were given by stomach tube in duplicate experiments two hours after the initial urine collection: 500 ml and 1000 ml of distilled water; 500, 750 and 1000 ml of sea water, and 750 ml of sea water which had been evaporated to give 1.5 times the normal sea water concentration of the H 150% ions to be studied (150% S.W.). In a Control experiment, the animal was restrained and sampled with no fluid being ingested. Each experiment lasted 16 hours with urine collected hourly.

Sampling Procedures. The hind flippers of the seal were strapped to a restraining board and a plexiglass speculum (3.5″ in length and 1.5″ in diameter) was inserted into the urogenital vestibule as far as the urinary papilla. A sterile X-ray catheter was then inserted into the bladder and the urine collected in a sterile polyethylene bag. The volume was recorded and the urine pipetted into containers for analysis. Between collections the flippers were free to move.

Analytical Procedures. The osmotic pressure (mOsm/L) of two milliliter aliquots of each urine sample was determined on a Fiske Osmometer (Model G-62). The samples were analysed within four hours after the completion of each experiment to minimize errors caused by precipitation of urea crystals. The specific gravity of urine samples was determined using a Goldberg T/C hand refractometer (American Optical Co.).

The chloride ion concentration (mEq/L) in the urine was determined using a Buchler-Cotlove chloridometer. Sodium and potassium ion concentrations (mEq/L) were determined using a Unicam flamephotometer (Model SP900). "Labtrol" (Dade Reagents, Inc.) was used as a standard in all chloride, sodium and potassium ion determinations.
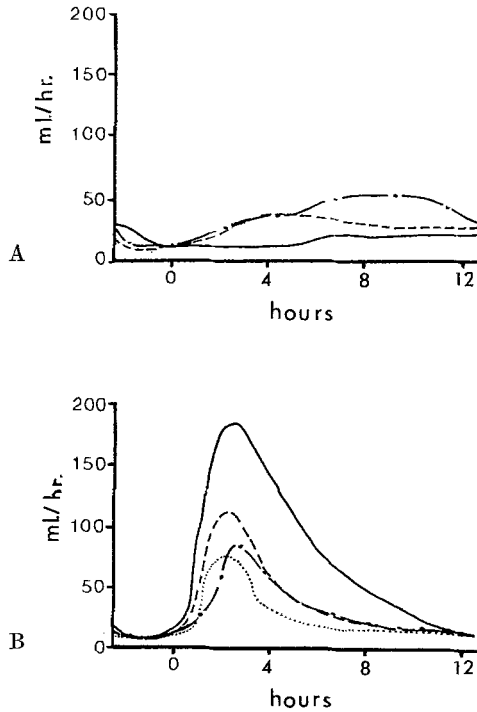
Fig. 1. Changes in mean urine volume (ml/hour).Tests A: ———— Control; ----- 500 ml distilled water; ——·—— 1 000 ml distilled water. Tests B: ...... 500 ml sea water; ——·—— 750 ml; sea water; ----- 1 000 ml sea water; —— 750 ml 150% sea water

Results and Discussion

Periods of dehydration (Control experiments) resulted in relatively low rates of urine production, with an average of 14 to 15 ml/hr produced in each case (Fig. 1). These were similar to the quantities determined for periods between meals by Smith (1936), Bradley and Bing (1942) and Schmidt-Nielsen *et al.* (1959). Man produces on the average 30 ml of urine/hour in cases of moderate hydropenia and can drop to 12 to 18 ml/hr in cases of extreme dehydration (Pitts, 1963). In man, the decreased urinary output is primarily due to changes in water reabsorption and not to alterations in the glomerular filtration rate (GFR). In more extreme dehydration, the changes in the filtration rate are caused by a reduced blood volume. In the seal, low urine volume during dehydration and starvation is attributed to increased electrolyte and water reabsorption (Bradley *et al.*, 1954) and to vasoconstriction with
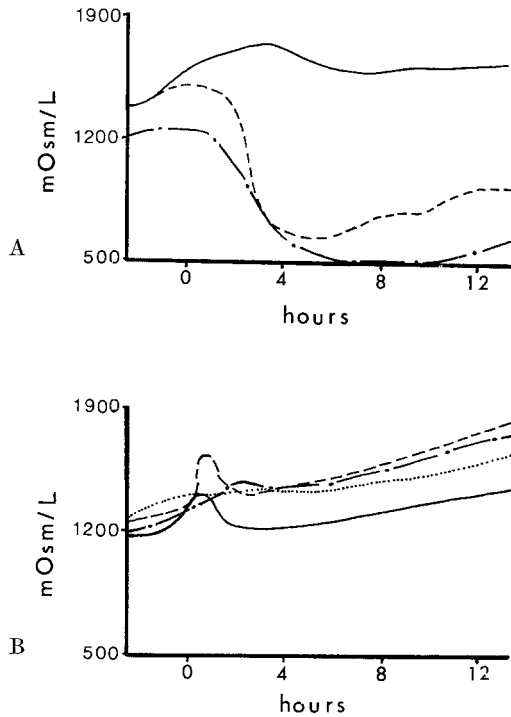
Fig. 2. Changes in mean urine osmolality (mOsm/L). Tests A: —— Control; ---- 500 ml distilled water; ——·—— 1 000 ml distilled water. Tests B: ..... 500 ml sea water; ——·—— 750 ml; sea water; -----1 000 ml sea water; —— 750 ml 150% sea water

the resultant reduction in the GFR (Hiatt and Hiatt, 1942). It was proposed by the Hiatts that the reduced urine flow between meals enables the seal to conserve its water supply. With low urine output there was a high urinary osmotic pressure (Fig. 2). This high osmotic pressure was probably due to a high urea output, which is the major osmotically active substance in the urine during fasting (Smith, 1936). Smith also found that the considerable quantities of ammonia, creatine and creatinine contributed to the osmolality of the urine 24 to 36 hours after the last meal.

In the Control tests, urine concentrations of sodium ions (Fig. 3) and chloride ions (Fig. 4) were low, indicating a near-maximum reabsorption of these two electrolytes. Urine potassium ion concentrations in the Controls were relatively higher than other electrolytes (Fig. 5). The effects of stress on potassium excretion (Pitts, 1963) and possible tissue damage caused by the catheterization and cannulation may, in part,
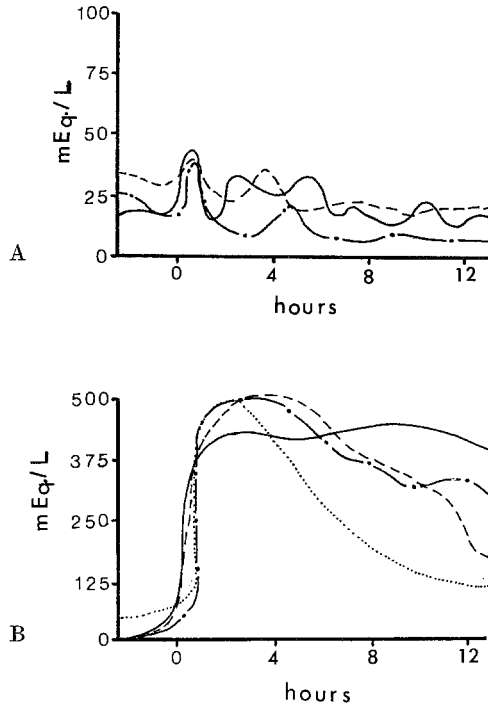
Fig. 3. Changes in mean urine sodium concentration (mEq/L). Tests A: ——— Control; - - - - 500 ml distilled water; ———·——— 1000 ml distilled water. Tests B: ...... 500 ml sea water; ———·——— 750 ml; sea water; - - - - - 1000 ml sea water; ——— 750 ml 150% sea water

account for the relatively high concentrations of this ion in the urine. It is also possible that the high urine potassium levels may be obligatory and an adaptation to a potassium rich piscivorous diet. The phenomenon of potassium secretion conditioning in the dog has been discussed by Pitts (1963, p. 125).

The pattern of urine volume changes after distilled water ingestion (Fig. 1) was similar to the excretory pattern in man and dog after ingestion of an isotonic solution (Pitts, 1963), in that the increase in urine volume was gradual. Albrecht (1950) and Bradley et al. (1954) reported a diuretic pattern for the seal similar to those of the dog and man. No measurements were made to determine whether the GFR changed during any of the tests. However, Bradley et al., and Page et al. (1954) and Schmidt-Nielsen et al. (1959) found that the GFR did not change during electrolyte and water loading. On the basis of their results, it seems probable that
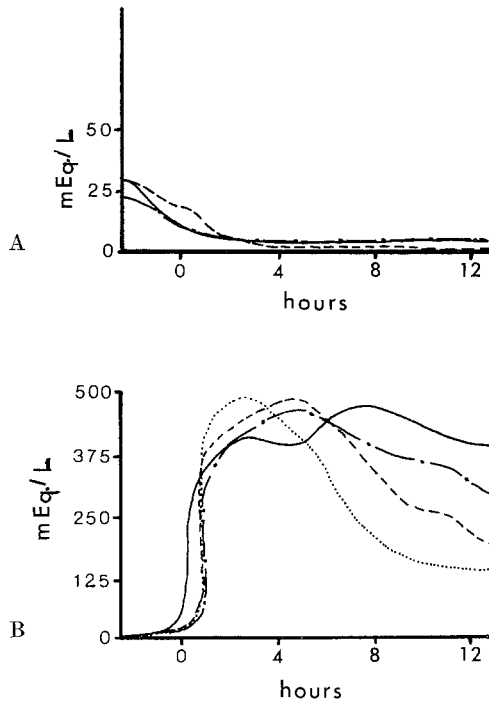
Fig. 4. Changes in mean urine chloride concentration (mEq/L). Tests A: —— Control; ---- 500 ml distilled water; ——·—— 1000 ml distilled water. Tests B: ..... 500 ml sea water; ——·—— 750 ml; sea water; ----- 1000 ml sea water; —— 750 ml 150 sea water

Table 1. Mean output of water and ions in 13 hours expressed as a percentage of total input

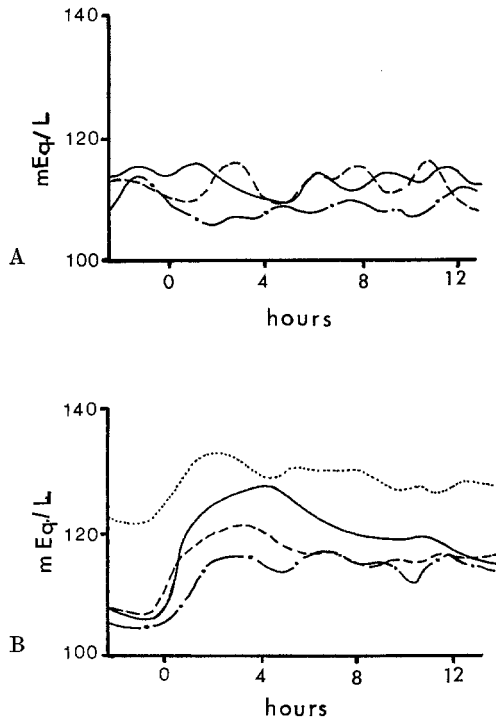| Volume input	Water output	Chloride output (%)	Sodium output (%)	Potassium output (%)
500 ml dist. water	68.5			
1000 ml dist. water	48.5			
500 ml sea water	61.5	45,5	53.5	431.0
750 ml sea water	54.0	44.0	55.0	261.0
1000 ml sea water	49.0	41.5	52.0	174.5
750 ml 150% sea water	130.0	71.5	94.0	357.5

Fig. 5. Changes in mean urine potassium concentration (mEq/L). Tests A: —— Control; ---- 500 ml distilled water; ——·—— 1000 ml distilled water. Tests B: ...... 500 ml sea water; ——·—— 750 ml; sea water; -----1000 ml sea water; —— 750 ml 150% sea water

if changes in filtration rate did not occur, then the changes in electrolyte concentrations and in urine volume in our study were due to alterations in the reabsorptive and secretory processes of the kidney. The reduced GFR that occurs in the seal during starvation may also have contributed to the low water output. Although the seals excreted only 21 to 50% of the introduced water over 13 hours (Table 1), it is possible that all the ingested water may have been removed after the experimental period.

After ingesting 500 ml of distilled water, the average rate of urine flow increased to 23 ml/hr (maximum = 48 ml/hr) after 4 hours, and after 1000 ml the rate increased to 32.9 ml/hr (maximum = 58 ml/hr) after 9 hours. The osmotic pressure of the urine decreased in the distilled water experiments (Fig. 2), but at no time was it hypoosmotic to the

plasma. If the pattern of water diuresis was similar to that in the dog (Pitts, 1963), the proportion of particles in the urine would perhaps have been low enough to make the urine hypoosmotic to the plasma. Even though there was a decreased electrolyte excretion, the other major constituents of the urine (urea, ammonia, creatine and creatinine) must be present in sufficient concentrations to maintain the recorded osmotic pressure. The osmolality is also affected by the gradual increase in urine volume which maintains a higher osmotic pressure and therefore conserves more water than would an abrupt increase.

Ingestion of hypertonic solutions results in an increased urine volume within three hours (Fig. 1) (Maximum urine volume for sea water tests: 500 ml = 82 ml/hr; 750 ml = 93 ml/hr; 1000 ml = 140 ml/hr; 750 ml of 150% = 210 ml/hr). The patterns of volume change for sea water and more concentrated salt solutions are similar to those reported by Albrecht (1950) and Bradley et al. (1954), respectively. In the sea water experiments, the urine osmolality increased progressively over the 13 hours following ingestion (Fig. 2) and reached a maximum of 2050 mOsm./L 13 hours after the ingestion of 1000 ml of sea water. Sodium ion (Fig. 3) and chloride ion (Fig. 4) concentrations increase rapidly after 1 to 2 hours and then may remain constant or decrease (Maximum urine sodium ion concentrations for sea water tests (mEq/L): 500 ml = 497; 750 ml = 523; 1000 ml = 490; 750 ml of 150% = 470. (Maximum urine chloride ion concentrations for sea water tests (mEq/L): 500 ml = 508; 750 ml = 490; 1000 ml = 500; 750 ml of 150% = 490). Potassium ion concentrations increased within the first two hours after sea water ingestion and reached a maximum of 136 mEq/L in the 500 ml test. (Maximum urine potassium ion concentration for sea water tests (mEq/L): 500 ml = 136; 750 ml = 121; 1000 ml = 123; 750 ml of 150% = 128). The increased urine volume and electrolyte concentrations may be accounted for by decreased aldosterone levels during the early stages, which would result in decreased sodium reabsorption and an osmotic diuresis. In the latter stages of the experiments the decreased electrolyte output and urine volume may be due to increased aldosterone levels which would increase electrolyte and water reabsorption. Similar effects due to varying levels of aldosterone have been demonstrated in the dog (Roemmelt et al., 1949).

With an initial increase in urine volume, the proportion of total solids (specific gravity) decreases (Fig. 6). At this time, the ion concentrations greatly increase, thus counteracting the decrease in osmotic pressure expected by a decrease in the concentration of solids excreted. The net result is an osmotic pressure that increases with time. This latter increase is possibly due to the ion concentrations remaining maximum or decreasing slightly, while the specific gravity increases.
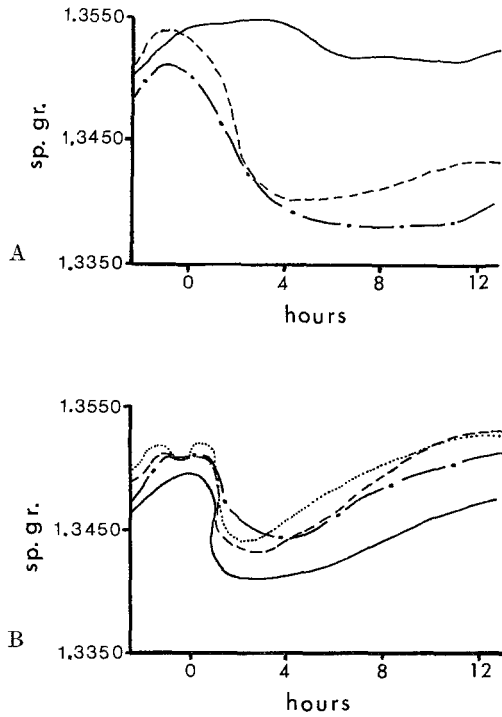
Fig. 6. Changes in mean urine specific gravity. Tests A: —— Control; ---- 500 ml distilled water; ——·—— 1 000 ml distilled water. Tests B: ..... 500 ml sea water; ——·—— 750 ml; sea water; ----- 1 000 ml sea water; —— 750 ml 150% sea water

Table 2. Maximum values recorded for urine osmolality and chloride, sodium and potassium ion concentrations

O.P. = osmotic pressure, U = urine concentration, S.W. = sea water concentration.

	Max. (mOsm/L)	S.W.	U/S.W.
O.P.	2 050	1 099	2.25
	Max. (mEq/L)		
Na+	523	447	1.17
CL−	508	548	0.93
K+	136	10	13.60

Open sea water (Barnes, 1954): Na+ = 470.20 mEq/L, Cl− = 548.30, K+ = 9.96.

The seal can concentrate sodium and chloride to approximately the concentrations found in open sea water (Table 2), and the results presented here show that to eliminate all of these ions introduced with sea water the seal has to draw on body water. Further evidence that this species cannot benefit from drinking large volumes of sea water is seen in the inability to eliminate both the water and electrolytes in sea water. Bradley *et al.* (1954) states that in the periods between meals, filtration as well as water and electrolyte excretion decreases, in fact, ". . . tubular activity may fail to operate in accordance with body needs, i.e., water and salt retention occurs despite the need to eliminate loads imposed experimentally." The results of the present experiments support this suggestion in that the seal retained up to 65% of the ingested water, 72% of the chloride and 65% of the sodium after 13 hours (Table 1). The results suggested that by continued drinking of sea water, the animal could become oedemic and increase its body electrolyte concentrations to toxic levels. If the animal takes in small quantities of sea water, as it may do when feeding (Depocas *et al.*, 1970), there would be sufficient water made available from the metabolic breakdown of the food, and with post-feeding hyperfiltration the body would be able to excrete the excess electrolytes. The seal spends up to one-third of its time submerged (Schmidt-Nielsen *et al.*, 1959), during which time the GRF, water and electrolyte output, and respiratory water loss are reduced, and there is little water loss by evaporation and in the faeces. Under these circumstances, the possibility of body hydration may be just as great a hazard as electrolyte intoxication following frequent ingestion of large quantities of sea water.

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