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SHORT COMMUNICATION

SODIUM BALANCE IN FRESH-RUN ATLANTIC SALMON

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Preliminary experiments have been carried out to determine the main features of salt balance in adult salmon immediately following transfer to fresh waters, both neutral and acidic. The processes of adaptation from hypo-osmotic regulation in sea water to hyperosmotic regulation in fresh water must involve many rapid adaptations of the gills, kidneys and endocrine systems. From the practical point of view these changes may affect the time spent by returning salmon in estuaries, where in Britain they are vulnerable to commercial netting. In addition, in a few rivers, the entry of salmon into fresh water may coincide with the most acidic episodes. Mass kills of fish were one of the factors which drew attention to the acid rain problem and have been reported in both Norway and Britain (e.g. Leivestad & Muniz, 1976; Crawshaw, 1984). This unfortunate coincidence of upstream migration and acidic episodes arises because of the high correlation between increased river flow and lowered pH, on the one hand and river flow and fish movements on the other, Gee (1980).

Adult salmon, *Salmo salar* L., were obtained from coastal nets in sea water at Carnoustie, Angus (fish nos 6, 7, 8, 9, 10, 11, 17 and 27). These were maintained in the DAFS laboratory at Almondbank, Perth in a tank of recirculating sea water at 28‰ salinity, at 12°C. Other adult salmon were caught in tidal fresh water in the Tay estuary at Inchyra, 2 km south of Perth. Some of these fish, which still had 'sea lice', *Salmonicola* species, on their bodies were transferred to the sea water tank for at least 5 days before use (fish 4 and 5), while others were transferred to running fresh water from the river Almond (fish 1, 2, 16, 22 and 28). The salmon ranged in weight from 1·73 to 3·71 kg. In addition 2-year-old parr approx. 150 g, reared in Almond river water were also used.

Key words: Salmon, sodium regulation, migration, acid water.

Influxes were measured with (10–40 μC) ^{24}Na (Amersham International), in fibreglass tanks containing 40 litres of water. When seawater-adapted fish were transferred to fresh water for influx measurements the fish were, when possible, first washed for 30 min in large tanks of running river water before being transferred to the experimental tank. They were then allowed to settle down for 30 min before the addition of the isotope, but in some of the rapid transfer experiments both the washing period and the settling period had to be reduced. When the settling period was omitted the isotope was added to the bath before the fish in order to obtain a uniform distribution at the beginning of the experiment. In the other cases the isotope was distributed over the surface of the tank at the beginning of the experimental period. The fish was removed, washed, killed by a blow on the head and a blood sample taken from the caudal blood vessels. The blood was centrifuged and 2-ml samples of plasma were counted in a well-type sodium iodide scintillation counter (Panax Reigate system). Samples (2 ml) of medium taken at the beginning and the end of the experiments were similarly counted. Corrections were made for decay. Na influxes (K_i) were calculated from the equation:

$$K_i = \frac{\text{Counts ml}^{-1}\text{ serum} \times \text{mean Na content of 1 ml of bath}}{\text{Counts ml}^{-1}\text{ of bath} \times \text{Na content of 1 ml of serum}}.$$

The mean sodium content of the bath was determined from the samples taken at the beginning and end of the experiment. Net sodium losses were calculated from the change in sodium content of the bath. Sodium concentrations were determined by flame photometry using an EEL 100 emission flame photometer. The water in the experimental tanks was continuously circulated by rotary pump (4 l min^{-1}) to maintain good mixing and vigorously aerated. Tank temperatures were maintained at 12 ± 1 °C with a cooling coil.

Most experiments were carried out in water taken from the river Almond. This contained (in mmol l^{-1}): Na, 0·25; Ca, 0·1–0·2; and K, 0·009; pH 7·0–7·3. Low sodium concentrations, 0·05 mmol l^{-1} were obtained by dilution with deionised Almond water, high sodium concentrations, 5 mmol l^{-1} by the addition of NaCl. Low pH was obtained by the addition of appropriate quantities of H_2SO_4. The pH was monitored continuously and adjusted if necessary.

Sodium taken up at the gills appears rapidly in the blood but equilibrates more slowly with the intracellular sodium of the other tissues. Estimates of fluxes based on changes in the specific activity of the blood will therefore not be exactly comparable with fluxes based on changes in the specific activity of the sodium in the whole body (Potts, Foster & Stather, 1970). To assess the magnitude of the discrepancy samples of white muscle were taken from fishes 1–6, 1 or 2 h after the beginning of the experiments. The mean value of the specific activity of the muscle sodium, including extracellular sodium, after 1 h was 67 ± 13 % from which we estimate that the specific activity of the blood would be 7 % higher than that of the total body sodium after 1 h. Estimated fluxes, caclulated from rate constants and an assumed value of 44·8 mmol l^{-1} Na kg^{-1} total body sodium, have

been reduced by this amount for comparison with fluxes calculated from changes in the sodium contents of the baths. Appropriate corrections were made for longer or shorter experiments.

Our results are based on 15 adult fish and a similar number of parr examined in a variety of conditions. Many of the experiments described below are based on only two or a few individuals. Nevertheless, the results are encouragingly consistent.

Two fish (1 and 2), which had been in fresh water for at least 5 days, had sodium influx rates of 0·94 and 0·59 % h^{-1} of total body Na, equivalent to 0·421 and 0·261 mmol $kg^{-1} h^{-1}$. Fish 1 had a net gain of 0·030 mmol $kg^{-1} h^{-1}$, fish 2 a net loss of 0·200 mmol $kg^{-1} h^{-1}$. The overall balances are shown in Table 1.

Preliminary experiments (unpublished) with the flounder (*Platichthys flesus*) between January and March 1984, showed that the average rate of sodium uptake between 2 and 4 h after transfer from sea water to fresh water was only $0{\cdot}079 \pm 0{\cdot}026$ % blood Na h^{-1} ($N=6$) and that the uptake rate increased slowly over the following 7 days.

In contrast, in the salmon all the influxes were comparable to those in the fish fully adapted to fresh water (Table 1). In the shortest experiment, fish 9, where the 'adaptation' period was reduced to only a 2-min washing period and the influx period to 5 min, the rate of uptake was still 0·67 % h^{-1}. Fish 9 showed a net rate of sodium loss of about 5 mmol h^{-1} but has not been included in Table 1 as this large loss may have been due in part to surface contamination as the washing time was so brief.

Fish 10 and 11 caught in sea water and maintained in sea water of 28 % salinity had high blood concentrations of sodium (Table 2). After 5 days or more in fresh

Table 1. *Sodium influxes and effluxes in fresh water (mmol $kg^{-1} h^{-1}$) in adult* Salmo salar

Fish	1	2	5	4	3	6	8	9
Beginning of expt	5+ days	5+ days	24 h	5 h	1 h	0·5 h	0·08 h	0·03 h
End of expt	5+ days	5+ days	25 h	6 h	2 h	1·5 h	0·25 h	0·11 h
Influx	0·421	0·261	0·296	0·179	0·291	0·408	0·188	0·300
Efflux	0·391	0·461	0·666	0·412	0·418	0·718	0·606	—
Net gain	0·030	−0·200	−0·370	−0·370	−0·233	−0·310	−0·418	—

Table 2. *Sodium content of the blood plasma of adult* Salmo salar *in sea water and following transfer to fresh water (mmol l^{-1})*

	Sea water		Time in fresh water							
			0·1 h	0·4 h	0·6 h	1·5 h	2 h	8 h	24 h	5+ days
	245	240	225	231	161	171	146	154	154	156 ($N=4$)
Fish no.	10	11	9	17	8	6	3	4	5	1,2,16,22

Table 3. *Rate of sodium uptake in parr of* Salmo salar *at various pH values (% h^{-1} blood Na and mmol kg^{-1} h^{-1})**

pH 7·0	pH 6·0	pH 5·5	pH 4·9
1·00	0·98	0·044	0·083
1·39	0·91	0·058	0·084
0·95	1·11	0·216	0·217
1·29	1·78	0·086	0·126
1·15 % h^{-1}	1·195 % h^{-1}	0·101 % h^{-1}	0·127 % h^{-1}
≡0·479 mmol kg^{-1} h^{-1}	≡0·497 mmol kg^{-1} h^{-1}	≡0·042 mmol kg^{-1} h^{-1}	≡0·052 mmol kg^{-1} h^{-1}

*Calculated on the assumptions that the parr contained 48·8 mmol kg^{-1} and that the total body sodium after 1 h had 93 % of the specific activity of blood sodium.

water the concentration of sodium in the blood of six fishes (1, 2, 5, 16, 22 and 28) averaged 155 ± 6 mmol l^{-1}.

The mean rate of sodium uptake of the eight salmon in fresh water of pH 7·0–7·3 was $0{\cdot}65 \pm 0{\cdot}07$ % body Na h^{-1}. Two adult fish (16, 28), in acidic water of pH 4·83 and 5·49, had uptake rates of 0·047 and 0·039 % h^{-1}, respectively. These rates are similar to those of the salmon parr, average weight 154 g, in acid water (Table 3).

The rates of sodium efflux from fish which had been in neutral water for 1 h or more ranged from 0·391 to 0·666 mmol kg^{-1} h^{-1} mean 0·47 mmol kg^{-1} h^{-1} (Table 1). This was higher than the mean rate of uptake, 0·29 mmol kg^{-1} h^{-1}, but the fish might not be expected to achieve balance so soon and the unavoidable handling would enhance sodium loss.

Two fish in acid water lost sodium much more rapidly. Fish 16, at pH 4·8, lost sodium during the first 30 min, at the rate of 10·88 mmol kg^{-1} h^{-1}. Fish 28, at pH 5·5, lost sodium at the rate of 3·35 mmol kg^{-1} h^{-1}.

Sodium uptake was found to be fully activated in the first 5 min following transfer to fresh water. Either the sodium uptake system is already activated before the fish enter the estuary or the uptake system is activated with extreme rapidity on entry into fresh water. Physiological adjustments to changed osmotic conditions generally take several hours or even days (Potts *et al.* 1970; Conte & Lin, 1967). If the sodium uptake pump in seawater-adapted salmon can adjust in 2 or 3 min it is markedly different from those previously examined and probably would need to be under nervous control, there is no evidence for such a mechanism.

The alternative hypothesis, that the pump is already triggered before the fish enters fresh water, raises some problems but also gives rise to a testable hypothesis. To pump sodium inwards in sea water would appear at first sight to be an act of supererogation as the salt taken up would then have to be excreted at some metabolic cost. In view of the limited number of fish available it was not possible to investigate the relationship between external concentration and

sodium uptake in detail but one fish, 17, adapted to fresh water for at least 5 days, took up sodium at the rate of only 1·72 % h^{-1} body Na, when transferred to a bath containing 5·6 mmol l^{-1} Na, which suggests that the pump has a limited capacity. If the pump saturates at an input of less than 2 % of total body salt per hour the metabolic cost would not be excessive. The rate of turnover of sodium in a large teleost such as the salmon would be of the order of 10 % h^{-1} in sea water. If an additional 2 % h^{-1} were due to active uptake it would not represent an excessive burden on the salt excretory system and the advantage conferred in enabling the salmon to enter fresh water immediately might outweigh the metabolic cost. It would seem to be unnecessarily expensive to take up sodium throughout its life in sea water and it would be more economical to start the uptake only as the salmon neared the coast. If this were the case then the returning salmon would be analogous to a smolt which is programmed for life in sea water while still in fresh water. If this hypothesis were correct then autumn-running salmon, caught at sea in the spring, should not show instantaneous salt uptake when transferred to fresh water.

The fish will not be in sodium balance immediately on entering fresh water, as sodium loss will continue at a high rate until the permeable junctions between the mitochondria-rich cells in the gills have been blocked (Sardet, Pisam & Maetz, 1979). In the smolt, net sodium loss averaged over 4 % h^{-1} of total body sodium during the first 4 h after transfer from sea water to fresh water and averaged 2 or 3 % h^{-1} during the next 8 h (Potts *et al.* 1970). Similarly sodium efflux from the adult salmon remains high for several hours even in neutral waters (Table 1) and the blood concentration drops by 37 % during the first few hours (Table 2).

The sodium uptake pump is very sensitive to external hydrogen ions, and sodium loss is increased in acid waters (McWilliams & Potts, 1978). In the two fishes examined, the initial rates of sodium loss following instantaneous transfer were 7·5 % h^{-1} at pH 4·8. The increased rate of sodium loss would become intolerable in a few hours but more work is required to see whether these high levels would be maintained.

The effect of aluminium ions is a further factor to be considered. During acidic episodes the concentrations of aluminium ions of various species increases dramatically and some of these species act synergistically with hydrogen ions in inhibiting sodium uptake. As the Almond river water is close to neutrality the aluminium content is negligible but in some rivers the fresh-run salmon must be faced with even more disadvantageous conditions.

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