

RENAL FUNCTION IN UNANAESTHETIZED RIVER LAMPREYS (*LAMPETRA FLUVIATILIS* L.): EFFECTS OF ANAESTHESIA, TEMPERATURE AND ENVIRONMENTAL SALINITY

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SUMMARY

1. Improved estimates of urine flow rates of lampreys in various salinities were obtained by the collection of urine for periods of up to 48 h from minimally-stressed, unanaesthetized fish, following catheterization of the urinogenital papilla.

2. The mean urine flow rate of freshwater lampreys was $200.7 \pm 14.3 \text{ ml kg}^{-1} \text{ day}^{-1}$.

3. Urine flow in freshwater lampreys was correlated with spontaneous changes in gill ventilation rate. MS222 anaesthesia reduced both ventilation and urine flow rates, but pronounced effects were only observed at concentrations greater than those needed to induce light anaesthesia ($50\text{--}55 \text{ mg l}^{-1}$). Urine flow rate in unanaesthetized fish was extremely sensitive to rapid (6°C h^{-1}) changes in temperature and Q_{10} ($6\text{--}16^\circ\text{C}$) was approximately 5.

4. Urine flow rate decreased rapidly as the osmotic difference between the body fluids and environment approached zero, and the rate of flow in 30‰ seawater lampreys was only 7.6% that of freshwater fish.

5. There was no evidence for an effect of environmental calcium concentration on branchial osmotic permeability.

6. Extensive tubular reabsorption of ions occurred in freshwater lampreys. The total daily excretion rate of sodium ions generally decreased in salinities hyperosmotic to the plasma, indicating enhanced reabsorption, but secretion of magnesium and sulphate ions was greatly increased. Urine osmolality was significantly increased in lampreys in hyperosmotic salinities.

7. Present data compare favourably with data obtained previously from anaesthetized animals, indicating that renal function in lampreys is not significantly impaired by light MS222 anaesthesia.

INTRODUCTION

The euryhaline river lamprey spawns in fresh water and experiences the same

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problems of osmotic and ionic regulation as freshwater teleosts, i.e. a large osmotic influx of water and a diffusional and urinary efflux of ions. The mechanisms of freshwater osmoregulation in lampreys are similar to those of teleosts (Morris, 1960) and include the excretion of large volumes of dilute urine. However, estimates of urine flow rate in lampreys vary widely (from 60–400 ml kg⁻¹ day⁻¹; Wikgren, 1953; Hardisty, 1954; Morris, 1956, 1960; Bentley & Follett, 1963; Malvin, Carlson, Legen & Churchill, 1970; Logan, Moriarty & Rankin, 1980a) and, although part of this variation is due to the highly variable flow rates which may be found in individual fish (Bentley & Follett, 1963), much of it probably reflects the different temperatures and variety of methods, all more or less stressful, which have been employed. Recent micropuncture experiments (Logan *et al.* 1980a; Logan, Morris & Rankin, 1980b), performed on anaesthetized animals, have yielded new data on the functioning of the lamprey kidney, but the relationship of these results to the normal physiology of lampreys would be clarified by studies on unanaesthetized, minimally-stressed lampreys. The present work set out to use chronically catheterized lampreys, which had been allowed a long period to recover from the stress of the operation, to identify factors possibly affecting urine production (temperature, anaesthesia, respiration, environmental calcium ion concentration) and to use the preparation to study effects of different environmental salinities on renal function.

The present work used fresh-run lampreys which had been adapted to a range of seawater dilutions. However, migrating lampreys rapidly lose the capability for marine osmoregulation as a result of breakdown of extra-renal osmoregulatory mechanisms (Morris, 1956, 1958; Pickering & Morris, 1970) and experiments performed on fish in 40 % and 50 % sea water were limited to the small numbers of fish which successfully adapted to these salinities.

MATERIALS AND METHODS

Animals

River lampreys were trapped on the River Severn during their autumnal and spring migrations, transported to Bangor with as little delay as possible after capture, and after slow adjustment of the water temperature to 10°C, were transferred to large tanks of aerated, copper-free, dechlorinated water maintained at 10°C. Batches of fresh-run fish were transferred to progressively increased seawater concentrations to provide lampreys adapted to a range of salinities up to 50 % sea water (500 mosmol l⁻¹). All lampreys were adapted to particular salinities for at least 10 days before use.

Experimental procedure

Lampreys were weighed after immobilization in a solution of MS222 (ethyl-*m*-aminobenzoate methane sulphonic acid salt, Sigma, 55 mg l⁻¹ water). Any water retained in the gill pouches or on the body surface was carefully removed before weighing. Body weights ranged from 27–82 g.

After weighing, the fish was laid on its back in a Perspex trough so that its head, gill region and dorsal surface were immersed in a circulating solution of MS222 (275 mg in 5 l) maintained at 10°C. The exposed body surface was covered in m

tissue paper to prevent dehydration. A catheter was constructed from approximately 40 cm of polypropylene tubing (PP60, Portex Ltd) by drawing out the tubing to provide a constriction about 1–2 mm from the tip. The catheter was filled with distilled water, carefully inserted into the urinogenital papilla of the lamprey, and a tie made around the papilla and tubing constriction, to prevent any forward or backward movement of the catheter. The catheter was secured by further ties to the tail approximately 1 cm and 2 cm posterior to the papilla.

The fish was then removed and transferred to a Perspex box (size 40 × 4 × 3 cm) which was connected to an anaesthetic-free, water-circulating system. The catheter was led to a fraction collector and urine was collected under water-saturated paraffin oil in tared plastic tubes. The system was covered in black polythene sheeting to reduce the risk of disturbance.

Ventilation rates were determined in some experiments using an impedance pneumograph (George Washington). A small silver electrode was inserted under the skin below the 3rd gill aperture of the lamprey and tied into position. A disc earth electrode was tied to the body about 1 cm anterior to the urinogenital papilla. Recordings were taken for 10–15 s at suitable intervals.

When required, 150–200 µl of blood was taken from the caudal vein of the fish and centrifuged immediately. Plasma samples were suitably diluted with double distilled water for analysis.

Effect of anaesthesia

Urine was collected from unanaesthetized lampreys in circulating fresh water, at 10°C, and MS222 was then added to give a range of concentrations of 0–80 mg l⁻¹. Urine was collected at each concentration for 20–30 min intervals for periods of up to 8 h.

Effect of temperature

The effect of rapid (approximately 6°C h⁻¹) changes in temperature on urine flow rates was determined over a range of 2–18°C. The water was held at the required temperature and urine collected for intervals of 20–60 min for periods of up to 4 h.

Effect of salinity

Urine was collected from unanaesthetized lampreys in fresh water and in salinities of up to 50 ‰ sea water. Water temperature was maintained at 10°C, and urine was collected for 60–90 min intervals for up to 48 h.

Effect of environmental calcium ion concentration

The apparatus was thoroughly washed in distilled water and urine was then collected from lampreys held in 10 l of circulating distilled water. Calcium chloride salt (Analar) was then added to the water to give a calcium concentration approximately equivalent to that of 100 ‰ sea water (10.5 mM). After urine collection, the water was drained and replaced with 0.3 ‰ or 0.6 ‰ sodium chloride (Analar) solutions with osmolarities (90, 206 mosmol l⁻¹) equivalent to those of 10 ‰ and 20 ‰ sea water respectively. Urine was collected for 90 min intervals over 20–30 h.

Analytical procedures and calculations

Electrolyte concentrations of suitably diluted samples of plasma and urine were measured by emission (sodium) or atomic absorption (potassium, calcium and magnesium) spectrophotometry (EEL 240 Atomic Absorption Spectrophotometer). Sulphate was measured by indirect atomic absorption spectrophotometry (Logan *et al.* 1980b). Osmolarities of plasma, urine and water samples were measured using a semi-micro osmometer (Knauer).

An initial 'settling down' period (6–8 h) was allowed for recovery from surgery. Urine flows were expressed as ml urine kg⁻¹ body weight day⁻¹. Statistical analysis was by Student's *t*-test.

RESULTS

The rate of urine flow in unanaesthetized lampreys in fresh water was 200.7 ± 14.3 ml kg⁻¹ day⁻¹ (Table 1) and decreased rapidly as the salinity of the external medium was increased (Fig. 1), so that the urine flow rate of 30 % seawater-adapted lampreys was only 7.6 % that of freshwater fish. This rapid decrease was associated with the approach of isotonicity between the body fluids and the environment. Urine

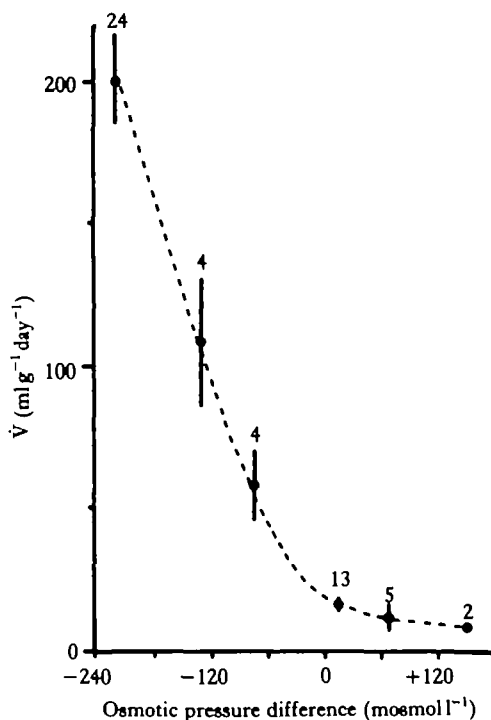


Fig. 1. Rate of urine flow (\bar{V} , ml kg⁻¹ day⁻¹) in lampreys in (from left to right) fresh water, 10, 20, 30, 40 and 50 % sea water, plotted against the difference in osmotic pressure (mosmol l⁻¹) between the external medium and the plasma. Values are mean flow rates \pm s.e.m. of individual means. Numbers of animals are shown.

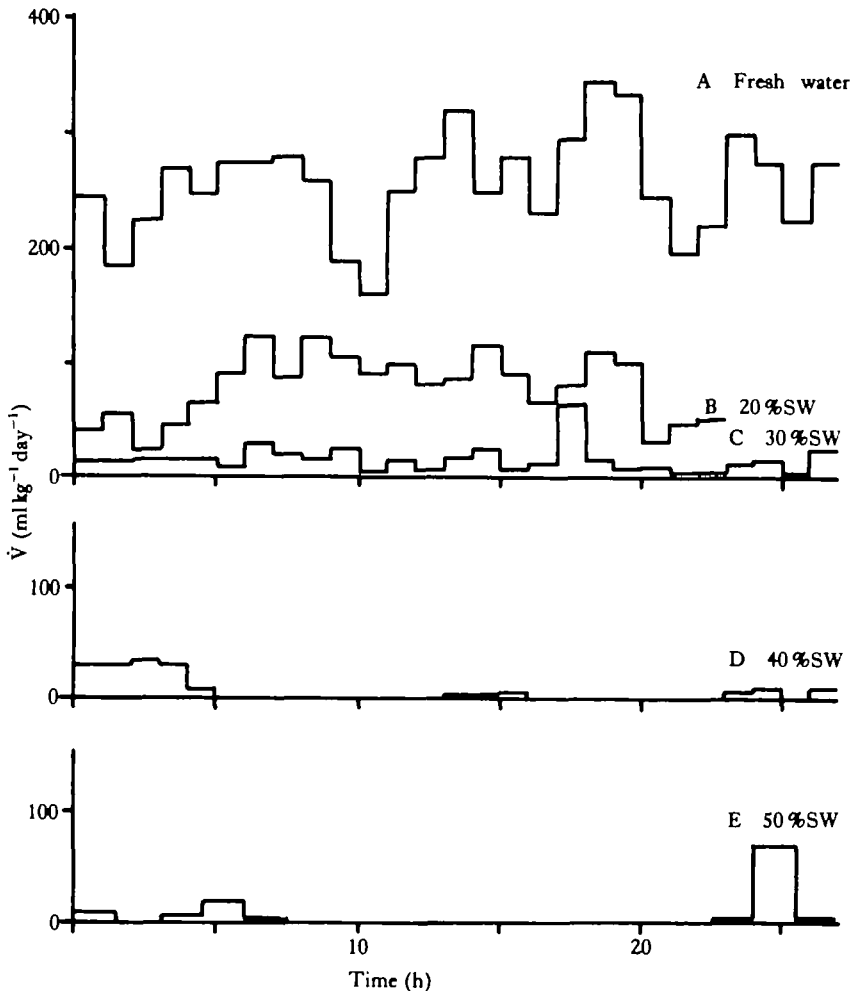


Fig. 2. Typical urine flow rate (\dot{V} , $\text{ml kg}^{-1} \text{day}^{-1}$) patterns of unanaesthetized lampreys in (A) fresh water, (B) 20 %, (C) 30 %, (D) 40 % and (E) 50 % sea water. Values are the mean flow rates calculated for 60–90 min collection periods.

was expelled at least once during each collection period when lampreys were in fresh water, 10 %, 20 % and 30 % sea water, but there were long anuric periods in 40 % and 50 % sea water (Fig. 2). Urine flow was highly variable in fish in all salinities studied, and in individual freshwater lampreys it correlated with spontaneous changes in gill ventilation rate (Fig. 3).

Urine collected from freshwater lampreys had an osmolality of 28.9 ± 7.0 mosmol l^{-1} (Table 1) and there was little change in urine osmolality with increasing water salinity up to 30 % sea water when there was a large increase ($P < 0.001$). Urinary ion concentrations were generally increased in these fish, but only those of magnesium ($P < 0.001$) and sulphate ($P < 0.001$) were significantly higher compared to freshwater

Table 1. Rate of urine flow ($\text{ml kg}^{-1} \text{ day}^{-1}$), urine and plasma electrolyte concentrations (mm) and osmolarities (mosmol l^{-1}), and urine : plasma ratios, of lampreys in 0 (fresh water) 10, 20, 30, 40 and 50% sea water (%SW)

%SW	0	10	20	30	40	50
Urine flow (mosmol l^{-1})	200.7 \pm 14.3 (24)	(102.5 \pm 2.8) 106.5 \pm 22.6 (4)	(204.6 \pm 7.4) 56.6 \pm 12.8 (4)	(309.7 \pm 5.9) 15.2 \pm 2.0 (13)	(412.0 \pm 6.0) 10.5 \pm 5.5 (5)	(510.6 \pm 3.0) 6.4 7.6
Urine Na^+	7.3 \pm 2.0 (8)	—	6.5 9.5 18.8	88.7 \pm 18.2 (5)	92.5 187.5 59.0	21.0 19.8
Plasma Na^+	130.9 \pm 3.9 (10)	—	134.8 \pm 13.6 (5)	145.4 \pm 22.6 (5)	210.0	170.8 \pm 7.3 (4)
Urine/plasma	0.06	—	0.09	0.61	0.54	0.12
Urine K^+	0.6 \pm 0.2 (11)	—	0.4 \pm 0.1 (5)	0.9 \pm 0.2 (5)	1.4 0.2	0.6 0.3
Plasma K^+	1.1 \pm 0.1 (10)	—	1.3 \pm 0.1 (6)	0.9 \pm 0.1 (5)	0.8	0.9 0.9
Urine/plasma	0.55	—	0.31	1.00	1.00	0.50
Urine Mg^{2+}	0.5 \pm 0.1 (10)	—	5.8 \pm 3.7 (4)	31.6 \pm 6.9* (5)	77.6 65.6	145.2 186.2
Plasma Mg^{2+}	2.5 \pm 0.8 (9)	—	2.4 \pm 0.5 (6)	4.8 \pm 1.9 (5)	5.1 3.8	2.7 \pm 0.3 (4)
Urine/plasma	0.20	—	2.42	6.58	14.04 34.4	61.37
Urine SO_4^{2-}	1.1 \pm 0.2 (8)	—	3.4 \pm 0.9 (5)	18.5 \pm 2.5* (6)	33.4 46.8	77.4 111.6
Plasma SO_4^{2-}	5.9 \pm 0.4 (9)	—	3.9 \pm 0.7 (8)	15.7 4.5 17.2	5.6 \pm 0.1 (4)	8.9 \pm 2.1 (4)
Urine/plasma	0.19	—	0.87	1.48	6.82	10.62
Urine Ca^{2+}	0.7 \pm 0.1 (7)	—	2.3 4.9	6.2 \pm 1.6 (4)	18.4 10.2	—
Urine osmolarity	28.9 \pm 7.0 (9)	—	34.3 \pm 5.8 (6)	121.3 \pm 23.5* (10)	331.8 \pm 59.0 (4)	505 423 403
Plasma osmolarity	217.3 \pm 15.6 (16)	235.0 \pm 3.2 (5)	268 288	294.4 \pm 13.3* (8)	347.4 \pm 10.0* (5)	361.8 \pm 9.5* (5)
Urine/plasma	0.13	—	0.13	0.41	0.96	1.23

Values are means \pm s.e.m. of individual means, except when $N < 4$ when individual means are shown.

Urine : plasma ratios were calculated from mean data.

Numbers of fish are given in parentheses.

* Highly significant ($P < 0.001$) difference from freshwater value.

fish. Urine osmolarity was further increased in lampreys adapted to higher salinities, and in a small number of 50 % sea water fish, the urine was slightly hyperosmotic to the plasma (Table 1).

The osmolarity of plasma from freshwater lampreys was 217.3 ± 15.6 mosmol l^{-1} (Table 1) and was significantly ($P < 0.001$) higher in fish in 30 % sea water. Plasma osmolarity was further increased with increasing water salinity so that lampreys adapted to 50 % sea water had a plasma osmolarity of 361.8 ± 9.5 mosmol l^{-1} .

Urine: plasma electrolyte concentration ratios were less than one in freshwater lampreys, but those of magnesium and sulphate ions rapidly increased with increasing water salinity, and very high urine: plasma concentration gradients for these ions were established in fish in 20–50 % sea water (Table 1) and the total daily excretion of these

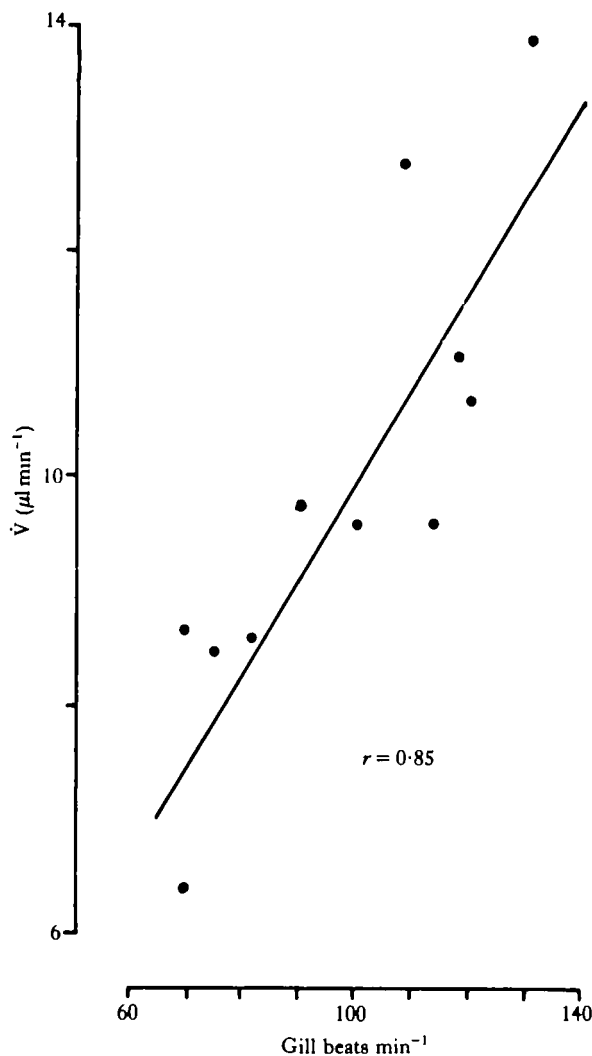


Fig. 3. Typical effect on urine flow rate (\dot{V} , $\mu l \text{ min}^{-1}$) of spontaneous variations in gill ventilation in an unanaesthetized, freshwater lamprey, at constant water temperature.

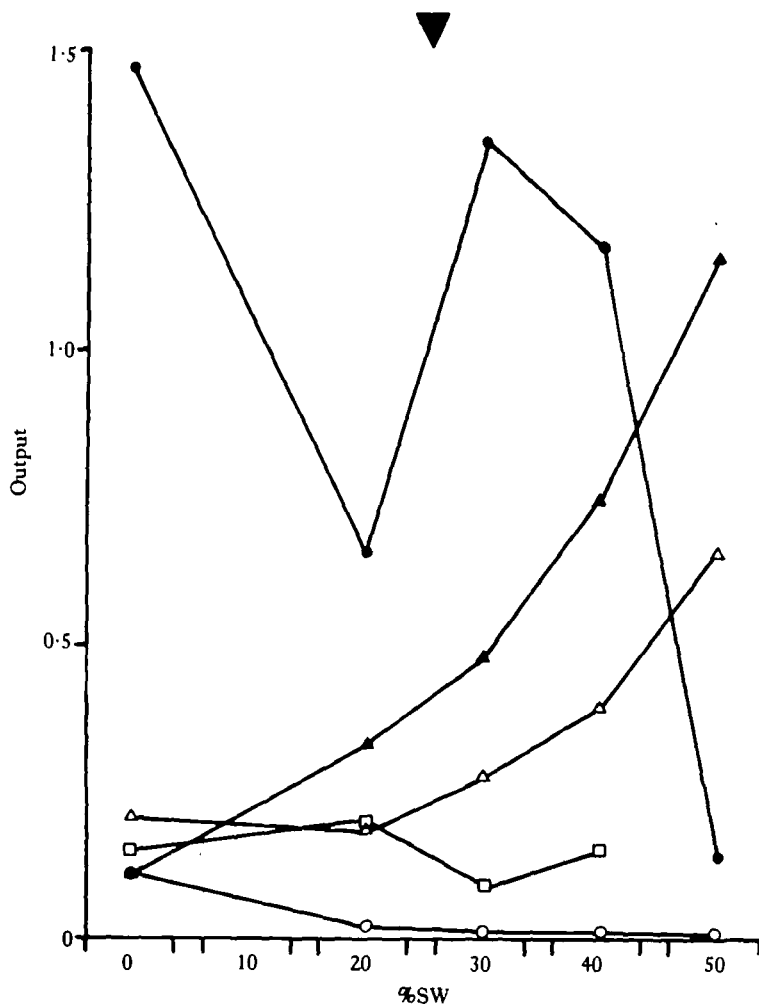


Fig. 4. Mean daily urinary excretion (output, calculated from Table 1, in $\text{mmol kg}^{-1} \text{day}^{-1}$ of sodium (●), potassium (○), calcium (□), magnesium (▲) and sulphate (△) ions in lampreys in 0 (fresh water), 20, 30, 40 and 50 % sea water (%SW). Arrow indicates approximate iso-osmoticity between plasma and environment.

ions was greatly increased (Fig. 4). Sodium excretion was greatly reduced in fish in 50 % sea water compared to all other groups.

The presence of calcium ions in the water did not have a significant effect on urine flow rate in lampreys. The urine flow rate ($206.7 \pm 42.3 \text{ ml kg}^{-1} \text{day}^{-1}$, $N = 5$) of lampreys held in a 10.5 mM -calcium chloride solution (osmolarity $30\text{--}33 \text{ mosmol l}^{-1}$) was not significantly different from that ($223.7 \pm 40.3 \text{ ml kg}^{-1} \text{day}^{-1}$, $N = 5$) of fish in distilled water alone. Transferring lampreys to 0.3% (osmolarity 90 mosmol l^{-1}) and 0.6% (osmolarity $206 \text{ mosmol l}^{-1}$) sodium chloride solutions (i.e. calcium-free) resulted in new urine flow rates of 194.3 ± 33.8 ($N = 4$) and 50.4 ± 8.6 ($N = 4$) $\text{ml kg}^{-1} \text{day}^{-1}$, respectively, but although the urine flow rate of fish in 0.6% sodium chloride solution was significantly ($P < 0.001$) lower than that of fish in distilled water,

was not significantly different from that of fish in 20% sea water (osmolarity $205 \text{ mosmol l}^{-1}$, calcium = 2.1 mM , Table 1).

Concentrations of MS222 anaesthetic ($50\text{--}55 \text{ mg l}^{-1}$), sufficient to induce anaesthesia, had little effect on urine flow rates of freshwater lampreys (Fig. 5), and no noticeable effect on gill ventilation rate was observed.

The effects of higher concentrations of MS222 were investigated in two lampreys, and urine flow rate was markedly decreased in both fish. Decreased gill ventilation rates were also observed in these fish.

Urine flow rates of freshwater lampreys were very sensitive to rapid temperature changes (Fig. 6). Q_{10} ($6\text{--}16^\circ\text{C}$) value was approximately 5. Gill ventilation rates were observed to increase as water temperature increased.

DISCUSSION

The present study confirms that the rate of urine production by freshwater lampreys is very high. Although the plasma osmolarity of lampreys is lower than that of teleosts (e.g. Hunn & Willford, 1970; Schmidt-Nielsen & Renfro, 1975) the resultant lower osmotic gradient between the body fluids and the environment is probably

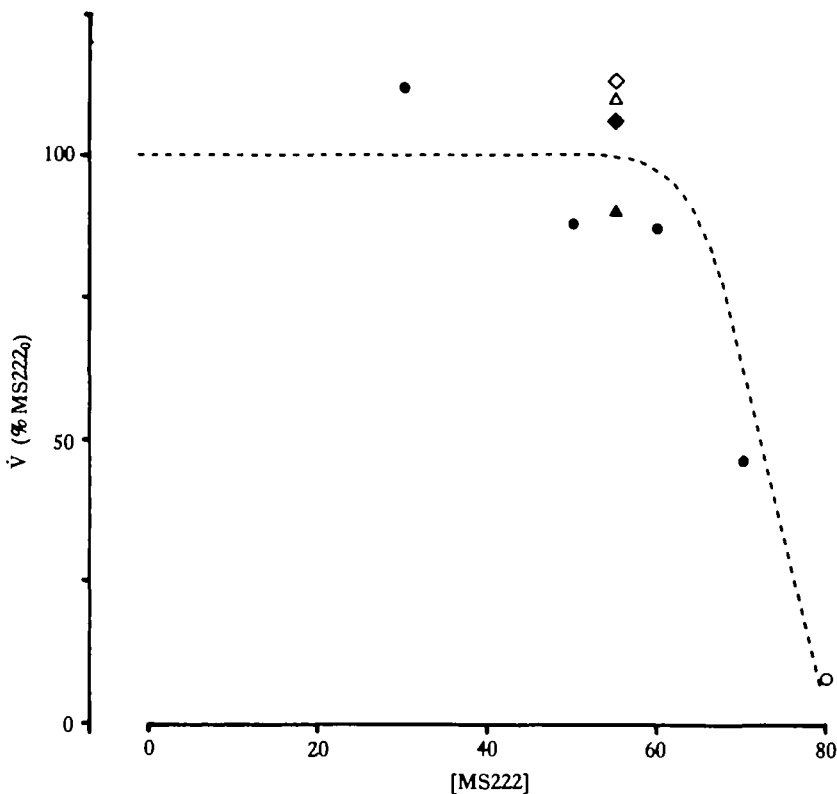


Fig. 5. The effect of environmental MS222 anaesthetic concentration (mg l^{-1}) on urine flow rate (\dot{V}) in freshwater lampreys, at constant water temperature. Values are individual means, expressed as percentage of anaesthetic-free value. Dotted line drawn by hand.

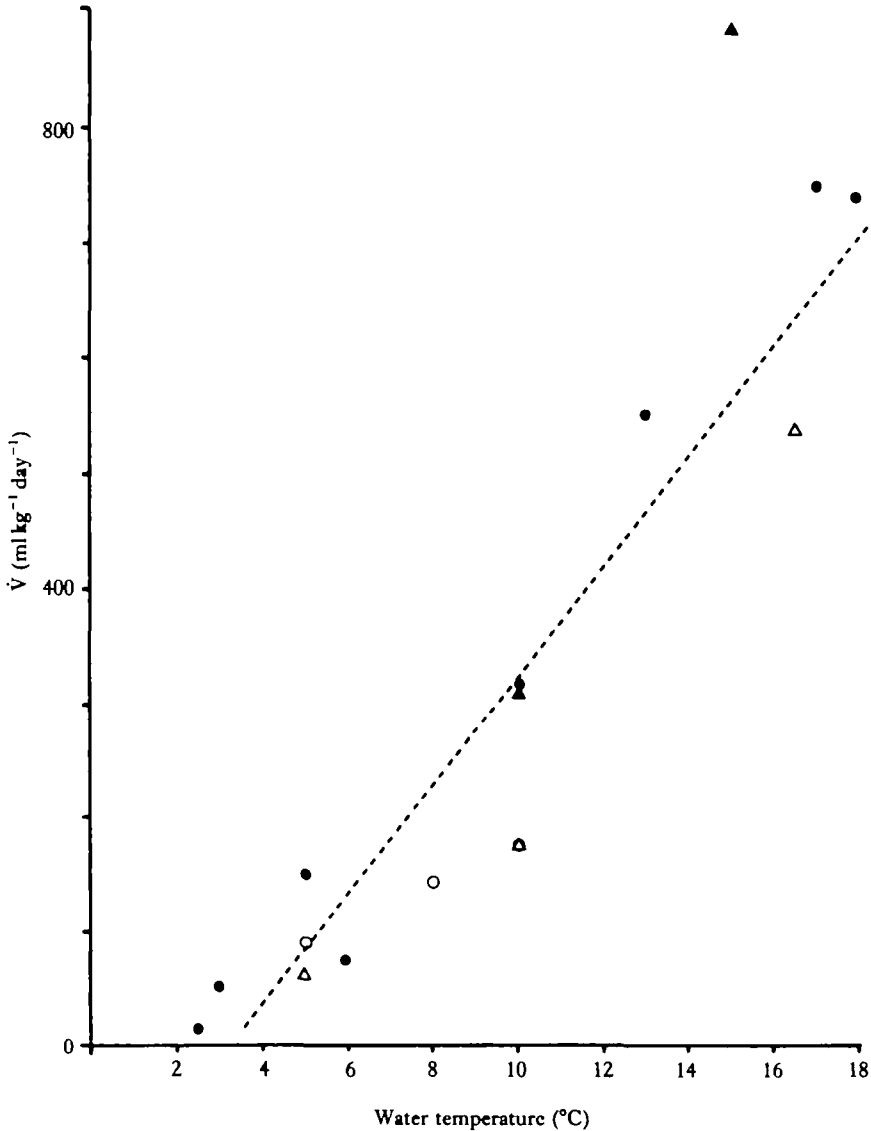


Fig. 6. The effect of successive increases in water temperature on urine flow rate (\dot{V} , ml kg⁻¹ day⁻¹) in unanaesthetized, freshwater lampreys. Values are individual means. Dotted line drawn by hand.

offset by the very high water permeability of freshwater lampreys (Wikgren, 1953; Bentley, 1962), resulting in a higher rate of urine flow. Urine flow rate in freshwater lampreys was positively correlated with gill ventilation rate, which indicates a high influx of water at high ventilation rates.

Urine flow rates of freshwater lampreys were extremely sensitive to changes in water temperature, and the Q_{10} (6–16°C) value was approximately 5. Teleosts acclimated to 20–25°C exhibited an increased water permeability when compared with fish acclimated to 5–10°C (Mackay & Beatty, 1968; Isaia, 1972; Motais & Isaia, 1972). However, when eels which were acclimated to one temperature were rapidly

transferred to water at a higher temperature, the change in urine flow was greater than when fish were allowed to acclimate to the higher temperature (Gaitskill & Chester-Jones, 1971; Motais & Isaia, 1972), and this indicates that the increase in water permeability which follows an increase in water temperature is greater when the changes in temperature are rapid, than when fish are allowed to acclimate to the new temperature. Similar changes in branchial water permeability, coupled with the observed increase in gill ventilation rate, could account for the higher Q_{10} value for urine flow found in lampreys in the present study compared with that found in temperature-acclimated lampreys (Wikgren, 1953).

High concentrations ($>55 \text{ mg l}^{-1}$) of MS222 anaesthetic caused large decreases in urine flow and gill ventilation rates in freshwater lampreys but both parameters were little affected at concentrations ($50\text{--}55 \text{ mg l}^{-1}$) sufficient to induce anaesthesia. Furthermore the osmolarity of urine from unanaesthetized freshwater lampreys was similar to that found in anaesthetized animals (Logan *et al.* 1980a): this indicates that renal tubular function is not impaired in lampreys under light MS222 anaesthesia.

The plasma and environment were isotonic in lampreys in salinities of between 20–30 % sea water, and in these salinities lampreys showed a greatly decreased urine flow rate when compared with freshwater fish. Similar changes have been found in anaesthetized lampreys and resulted from a decrease in single nephron (SNGFR) and whole kidney (GFR) glomerular filtration rates (Rankin, Logan & Moriarty, 1980), with tubular water reabsorption essentially unchanged. The present data indicate that changes in renal function in these fish were in response to an increase in environmental osmotic pressure and not to calcium-mediated decreases in water permeability and hence water influx.

Lampreys in salinities hyperosmotic to the plasma (i.e. greater than 30 % sea water) replace osmotic losses by drinking large volumes of the medium (Morris, 1958; Pickering & Dockray, 1972) and by increasing tubular reabsorption of water (Logan *et al.* 1980b; Rankin *et al.* 1980). Excess magnesium and sulphate ions, absorbed in the gut as a consequence of ingesting sea water, are excreted renally and the urinary concentrations of these ions were very high in anaesthetized 50 % and 100 % seawater-adapted lampreys (Logan *et al.* 1980b). The SNGFR of anaesthetized lampreys in 50 % sea water was not significantly different from that of fish in 20 % (i.e. hypo-osmotic) sea water (Rankin *et al.* 1980). It is of significance that, in the present study, marked changes in tubular function occurred in unanaesthetized lampreys in salinities above 20–30 % sea water. Lampreys in 50 % sea water had very high magnesium and sulphate ion excretion rates, indicating that a marked tubular secretion of ions had occurred. The excretory rate for sodium ions was lower in these lampreys than in fish in any other salinity, indicating that tubular sodium reabsorption was enhanced.

Unanaesthetized lampreys in 50 % sea water excreted a urine which was slightly hyperosmotic to the plasma, largely due to very high urinary concentrations of magnesium and sulphate ions. A hyperosmotic urine has previously been reported in anaesthetized lampreys adapted to 100 % sea water, but not in those adapted to 50 % sea water (Logan *et al.* 1980b).

Generally, the present data obtained from unanaesthetized lampreys compare favourably with data obtained from anaesthetized lampreys. Renal function is

minimally affected by light MS222 anaesthesia, and the intrarenal mechanisms, recently determined in anaesthetized animals (Logan *et al.* 1980a,b; Rankin *et al.* 1980; Rankin, Griffiths, McVicar & Gilham, 1982), probably relate to the normal renal physiology of lampreys.

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