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A MICROPUNCTURE STUDY OF KIDNEY FUNCTION IN THE RIVER LAMPREY *LAMPETRA FLUVIATILIS* ADAPTED TO SEA WATER

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SUMMARY

Micropuncture techniques have been used to investigate kidney function in lampreys adapted to hyperosmotic media. Plasma electrolyte concentrations were maintained well below corresponding concentrations in the external environment. Urine composition was variable, but generally showed high concentrations of magnesium, sulphate and chloride ions. Lampreys in 50% sea water produced urine which was hypo or iso-osmotic to plasma, whereas those in 100% sea water produced hyperosmotic urine. Urine flow rate in 50% sea water was one tenth of that in fresh water, due to a reduction in filtration rate and an increase in water reabsorption by the kidney. As in fresh water, little if any filtered water was reabsorbed by the proximal segment. Almost 90% of filtered water was reabsorbed by the kidney of 100% sea water lampreys and most of this must have occurred in the distal and collecting segments.

INTRODUCTION

Studies on osmoregulation in lampreys have been largely confined to the fresh-water phase of their life cycle (reviewed by Morris, 1972). It has been established that in sea water, lampreys maintain plasma electrolyte levels well below those of the external environment (Burian, 1910; Robertson, cited by Morris, 1972; Mathers & Beamish, 1974) but the technical difficulties involved in capturing feeding lampreys at sea seem to have prevented a thorough study of the osmoregulatory mechanisms involved.

Despite the rapid decline in marine osmoregulatory ability on entering fresh water, some 'fresh-run' river lampreys have been re-adapted to dilute sea water (Hardisty, 1956; Morris, 1956). Attempts at re-adapting early migrants to full strength sea water have failed (Abou-Seedo & Potter, 1979), although Beamish, Strachan & Thomas (1978) found that sea lampreys, *Petromyzon marinus*, removed from migrating Atlantic salmon could osmoregulate in sea water. Kidney function was studied only in a few fresh-run river lampreys osmoregulating in 50% sea water. Urine flow was so low, however, that it was measurable in only one fish at 1·3 ml kg^{-1} day^{-1} (Morris, 1958). An analysis of urine from six 'fresh-run' fish transferred abruptly from fresh water to 50% sea water indicated that the kidney functions as in marine teleosts, by excreting calcium and magnesium ions (Pickering & Dockray, 1972).

The need for further information is obvious and the present study assesses kidney f[redacted]tion in 'fresh-run' lampreys after long-term adaptation to 50% sea water and in lampreys caught under estuarine conditions.

MATERIALS AND METHODS

Adult river lampreys were caught in eel traps set on mud flats in the Humber estuary and lower reaches of the river Trent. They were transported to Bangor and Nottingham in tanks of freshly prepared 50% sea water and kept in aquaria at 12 °C. The tank water was gradually increased to full strength sea water within a week of capture.

River lampreys were also trapped at the beginning of their migration up the river Severn (Logan *et al.* 1980*a*) and a number of these caught early in the 'season' were progressively adapted to 50% sea water.

Lampreys were adapted to a particular salinity for at least two weeks before use. The osmolarity of undiluted sea water was 1037·1 ± 18·8 (mean ± S.E.M.).

Experimental and analytical procedures

The method used for blood and urine sampling was described by Logan, Moriarty & Rankin (1980*b*). A polyethylene catheter (PP60, Portex Ltd, Hythe, Kent) was inserted into the urinary papilla and urine collected under oil in plastic tubes. Fluid was sometimes taken directly from the urinary ducts by puncturing them with large micropipettes. Because of the low urine flow rate in 100% sea water, a rapid method of urine collection was sometimes used. This involved anaesthetizing the fish (in ethyl-m-aminobenzoate methane sulphonic acid salt, Sigma, 0·05 g per litre sea water) and applying gentle manual pressure down the ventral surface of the animal so that fluid from the urinary ducts drained through the urinary papilla into tapered glass capillary tubes. The anus was blocked temporarily to avoid contamination by gut fluid.

Lampreys were prepared for kidney micropuncture in the manner described by Moriarty, Logan & Rankin (1978). Methods used for measuring inulin clearance and single nephron filtration rate were those of Logan *et al.* (1980*b*). To measure inulin clearance, 50 μCi[^{3}H] inulin (> 300 mCi/mmol: Radiochemical Centre, Amersham), in 0·2 ml distilled water, was injected intraperitoneally approximately 15 h before each experiment. The inulin dose was increased to 250 μCi in 0·3 ml water for single nephron determinations, giving approximately 100 counts per min above background in kidney tubular fluid samples. 150 μl blood was taken from the caudal vein prior to the first urine collection period. Further blood samples were taken at 2 h intervals. Plasma inulin counts were plotted against time, so that plasma counts at the mid-point of each urine and tubular fluid collection period could be obtained from the graph. Consequently, urine/plasma and tubular fluid/plasma inulin ratios were determined.

Electrolyte concentrations in suitable dilutions of plasma and urine were measured by emission (sodium) or atomic absorption (K, Ca, Mg) spectroscopy (EEL 240 or Unicam SP 90 Atomic Absorption Spectrophotometers). Chloride concentrations were determined by titration with an Aminco (American Instruments Co.) or CMT10 (Radiometer, Copenhagen) chloride meter.

Sulphate concentrations in suitably diluted urine samples were determined by a modification of the method of Dunk, Mostyn & Hoare (1969). 1 ml of sample plus 1 ml 750 μmol barium chloride ('Analar' grade, BDH Chemicals, Ltd) solution containing 2000 p.p.m. potassium chloride were shaken, stood for at least 18 h to ensure complete precipitation of barium sulphate, and then centrifuged at 1500 g for

Table 1. *Electrolyte concentrations (mM) in plasma and urine of lampreys adapted to fresh water, 50% sea water and 100% sea water*

	Na^+	Cl^-	K^+	Ca^{2+}	Mg^{2+}	SO_4^{2-}
FW plasma†	122·1 ± 2·9 (27)	108·0 ± 4·3 (28)	3·2 ± 0·7 (17)	2·4 ± 0·2 (20)	1·1 ± 0·2 (20)	—
50% SW plasma	151·0 ± 5·4*** (5)	138·8 ± 4·6*** (5)	3·3 ± 0·5 NS (5)	2·2 ± 0·1 NS (5)	2·6 ± 0·8* (5)	—
100% SW plasma	141·6 ± 2·2** (7)	143·2 ± 7·2*** (6)	3·3 ± 0·3 NS (7)	3·0 ± 0·2* (6)	2·5 ± ±0·4** (7)	—
FW urine†	16·5 ± 1·8 (20)	11·0 ± 3·5 (19)	2·2 ± 0·6 (13)	—	—	—
50% SW urine	67·6 ± 17·0*** (10)	85·5 ± 13·1*** (10)	1·8 ± 0·8 NS (10)	7·8 ± 1·8 (10)	50·4 ± 10·1 (10)	—
100% SW urine (a)	62·9 ± 15·3 (8)	150·0 ± 18·5 (8)	1·4 ± 0·5 (8)	12·1 ± 1·3 (8)	127·1 ± 14·9 (8)	93·5 ± 7·9 (8)
100% SW urine (b)	34·7 ± 10·4 (9)	162·3 ± 13·6 (9)	1·7 ± 0·5 (9)	17·5 ± 3·4 (9)	129·9 ± 15·5 (9)	96·7 ± 13·6 (9)
100% SW urine (a + b)	47·9 ± 9·5*** (17)	156·4 ± 11·0*** (17)	1·5 ± 0·4 NS (17)	14·9 ± 1·9 (17)	128·6 ± 10·5 (17)	95·2 ± 7·9 (17)

Results are given as means ± S.E.M. The number of estimates are given in parentheses. Significance of differences from fresh water fish plasma and urine electrolyte concentrations are given: NS, not significant; $*P < 0.1$; $**P < 0.01$; $***P < 0.001$.

† Taken from Logan *et al.* (1980*b*).

20 min. Residual barium was measured by atomic absorption spectrophotometry (EEL model 240) at 553·6 nm using a nitrous oxide/acetylene flame. Calibration was by magnesium sulphate (Analar) solutions and was linear in the range 100–500 μmol/l. Sulphate concentrations below this range gave anomalous readings due to the slight solubility of barium sulphate. This also meant that calibration with barium standards was not possible. The solutions were not acidified as no interference was detectable with any of the ions present in lamprey urine.

Osmolarities of all samples were measured in a nanolitre osmometer (Clifton Technical Physics, N.Y.) or Osmette S (Precision Instruments Ltd).

Table 2. *Osmolarity (m-osmol) of blood plasma and fluid samples from the kidneys of marine lampreys*

	Plasma	Proximal tubular fluid	Urinary duct fluid	Urine
50% sea water lamprey	296·1 ± 14·3 (7)	288·2 ± 7·9 (19)	294·0 ± 36·7 (7)	235·1 ± 36·4 (10)
100% sea water lamprey	309·1 ± 5·7 (5)	330·2 ± 2·3 (5)	—	389·1 ± 13·0 (7)

Results are given as means ± S.E.M. The number of estimates are given in parentheses.

RESULTS

There were no significant differences in plasma concentrations of sodium, chloride, potassium and magnesium between lampreys adapted to 50% sea water and those adapted to 100% sea water. Concentrations of sodium and chloride in both groups were, however, significantly higher than in fresh water lampreys, and magnesium levels were more than double those in fresh water (Table 1).

The plasma osmolarity of seven lampreys osmoregulating in 50% sea water was 296·1 ± 14·3 m-osmol (Table 2). Proximal tubular fluid at 288·2 ± 7·9 m-osmol (mean ± S.E.M.) (n = 19) was near isosmotic. A number of urine and urinary duct samples were significantly hyposmotic, but mean osmolarity of urinary duct fluid was 294·0 ± 36·7 m-osmol (n = 7). Urine samples varied from 42 up to 360 m-osmol, but the mean, 235·1 ± 36·4 m-osmol (n = 10) was not significantly different from that of urinary duct fluid.

The plasma osmolarity of five lampreys adapted to 100% sea water was 309·1 ± 5·7, similar to that in 50% sea water fish and significantly higher ($P < 0.001$) than in fresh water fish. Proximal tubular fluid in 100% sea water lampreys was slightly hyperosmotic to plasma ($P < 0.01$) at 330·2 ± 2·3 (n = 5) (mean ± S.E.M.) and urine was consistently hyperosmotic, giving a mean of 389·1 ± 13·0 m-osmol (n = 7) which was significantly higher ($P < 0.001$) than that of blood plasma. Unfortunately, plasma and urine samples were not measured in the same fish.

The urine of lampreys adapted to 50 or 100% sea water was very different in its electrolyte composition to that produced by fresh water fish (Table 1) and urinary concentrations of chloride, calcium and magnesium were significantly higher ($P < 0.001$) in 100% sea water fish than in 50% sea water fish. Sodium concentrations were lower in 100% than in 50% sea water fish, but the difference was

significant. There were no significant differences in electrolyte concentrations between 100% sea water fish urine collected either by cannulation (urine (*a*) in Table 1) or by forcibly draining the ducts (urine (*b*)): therefore, the results were pooled. Concentrations of sodium, chloride, calcium and magnesium in the urine of 50% and 100% sea water lampreys were very variable. Thus, for example, mean urinary sodium concentration in 50% sea water fish was 67·6 mM, but individual values ranged from 20 to 160 mM. There was a similar range of variation in the urinary magnesium concentrations of 100% sea water fish, from 48 to 187 mM.

Table 3. *Urine flow rate and inulin clearance in lampreys adapted to fresh water, 50% sea water and 100% sea water*

	Inulin clearance ml kg^{-1} day^{-1}	Urine/Plasma Inulin	% water reabsorption	Urine flow ml kg^{-1} day^{-1}
fresh water†	601·7 ± 55·7	1·8 ± 0·1	44·4 ± 2·3	337·1 ± 29·1
lamprey	(19)	(19)	(19)	(19)
50% sea water	111·8 ± 36·8***	8·0 ± 1·7	83·1 ± 4·3***	35·3 ± 13·2***
lamprey	(5)	(7)	(7)	(9)
100% sea water	—	9·5 ± 1·5	89·1 ± 1·4***	19·5 ± 2·0***
lamprey		(3)	(3)	(7)

Results are given as means ± S.E.M. The number of estimates are given in parentheses. Significance of differences from fresh water values are given: *** $P < 0.001$.

† Taken from Logan *et al.* (1980*b*).

There was no correlation between concentrations of sodium and magnesium in 50% sea water urine ($r = -0.1$) but good correlation in the 100% sea water urine samples ($r = -0.69$, $P < 0.01$).

Inulin clearance in five lampreys adapted to 50% sea water was 111·8 ± 36·8 ml kg^{-1} day^{-1} (Table 3). Assuming that inulin clearance equals glomerular filtration rate, water reabsorption by the kidney amounted to 83·1 ± 4·3%.

Urine flow rate was almost a tenth of that in fresh water fish. Tubular fluid: plasma inulin in proximal tubular fluid of these 50% sea water fish was 1·10 ± 0·11 ($n = 7$), indicating that little, if any, of the filtered water was reabsorbed along this segment. In 100% sea water, the lamprey kidney reabsorbed 89·1% of filtered water so that urine flow, at 19·5 ml kg^{-1} day^{-1}, was even lower than in 50% sea water. It should be pointed out that due to a shortage of experimental animals, inulin clearance was not measured in 100% sea water lampreys. The estimate of water reabsorption was therefore based on inulin concentrations in urinary duct fluid.

Single nephron filtration rate in 6 lampreys adapted to 50% sea water was 3·1 ± 0·4 nl min^{-1} ($n = 30$). This was not significantly different from that found in 100% sea water fish, which was 2·9 ± 0·3 nl min^{-1} ($n = 9$).

DISCUSSION

Before the onset of degenerative changes accompanying sexual maturity (Morris, 1958), lampreys are capable of osmoregulation in sea water and the kidney plays a vital role in maintaining plasma electrolyte concentrations well below those of the internal medium.

The urine of lampreys adapted to 50% sea water was isosmotic or hyposmotic as in marine teleosts (Hickman & Trump 1969). The dilute urine produced by some of these lampreys indicated they were osmoregulating, but because of the scarcity of such animals, none were put at risk by transferring to higher salinities. The changes described by Morris (1958) which occur on entering fresh water, or even earlier, seemed to be reversed during gradual re-adaptation to hyperosmotic media.

Lampreys caught in the Humber estuary were found in large numbers only during the autumn months, suggesting they were beginning their spawning migration. They were still truly euryhaline however and could tolerate extremes of exposure and salinity while held in traps on tidal mud flats. The urine produced by these lampreys in the laboratory was consistently hyper-osmotic to plasma. Further evidence for hyper-osmotic urine was provided by the results of analyses on 17 urine samples given in Table 1. The total concentration of measured electrolytes in blood plasma was 294 mM, compared with 445 mM in urine. There was very little variation in osmolarity of plasma from sea water lampreys and none of the evidence suggested that plasma electrolyte levels were ever elevated sufficiently for the kidney to produce ultrafiltrate of about 400 m-osmol. No explanation of this phenomenon can be offered until further work is carried out. Youson & McMillan (1971) and Natochin (1977) have commented on the anatomical similarity between the nephron loop in lampreys and the loop of Henlé. This raises the intriguing possibility that the former might be involved in the production of hyperosmotic urine in the sea water lamprey.

The urine flow rate of lampreys adapted to hyperosmotic media was higher than that of lampreys held in 50% sea water for 24 h (Morris, 1958; Pickering & Dockray, 1972), suggesting that the results of short-term salinity change experiments must be treated with caution. Urine flow was still considerably lower than in fresh water lampreys, partly because of reduced filtration rate, seen at the single nephron level and in overall GFR. The absence of a renal portal system, which may permit a continuation of tubular function when glomerular blood flow is reduced, suggests glomerular recruitment is unlikely in the lamprey. In the short-term, such as in salinity change experiments described by Rankin *et al.* (1980), changes in GFR were probably related to blood pressure in the renal arteries. Blood flow in these arteries was visibly reduced.

Similar reversible changes in GFR have been induced in rainbow trout (Holmes & McBean, 1963) and the rapid responses suggested there were no short-term changes in kidney morphology. There has been no histological investigation of the marine lamprey kidney, but it is possible there may be significant differences from the fresh water condition, such as those seen in the sea water adapted stickleback (Wendelaar-Bonga, 1973). These changes included reduced cellular activity of the glomerular podocytes, perhaps reflecting reduced filtration in sea water. There was also an increase in number and development of mesangial cells, which would increase the barrier to filtration.

The relatively low urine flow rate of 50% and 100% sea water lampreys was also due to the fact that net tubular water reabsorption was double the fresh water level. No more than about 9% of filtered water was reabsorbed by the proximal segment, as in fresh water lampreys (Logan *et al.* 1980*b*): therefore, most water reabsorption probably occurs in the distal and collecting segments. The main function of

proximal segment in sea water lampreys is to excrete magnesium (Rankin *et al.* 1980) and probably sulphate ions.

Mean urine flow rate of lampreys during the 24 h after abrupt transfer from fresh water to 50% sea water was 18·1 ml kg^{-1} day^{-1} and urinary Mg^{2+} concentration was 94·2 mM (Pickering & Dockray, 1972), giving a magnesium excretion rate of 1·7 mmol kg^{-1} day^{-1}. This is similar to the Mg^{2+} excretion rate of lampreys after long-term adaptation to 50% sea water (1·8 mmol kg^{-1} day^{-1}, calculated from Tables 1 and 3), suggesting that lampreys can switch-on magnesium secretion rapidly. This may be a response to elevated plasma magnesium concentration, as in teleosts (Bieter, 1931, 1933, 1935; Berglund & Forster, 1958; Hickman, 1968*a*). The magnesium excretion rate of 100% sea water lampreys was 2·5 mmol kg^{-1} day^{-1}.

Estimates of magnesium excretion by marine teleosts include 0·6–1·0 mmol kg^{-1} day^{-1} by the flounder (Hickman, 1968*a*, 1968*b*; Foster, 1975), 1·2 mmol kg^{-1} day^{-1} by *Oncorhynchus kisutch* (Miles, 1971), 1·4 mmol kg^{-1} day^{-1} by *Lophius americanus* (Hickman & Trump, 1969) and 2·1 mmol kg^{-1} day^{-1} by *Salmo gairdneri* (Beyenbach & Kirschner, 1974, 1975).

The rate of magnesium excretion by lampreys, particularly those in 50% sea water, was therefore rather higher than by marine teleosts. Morris (1958), however, found that extra-renal loss of water was greater in 50% sea water lampreys than in marine teleosts. To compensate for this, 50% sea water lampreys drank up to 220 ml kg^{-1} day^{-1} and absorbed up to 80% of swallowed water. Estimates of drinking rate in marine teleosts range from 8·14 and 12·33 ml kg^{-1} day^{-1} in intertidal species (Evans, 1967, 1968) to 234 and 266 ml kg^{-1} day^{-1} in *Tilapia mossambica* (Potts *et al.* 1967; Evans, 1968). The drinking rate in sea water eels was 36 ml kg^{-1} day^{-1} (Gaitskell & Chester Jones, 1971). Therefore, it appears that lampreys in 50% sea water drank more than a number of teleosts in full strength sea water and more than rainbow trout adapted to 50% sea water (Shehadeh & Gordon, 1969). Consequently, more magnesium may have been absorbed across the gut wall and excreted by the kidney.

The mechanism of magnesium secretion by the fish kidney is not known, but sodium-magnesium exchange has been postulated (Natochin & Gusev 1970; Vinnichenko, Natochin & Sabinin, 1975). There was an inverse correlation between sodium and magnesium concentrations in urine from isolated perfused kidneys of the anglerfish, *Lophius piscatorius* (Babiker & Rankin, 1979); this may have arisen in the proximal tubule as the *Lophius* nephron has no distal segment. There was an inverse correlation between sodium and magnesium concentrations in the urine of 100% sea water lampreys but not in that from 50% sea water animals. Evidence presented by Beyenbach & Kirschner (1974, 1975) however, has shown that the inverse relationship between sodium and magnesium concentrations in the urine of rainbow trout was due to reabsorption of sodium and water by the bladder wall, with consequent concentration of the residual magnesium. Such a mechanism could not explain the high magnesium concentrations found in lamprey proximal tubular fluid (Rankin *et al.* 1980) since this segment reabsorbed little, if any, of the filtered sodium and water. Water reabsorption could, however, account for the increase in magnesium concentration between the end of the proximal segment and the urinary duct. There were insufficient data on sea water lampreys to determine any correlation between renal water reabsorption and urinary sodium and magnesium concentrations.

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