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# Experimental evidence of seawater drinking in juvenile hooded (*Cystophora cristata*) and harp seals (*Phoca groenlandica*)

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**Abstract** This study was undertaken to measure whether young harp seals (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) drink seawater and, if so, to investigate how the excess salt load is handled. Blood and urine samples were collected from hooded seal pups ($n = 3$) and harp seal pups ($n = 3$) after 2 weeks of freshwater exposure, at intervals during 3 weeks of seawater exposure and, finally, after 2 weeks of re-exposure to fresh water. Total water turnover, as measured by injection of tritiated water, was 2200 ml · day$^{-1}$ and 3300 ml · day$^{-1}$ in hooded seals and harp seals, respectively. The extent of mariposia was taken as the difference between total water turnover and influx of water through food (free and metabolic water) and respiratory water exchange. Seawater drinking amounted to 14% and 27% of total water turnover ($r_{H_2O}$) for the hooded seals and harp seals, respectively. Further evidence of mariposia was obtained from an increase in the excretion rate of the urine osmolytes $Na^+$, $Cl^-$ and $Mg^{2+}$, during the period of seawater exposure. It is concluded that water influx due to seawater drinking can not be excluded as a source of error when estimating food consumption of free-ranging harp seals and hooded seals, by use of labeled water techniques.

**Key words** Tritiated water · Mariposia · Osmolytes · Homeostasis · Harp seal

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**Abbreviations** $ADMR$ average daily metabolic rate · $H_2O_{food}$ water intake from food · $H_2O_{resp}$ water influx via respiration · $r_{H_2O}$ total water turnover · $SA$ specific activity · $TBW$ total body water · $V$ respiratory minute volume

## Introduction

Pinnipeds have three main routes of water loss; water loss via respiratory and cutaneous evaporation, urine production and water in feces. Experimental studies of grey seals (*Halichoerus grypus*) show that respiratory evaporative water loss constitutes only between 2% and 11% of total measured water loss (Folkow and Blix 1987). Respiratory water loss is restricted by the nasal heat exchange mechanism, which is also an efficient water saving mechanism (Huntley et al. 1984; Folkow and Blix 1987). Seals have sweat and sebaceous glands, but they do not appear to sweat (Ridgeway 1972; Whittow et al. 1972). This combined with a thick skin (King 1964), results in a low cutaneous evaporative water loss. Finally, the reniculated kidney of pinnipeds (Vardy and Bryden 1981) is able to produce urine with a maximum osmolality of 2000–2700 mosmol · kg$^{-1}$ (e.g., Tarasoff and Toews 1972; Hong et al. 1982; Skog and Folkow 1994), of which $Na^+$ and $Cl^-$ combined may contribute up to about 1000 mosmol · kg$^{-1}$. Such a concentrating capability may also limit obligatory water loss and help maintain homeostasis, when supply of fresh water (or snow/ice) is restricted.

These facts have led many researchers to question whether marine mammals need any additional oral water intake and thus drink seawater. Studies of harbour seals (*Phoca vitulina*) suggest that this species is not able to drink seawater with a net gain of water (Tarasoff and Toews 1972), neither does it voluntarily drink seawater (Depocas et al. 1971). This is contrary to the observations by Renouf et al. (1990) who observed that some of their harbor seals occasionally drank seawater from a small pool. Brown (1952),

moreover, observed that a captive female leopard seal (*Hydrurga leptonyx*) drank large quantities of seawater when given access to it. Gentry (1981) observed behavior resembling seawater drinking in four species of free-ranging otariids, while Costa (1978) reported extensive drinking of seawater in sea otters (*Enhydra lutris*). More recently, Renouf et al. (1990) reported that captive harp seals regularly ate significant amounts of ice cubes (up to 1000 g $day^{-1}$) when offered ad libitum. Water turnover studies of harp seals kept in freshwater tanks have moreover indicated that as much as 50% of water influx, or 1900 ml $day^{-1}$, was due to freshwater drinking (Lager 1992). Water influx through drinking of this order constitutes a large source of error in estimates of food consumption of free-ranging harp seals, based on labeled-water methods. Singly labeled water, like tritiated water, has been used to measure the food intake of free-living animals (e.g., Costa and Gentry 1986). One prerequisite for using this approach is that the animal does not drink water (Costa et al. 1989), since it is assumed that all the water influx is derived from the food. The influx of water via respiration is so small that it can be neglected. When the approximate diet of the animal and the gross chemical composition and water contents of this food is known, food intake can be calculated. Seawater intake from drinking thus causes an overestimation of the food intake of free-living seals.

When harp and hooded seals reside in pack ice areas, they have access to fresh water in the form of ice and snow. Satellite telemetry studies show that both hooded and harp seals migrate in open water for extended periods of the year (Folkow and Blix 1995; Nordøy et al. 1995, 1998; Folkow et al. 1996). During these periods these seals do not have access to any fresh water and must drink seawater if additional water, besides that obtained through food, is needed.

This study was undertaken to measure the extent of seawater drinking in young harp and hooded seals, and to estimate the potential source of error when the labeled-water method is used to measure food intake.

## Materials and methods

Three hooded seal pups (*Cystophora cristata*) and three harp seal pups (*Phoca groenlandica*) were captured on the pack ice of the Greenland Sea in April 1995. The animals were kept at the Department of Arctic Biology, University of Tromsø, in a 35,000-l freshwater tank under continuous flow and natural light conditions. The hooded seals (nos. 39, 40 and 42) were about 3 months old and weighed 28–30 kg, and the harp seals (nos. 44, 45 and 46) were about 6 months old and weighed 43–46 kg, when the experiments started. The number of animals was limited to six due to space limitations as many other experiments on other seals were performed at that time.

Prior to experiments the seals were trained to come up on a ledge where they could be fed by hand. This was done to prevent accidental seawater intake due to feeding in the water. The animals were fed individually pre-weighed, recently thawed capelin (*Mallotus villosus*) twice daily. A vitamin B complex was supplemented daily according to Blix et al. (1973).

The first and the last part of the experiment took place in a freshwater tank at the Department of Arctic Biology. The main part of the experiment took place in a 23,000-l outdoor, continuous flow seawater tank at the Centre of Aquaculture Research, Norwegian Institute of Fisheries and Aquaculture, in Tromsø. During the first experimental period (June–July) the average ambient temperature was 9.3 °C (range 6.3–15.7 °C), while the average temperature during the second period (September–October) was 8.6 °C (range 5.3–14.3 °C).

Water influx due to either seawater or freshwater drinking was calculated by the use of the following equation:

$$\text{Drinking} = r_{H_2O} - H_2O_{food} - H_2O_{resp} \quad (1)$$

where $r_{H_2O}$ is total water turnover, $H_2O_{food}$ is water intake from food (both free and metabolic water) and $H_2O_{resp}$ is water influx via respiration, assuming minimal influx of water through the skin.

### $r_{H_2O}$ calculations and corrections

$r_{H_2O}$ was measured by using the tritiated water method. After 14 days (the hooded seals) or 3 months (the harp seals) in freshwater tanks, the seals were transferred to the seawater tank. After 6–14 days of habituation to the new place and the new water, tritiated water (between 5 μCi $kg^{-1}$ body weight and 10 μCi $kg^{-1}$ body weight; Dupont, NEN Products, Boston, USA), diluted in approximately 10 ml saline, was injected into the intravertebral extradural vein through a 16-cm polyethylene venflon catheter (diameter 1.7 mm). Prior to the injection of tritiated water, blood samples were collected to measure the background level of radioactivity. After an equilibration period of between 1 h and 2 h after injection, blood samples were collected to measure total body water (TBW). Blood samples were then collected after 6, 13 and 22 days for the hooded seals and after 7, 14 and 27 days for the harp seals. After about 2 weeks in the seawater tank, tritiated water was re-injected to measure the change in TBW and to measure $r_{H_2O}$ when the animals were re-exposed to fresh water. After re-injection, the animals were brought back to the freshwater tank for another 9–13 days of freshwater exposure before the last blood samples were collected. Ice-chilled blood samples were immediately centrifuged (Kubota KS, Tokyo, Japan) at 1880 *g* for 10 min and stored at −20 °C until analysis. Plasma samples were deproteinised using ~71% perchloric acid and tritium concentration determined by standard liquid scintillation techniques using a Packard Tri-Carb Liquid Scintillation Spectrometer (model 3375, Warrenville, Downers Grove, USA).

The natural logarithm of the specific activity (SA) of tritium in plasma was plotted against time (Fig. 1), where the inclination of the decay (−k) of the SA in plasma is the fractional turnover of the tritiated water. Since the experimental animals were growing, Eq. 15 from Lifson and McClintock (1966) was used to calculate $r_{H_2O}$, which assumes a linear change in TBW. A maximum error of 5% is produced, provided TBW changes less than 40% during the measurement period (Nagy and Costa 1980). During the period kept in fresh water, $r_{H_2O}$ was not corrected for change in TBW. Due to small changes in body mass during this period, the error of the calculated $r_{H_2O}$ is less than 1%.

The final estimates of $r_{H_2O}$ were corrected for exchange and fractionation (Lifson and McClintock 1966). Exchange was corrected for by assuming an average daily metabolic rate (ADMR) of our seals being 3.5 times the basal metabolic rate (BMR) predicted by the Kleiber equation (Kleiber 1975), and by using the following equation from Folkow and Blix (1987) to determine the respiratory volume per day:

$$V = 0.042\ \text{ADMR} + 0.119\text{l}\ \text{min}^{-1} \cdot \text{kg}^{-0.75} \quad (2)$$

where V is the respiratory minute volume and ADMR is the average daily metabolic rate.

Knowing the ambient temperature, and assuming 100% relative humidity of the air, the partial pressure of water vapor of inspired air was calculated. Total water influx via respiration was then

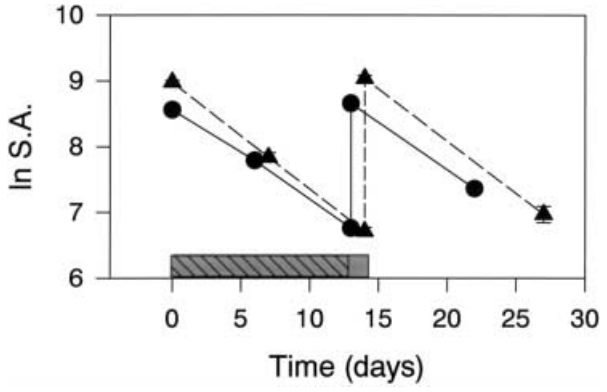


**Fig. 1** The natural logarithm of the specific activity (SA) of tritiated water in plasma plotted as a function of time (days) in three hooded seals (●) and three harp seals (▲). The initial SA was about 8000 cpm·ml$^{-1}$. The period of seawater exposure is marked along the *abscissa* with *crosshatching* for the hooded seals and in *grey* for the harp seals. This plot is made to estimate the fractional turnover, $k$, of tritiated water. At day 13 and day 14 for the hooded seals and harp seals, respectively, tritiated water was reinjected to determine total body water

obtained by multiplying respiratory volume and partial pressure of inspired water. By using eq. 39 from Lifson and McClintock (1966), exchange of tritiated water was calculated to overestimate calculated water turnover by 4–5% in these experiments.

The fraction of water efflux which is subjected to fractionation disappear either as cutaneous or respiratory evaporative water. This fraction was taken as the difference between total water turnover and urine produced. By assuming that about 90% of water was subjected to fractionation and using eq. 32 from Lifson and McClintock (1966), an underestimation of $r_{H_2O}$ of about 6% is indicated. This value represents a maximum error since the fraction of water efflux as evaporative water is overestimated due to the method of measuring urine production (urine measurements, see later).

### $H_2O_{food}$ and $H_2O_{resp}$

The free water content of the food was measured by drying seven subsamples (50 g each) of a total sample of 2000 g grinded capelin, at 60 °C to constant mass (~48 h). The amount of metabolic water (water resulting from chemical oxidation) from food was determined by measuring the fat and protein contents of capelin. The fat content was determined using the ethyl acetate extraction method in principle as described by Nordøy (1995) and the protein content was measured by the Kjeldahl protein analysis (Skoog et al. 1988). One gram oxidized fat produces 1.07 g metabolic water, while 1 g protein produces 0.39 g water (Schmidt-Nielsen 1990). Water intake via respiration was calculated as described previously.

### Urine and blood samples

On experimental days, the tank was drained, the seals were caught and restrained for collection of blood samples 1–2 h after having been in water. The seal pups were then put in specially made cages designed for continuous collection of urine (Nordøy et al. 1990). The urine passed through a funnel and was collected in flasks kept in iced water. The flasks were read every hour for urine volume. The seals were returned to the tank the following morning. Blood samples were collected from the hooded seals after 14 days of freshwater exposure, after 6, 13 and 22 days in seawater and, finally, 7 days after re-entry into fresh water. For the harp seals, blood samples were collected after 14 days of freshwater exposure, after 7, 14 and 27 days in seawater and, finally, 13 days after re-entry to the freshwater tank. The blood samples were collected by the procedure previously described, and centrifuged using either a CR4-22 centrifuge (Jouan, Saint Nazaire, France) at 2774 *g* for 8 min or a Kubota KS centrifuge (Tokyo, Japan) at 1880 *g* for 10 min.

Plasma samples were analyzed for osmolality (Osmomat 030, Berlin, Germany), $Cl^-$ (925 Chloride Analyzer, Halstead, Essex, England), $Na^+$ and $K^+$ (CIBA Corning 614 ISE $Na^+/K^+$ Analyzer, Halstead, Essex, England). Plasma aldosterone was determined by radio immunoassay (RIA) with a kit from Diagnostic Product Corporation (La., USA). This is a second-antibody-coated tube method using $^{125}$I-labeled aldosterone as a tracer. Urine was analyzed for osmolality and $Cl^-$, $Na^+$, $K^+$ and $Mg^{2+}$ (Perkin-Elmer 2380 atom absorption spectrophotometer, Conn., USA).

### Statistics

Wilcoxon's rank-sum test was used to test for significant changes between the measured values (Bhattacharyya and Johnson 1977). $P < 0.05$ was regarded as significant. Values are presented as averages ± SEM.

## Results

During seawater exposure, the average total turnover of water was 2162 ± 71 ml·day$^{-1}$ and 3339 ± 48 ml·day$^{-1}$ in hooded seal pups and harp seal pups, respectively. This amounts to about 70 ml·day$^{-1}$·kg$^{-1}$ in both species (Fig. 2). The free water content of the capelin was 67%. Daily consumption of capelin of hooded seals was 1.9 kg, giving a free water intake of 1270 ml·day$^{-1}$ water. Corresponding values for the harp seals were 2.5 kg·day$^{-1}$ capelin and 1680 ml·day$^{-1}$ water. The capelin contained 16% fat and 13% protein by wet mass. Assuming that all fat and protein is oxidized to its end products, about 400 ml and 600 ml metabolic water is produced per day in the hooded and harp seal pups, respectively. Thus, the free and metabolic water of ingested food amounts to about 81% of $r_{H_2O}$ of hooded

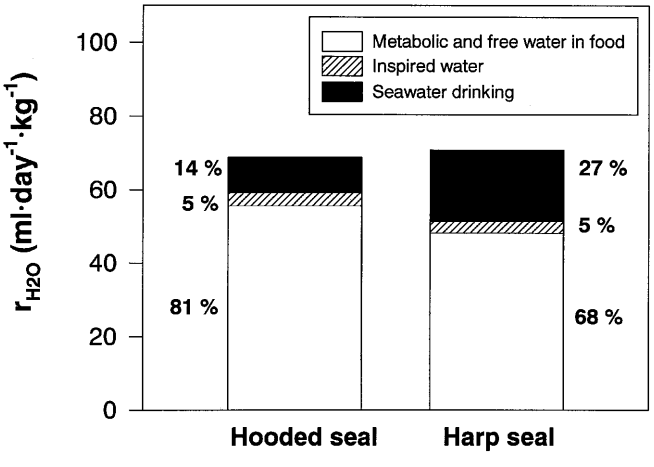


**Fig. 2** The total water turnover ($r_{H_2O}$; ml·kg$^{-1}$·day$^{-1}$), metabolic and free water from food, water intake from respiration and seawater drinking, for three hooded and three harp seals. The percentage contribution of the different routes of water influx to the total water turnover is also given

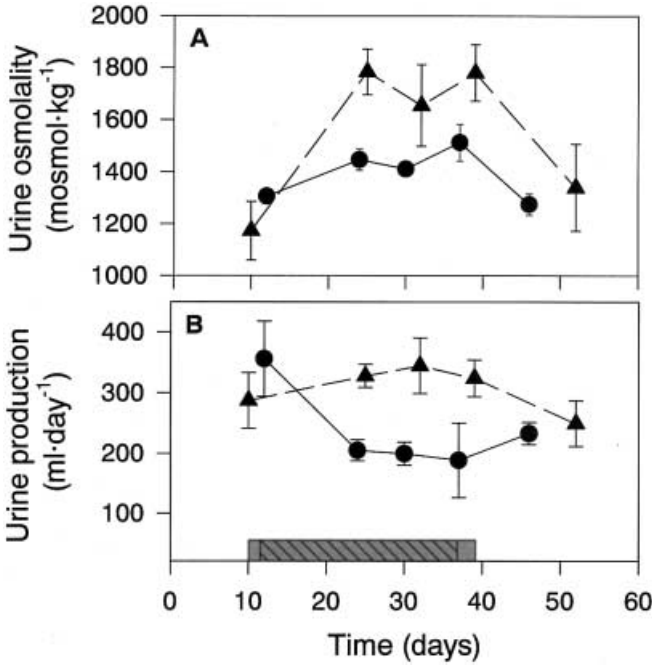


**Fig. 3** **A** Urine osmolality (mosmol·kg$^{-1}$) in three hooded (●) and three harp seals (▲) during periods of freshwater and seawater exposure. The period of seawater exposure is marked along the *abscissa* with *crosshatching* for the hooded seals and in *grey* for the harp seals. **B** Urine production (ml·day$^{-1}$) plotted as a function of time (days) for three hooded (●) and three harp seals (▲). The period of seawater exposure is marked along the *abscissa* with *crosshatching* for the hooded seals and in *grey* for the harp seals

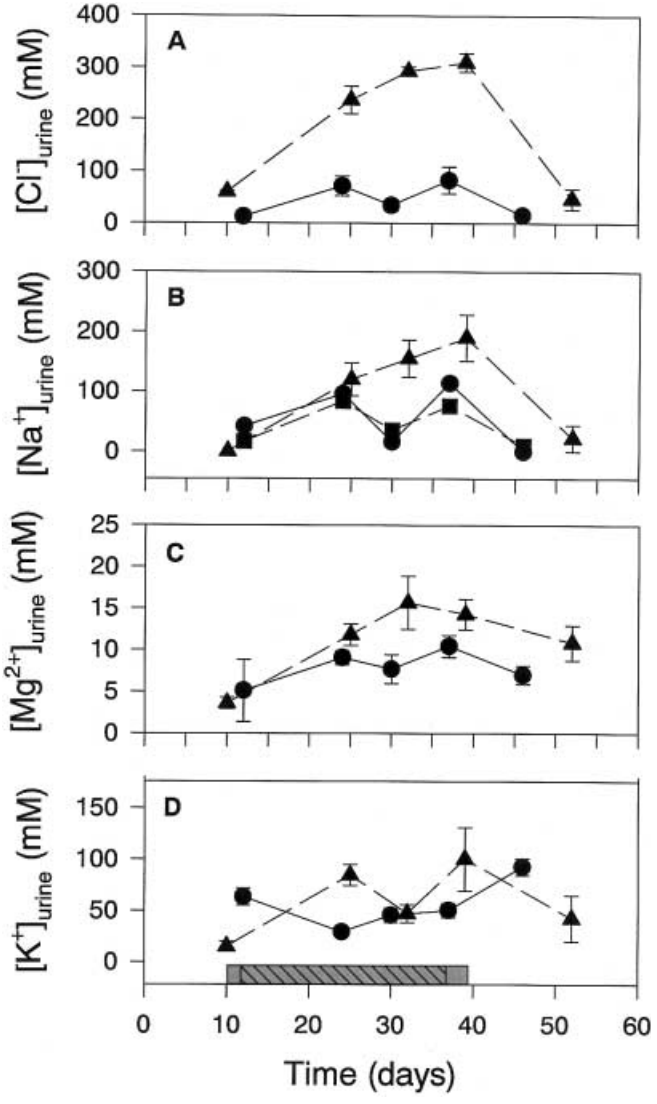


**Fig. 4** Urinary concentrations of $Cl^-$ (**A**), $Na^+$ (**B**), $Mg^{2+}$ (**C**) and $K^+$ (**D**) in three hooded seal pups (●) and three harp seal pups (▲) during periods of freshwater and seawater exposure. The period of seawater exposure is marked along the *abscissa* with *crosshatching* for the hooded seals and in *grey* for the harp seals

seals, and about 68% of the total water influx of harp seals (Fig. 2). Respiratory water intake was calculated to be 114 ± 2 ml·day$^{-1}$ and 152 ± 4 ml·day$^{-1}$ in the hooded and harp seals, respectively. This amounts to about 5% of $r_{H_2O}$ of the animals (Fig. 2). The hooded seals drank 300 ± 55 ml·day$^{-1}$ seawater, or 9 ml·day$^{-1}$·kg$^{-1}$, being 14% of $r_{H_2O}$, while the harp seals drank 900 ± 12 ml·day$^{-1}$ seawater, or 19 ml·day$^{-1}$·kg$^{-1}$, being about 27% of $r_{H_2O}$ (Fig. 2). Total water turnover in fresh water was the same as when the seals were kept in seawater, while freshwater drinking amounted to about 16% and 34% of $r_{H_2O}$ in the hooded seals and harp seals, respectively.

Urine osmolality (Fig. 3A) increased from 1307 ± 17 mosmol·kg$^{-1}$ and 1173 ± 113 mosmol·kg$^{-1}$ during the first period in fresh water to 1472 ± 40 mosmol·kg$^{-1}$ and 1739 ± 88 mosmol·kg$^{-1}$ during the time they were kept in seawater ($P < 0.05$), while there was a decrease to 1275 ± 41 mosmol·kg$^{-1}$ and 1340 ± 167 mosmol·kg$^{-1}$ for the hooded and harp seals, respectively, when re-introduced to fresh water ($P < 0.05$). Urine production in the hooded seals decreased from 365 ± 62 ml·day$^{-1}$ when kept in fresh water to 197 ± 18 ml·day$^{-1}$ when kept in seawater ($P < 0.05$). There was, however, no significant increase in urine production when the animals were re-introduced to the freshwater tank. The urine production of the harp seals was 287 ± 46 ml·day$^{-1}$ when kept in fresh water and 330 ± 19 ml·day$^{-1}$ when swimming in seawater (Fig. 3B).

Urine $Cl^-$ increased from 12 ± 6 mM and 60 ± 3 mM to 72 ± 19 mM and 332 ± 27 mM from freshwater to seawater exposure, for the hooded seals and harp seals, respectively ($P < 0.05$). When re-exposed to fresh water there was a return to a low 15 ± 3 mM and 47 ± 20 mM for the hooded and harp seals, respectively ($P < 0.05$; Fig. 4A). For the harp seals, the urine $Na^+$ increased from less than 10 mM during freshwater exposure to 155 ± 25 mM during seawater exposure ($P < 0.05$). By re-exposure to fresh water, the values decreased to 22 ± 22 mM ($P < 0.05$). The average values for two of the hooded seals were 30 mM during the first period of freshwater exposure, 70 mM during seawater exposure, and 5 mM when re-exposed to fresh

**Table 1** Average values and SEM for blood plasma osmolality, $Cl^-$ and $Na^+$ in three hooded seal pups and three harp seal pups after 14 days of freshwater exposure (*I*), during seawater exposure and after 7 and 13 days of re-exposure to fresh water (*II*), respectively. The figures for seawater exposure represent the average values of three different measurements during this period ($n = 9$)

| | Hooded seals | | | Harp seals | | |
|---|---|---|---|---|---|---|
| | Osmolality ($mosmol \cdot kg^{-1}$) | $[Cl^-]$ (mM) | $[Na^+]$ (mM) | Osmolality ($mosmol \cdot kg^{-1}$) | $[Cl^-]$ (mM) | $[Na^+]$ (mM) |
| Fresh water (I) | 329 ± 5 | 99 ± 1 | 150 ± 1 | 318 ± 4 | 101 ± 2 | 152 ± 2 |
| Seawater | 332 ± 4 | 100 ± 4 | 153 ± 2 | 319 ± 6 | 103 ± 2 | 153 ± 2 |
| Fresh water (II) | 335 ± 4 | 98 ± 3 | 153 ± 2 | 307 ± 2 | 100 ± 1 | 143 ± 2 |

water (Fig. 4B). Urine $Mg^{2+}$ increased from 5 ± 2 mM during the stay in fresh water to 9 ± 1 mM during seawater exposure in the hooded seal pups, and decreased to 7 ± 1 mM when re-exposed to fresh water ($P < 0.05$). Urine $Mg^{2+}$ of the harp seals increased from 4 ± 1 mM to 14 ± 1 mM when introduced to seawater ($P < 0.05$), while there was a tendency to a decrease when the animals were re-exposed to fresh water ($P > 0.05$; Fig. 4C). Urine $K^+$ decreased from 63 ± 8 mM to 42 ± 3 mM when the hooded seals were transferred from fresh water to seawater ($P < 0.05$). During re-exposure to fresh water there was an increase to 93 ± 8 mM ($P < 0.05$). The harp seals increased their urine $K^+$ from 15 ± 5 mM during freshwater exposure to 77 ± 10 mM when exposed to seawater. After 21 days of seawater exposure, there was a decrease in $K^+$ concentration ($P < 0.05$; Fig. 4D).

Plasma osmolality was not affected by seawater exposure (did not change during the course of the experiment) and was maintained at 332 ± 4 $mosmol \cdot kg^{-1}$ in the hooded seals and at 317 ± 6 $mosmol \cdot kg^{-1}$ in the harp seals. In accordance with this, the plasma osmolyte $Cl^-$ was maintained at 99 ± 3 mM and 102 ± 2 mM for the hooded and harp seals, respectively, and the plasma osmolyte $Na^+$ was 152 ± 2 mM for both the hooded and harp seals (Table 1). There were no significant changes in these plasma parameters, and homeostasis was therefore maintained in both species during the experiment, despite significant amounts of seawater drinking.

Aldosterone in plasma for the hooded seals ranged from 697 pM to 1252 pM during the first period of freshwater exposure, from 570 pM to 1687 pM during seawater exposure and from 647 pM to 2999 pM during the second period of freshwater exposure. For the harp seals the values ranged from 721 pM to 3332 pM, 373 pM to 2318 pM and from 480 pM to 1545 pM during freshwater, seawater and freshwater exposure, respectively (Fig. 5).

## Discussion

The difference between the daily total water turnover and different routes of water influx (respiratory water, metabolic and free water of the food), suggests that both harp seals and hooded seals drink significant amounts of seawater. In young harp seals this seawater intake amounts to as much as 27% of water turnover, or close to $1\,l \cdot day^{-1}$ seawater, while in young hooded seals the water influx due to drinking seawater amounts to 14% of total turnover rate (Fig. 2). With regard to harp seals, the indicated seawater drinking is supported by changes in the excretion rate of the major urinary osmolytes, $Na^+$ and $Cl^-$, as evidenced by an increased urine production (Fig. 2B) and increased urine concentration of these osmolytes, during the stay in seawater (Fig. 4A, B). Also, the increased excretion rate of the important divalent ion $Mg^{2+}$ of seawater supports the measured mariposia (Fig. 4A, B). The changes in total urine

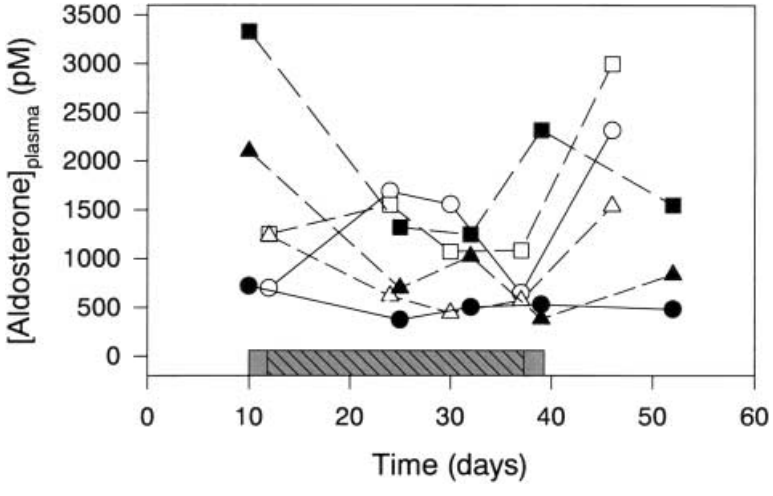


**Fig. 5** Plasma aldosterone during fresh and seawater exposure in three hooded (*open circle* No. 39, *open square* No. 40, *open triangle* No. 42) and three harp seals (*closed circle* No. 44, *closed square* No. 45, *closed triangle* No. 46). The period of seawater exposure is marked along the *abscissa* with *cross-hatching* for the hooded seals and in *grey* for the harp seals

osmolality supports these changes in urine osmolytes (Fig. 3).

Since both species were hand-fed on the ledge, the seawater intake was not due to accidental water intake caused by feeding under water, as suggested for harbour seals undergoing similar experiments (Depocas et al. 1971). Moreover, the level of mariposia was considerably higher than in harbour seals, where it amounts to only 9% of $r_{H_2O}$ (Depocas et al. 1971). In accordance with this it has also been concluded that the water excreted in the urine of harbour seals is almost exclusively derived from water which is made available from food (Irving et al. 1935; Smith 1936). Our experiments show that this is not the case in hooded seals and harp seals.

It is important, moreover, to note that our estimate of seawater drinking is an underestimate, since it has been assumed in our calculations that all fat and protein of food ingested are metabolized immediately, contributing to the daily water influx. In all experiments, however, body mass increased (2.7–13.1%) during the course of the experiment, indicating that some of the absorbed energy was stored, instead of being oxidized to $CO_2$ and water. We have, moreover, not accounted for incomplete absorption of food in the intestine (about 94% apparent digestible efficiency of capelin according to Mårtensson et al. 1994). Thus, since not all of the ingested fat and protein is available for metabolic water production, this will also contribute to an underestimate of seawater drinking.

Despite this obvious evidence of seawater drinking, plasma osmolality, $Cl^-$ and $Na^+$ were unchanged in both hooded and harp seals, during their stay in seawater (Table 1). In addition, there was no noticeable change in plasma parameters from freshwater to seawater exposure. The measured levels of different electrolytes in plasma are also in accordance with previous measurements in other pinniped species (Hong et al. 1982; Nordøy et al. 1992; Skog and Folkow 1994). This indicates that the kidneys are able to concentrate the urine to such an extent that the extra salt load is excreted, and homeostasis is maintained despite the measured minimum intake of 300–900 $ml \cdot day^{-1}$ seawater.

Considerable individual variation in plasma aldosterone levels were observed during the experimental periods (Fig. 5). When the values for the hooded and harp seals were pooled, however, there was a trend of decreased plasma aldosterone from freshwater to seawater exposure, and a concomitant increase when the animals were re-exposed to fresh water. The increased $Na^+$ load due to seawater ingestion, may give the tendency to decreased plasma aldosterone in order to reduce $Na^+$ reabsorption. When in fresh water, however, the only influx of $Na^+$ is through the food, and plasma aldosterone may be elevated to increase tubular reabsorption of this electrolyte. In harp seal pups subjected to 4 weeks of fasting without access to water (Nordøy et al. 1993) plasma aldosterone increased 10-fold to a maximum average value of 6800 pM after 30 days fasting. This suggested that aldosterone had an important function in these seals to increase $Na^+$ reabsorption and thus facilitate passive water reabsorption, to limit urinary water loss during fasting.

Our measurements of mariposia confirm indirect evidence of mariposia in harp seals provided of Gales and Renouf (1993). They demonstrated by use of stomach temperature telemetry, that swimming harp seals may display shorter periods of a profound decrease in stomach temperature (down to 17 °C), in absence of either snow, ice or food, which indicated seawater ingestion. Generally, it has been concluded that seals do not need to drink seawater because they are able to maintain water balance by way of the free and metabolic water from food (Hiatt and Hiatt 1942; Bradley et al. 1954; Depocas et al. 1971; Tarasoff and Toews 1972). A low urine flux, a thick skin (King 1964) and an effective nasal heat exchange (Huntley et al. 1984; Folkow and Blix 1987) are adaptations suggested to prevent excessive water efflux and thus reduce the need for additional water intake (seawater or fresh water). Despite these obvious logical elucidations, others have observed seawater drinking at various occasions in a number of different species of pinnipeds (Brown 1952; Gentry 1981; Tedman and Green 1987; Renouf et al. 1990; Gales and Renouf 1993; this study).

Why then do hooded seals and harp seals, in particular, drink seawater? The hypothesis of Gentry (1981) that otartiid species may drink seawater when dehydrated under hot conditions does not apply to present situation, since our seals where kept at rather low ambient temperatures. One intriguing hypothesis is that ingested seawater may provide urinary osmotic space for urea formed from catabolism of a high protein diet (Wolf et al. 1959). This has been suggested to be the case for sea otters feeding on a high protein diet (Costa 1978). Our seals, however, ate capelin with a relatively low protein content (13% protein $\cdot kg^{-1}$ wet mass), making the latter hypothesis less likely as an explanation for the measured mariposia. One plausible explanation may be the suggestion by Ridgeway (1972) that pinnipeds may drink seawater to maintain mineral balance.

When using the tritiated water method for measuring food intake in free-living seals, it is assumed that all water influx is derived from the food consumed (e.g., Costa 1988). The influx of water via respiration is so small that it can be neglected. When the approximate diet of the animal and the gross chemical composition and water contents of this food is assumed, food intake can be calculated, based on water influx. If seals, however, drink seawater the food intake will be gradually overestimated the more seawater is consumed. Our experiments show that with regard to hooded and harp seals, an overestimation of food consumption rates in the order of 15–30% is likely to be made, if mariposia is neglected. Thus this is an important source of error that must be accounted for in future calculations of food intake, particularly using the singly labeled water method in harp seals.

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