J. Exp. Biol. (1970), **52**, 553–564
With 3 text-figures
Printed in Great Britain

SALT AND WATER BALANCE IN SALMON SMOLTS

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(*Received* 18 *November* 1969)

INTRODUCTION

Although the salmon is probably the best known euryhaline fish, for the first 2 or 3 years of its life it is stenohaline. The salmon becomes euryhaline only in the smolt stage, the process of 'smoltification' taking place in April or May in fish 2 or 3 years old, although a proportion of late parr can tolerate sea water. In recent years a more detailed picture has emerged of salt and water balance in both marine and fresh-water teleosts as the result of a number of studies with isotopic tracers. It is now known that the greater part of the salt influx in sea-water teleosts takes place through the body surface (Motais & Maetz, 1964; Potts & Evans, 1967; Evans, 1967) and not through the gut alone as had previously been assumed. This salt, together with salt drunk in sea water, is continuously excreted. These processes result in a large turnover of salt in marine teleosts, usually of the order of 10–20% of the total sodium and chloride per hour. In contrast, in fresh water the permeability to salt is low, and although some drinking may occur the salt turnover is low, usually $\frac{1}{2}$–1% of the total body salt per hour. Studies of the process of adaptation of marine fish to fresh water and back again show that adaptation to different media is associated with both rapid and slow changes in permeability and indicate that although in some species exchange diffusion may be an important component of the salt fluxes in other species it is of minor importance (Motais, Romeu & Maetz, 1966). In the light of these developments the exchanges of sodium and chloride ions and water have been investigated in salmon smolts in both fresh water and sea water. For comparison similar measurements have been made on salmon parr where possible.

MATERIALS AND METHODS

The smolting salmon used in this investigation were obtained from the rivers Lune, Greta and Crayke (Lancashire). The work was undertaken in May 1967, 1968 and 1969. The fish were 2 years old and weighed between 20 and 45 g. Both stock fish and experimental fish were kept in a cold room at 10° C.

Fresh water (Lancashire tap water) contained 0·2 mM/l. Na^+ and sea water contained 420 mM/l. Na^+. The latter was obtained from Morecambe Bay, and as the concentration was found to vary it was made up to this fixed concentration by the addition of suitable amounts of a sea-salt mixture.

Total body sodium, chloride and water

Sodium was estimated by digesting the fish in concentrated nitric acid, diluting with distilled water and measuring the sodium concentration of this solution using an EEL flame photometer. Chloride was estimated in a water extract of the fish obtained by cooking the animals in a pressure cooker for 6 min. at 15 lb./sq. in. and homogenizing with water in a Waring blender. The homogenate was made up to a constant volume and left for the chloride to diffuse out of the broken tissue. The chloride in this extract was measured using an Aminco chloride titrator.

Isotope measurement techniques

It was possible by utilizing the different physical properties of the three isotopes ^{22}Na, ^{36}Cl, and ^{3}H simultaneously to monitor their efflux rates. ^{22}Na emits gamma rays (0·51 and 1·28 MeV.) and these were monitored without interference from the emissions of the other two isotopes by using a gamma counting apparatus. This was a Nuclear Enterprise NE 8111 arm counter, the detector consisting of a plastic scintillator encased in an aluminium can. This could be used to count either a living fish or large volumes of liquid.

^{36}Cl gives rise to beta particles of energy 0·71 MeV, whilst ^{22}Na gives rise to positrons of energy 0·54 MeV. These particles were counted with a liquid Geiger counter (M12 from 20th Century Electronics). The efficiency for counting the radiation emitted by ^{22}Na was considerably lower than for ^{36}Cl and in order to obtain values for the amount of ^{36}Cl present in a sample a correction for the proportion of the count contributed by ^{22}Na was made by suitable intercalibration between NE 8111 and the M12 liquid beta counter.

Tritium emits low-energy beta particles (0·018 MeV.) and these could not be detected by either the M12 or the NE8111. In order to assay the amount of $^{3}H_2O$ present in any sample a freeze-drying technique was used to obtain aliquots of pure water from the samples taken from the efflux baths (Rudy, 1967). $^{3}H_2O$ was counted by liquid scintillation counting (in a Nuclear Enterprises liquid scintillation counter).

Measurement of efflux rates of Na, Cl and H_2O

Efflux rates were obtained by injecting known amounts of the three isotopes into fish anaesthetized with MS222 (0·01%). The fish were then placed in either 1·5 or 3 l. of medium from which samples were taken at suitable intervals of time to monitor the loss of activity from the animal. The efflux rate during the first half hour following injection was discounted as this could be due to leakage from the wound, and the loss would be taking place when the isotope was unequally distributed throughout the body.

The activity in the samples was compared with standards prepared from aliquots of the injected dose made up in the same volume of medium as the efflux bath. The activity of the standard then corresponded to that of the experimental bath when all the activity in the fish had been lost to the bath. The activity remaining in the fish was obtained by subtracting the activity in the experimental bath from that in the standard. Normally 1 mC. $^{3}H_2O$ 4 μC. each of ^{22}Na and ^{36}Cl were injected into each fish.

Transfer experiments

The fish were injected with the isotopes and left in the efflux bath until a value for the rate of loss in a particular medium had been obtained. The fish were then transferred to the appropriate second medium and the rate of loss of the isotopes was followed by sampling of this medium. Corrections were made for activity lost into previous efflux baths during the course of the same experiment.

The efflux rate was calculated from the formula

$$K = \frac{1}{t} \log_e \frac{N_0}{N_t},$$

when K is the rate constant of the efflux, N_0 the initial activity in the fish and N_t the activity remaining in the fish after time t.

Drinking rates

Drinking rates were measured by a method similar to that of Evans (1968). The fish were immersed for 2 hr. in a medium containing ^{125}I-polyvinyl pyrrolidone (PVP). At the end of this period they were transferred to inactive medium for 30 min. to allow the active water to pass well down into the gut so that none was lost during dissection. MS222 (Sandoz) was added to the inactive medium to a concentration of 0·01 % and the animals were left until dead. They were then opened up and the entire gut was removed. The ^{125}I activity in the gut was counted using an EKCO 610B scaler and sodium iodide (thallium) well crystal. The activity in the medium was also measured in the same way and from the activity of the medium the volume ingested by the fish was estimated.

Measurement of effluxes during rapid changes in salinity

Salmon smolts or parr were injected intraperitoneally with 10 μC. of ^{24}NaCl. In isotonic solution the volumes injected did not exceed 0·1 ml. The fish were then placed in a short cylinder containing 200–300 ml. of water connected by a rubber tubing to a 10 ml. vessel in the well of a Nuclear Enterprises scintillation counter. The cylinder containing the fish and the counting vessel formed a closed circuit driven by a flow-inducer pump. Water in the system could be circulated at a rate of more than 2 l./min. and water was changed by breaking the circuit at one point and inserting one end of the tubing into the new medium. The medium could be almost totally replaced (> 99%) in 1 min. A small volume of air, 40 ml., was left in the first chamber to oxygenate the water. The counting chamber was shielded by lead bricks from the activity in the fish. Activity appearing in the solution was monitored by a Nuclear Enterprises rate meter and plotted directly by a Beckman potentiometric pen recorder. The slope of the graph was proportional to the rate of efflux of sodium.

RESULTS

The water, sodium and chloride content of smolts adapted to fresh water and sea water are shown in Table 1, and the rate constants of exchange in Table 2.

Fresh-water smolts. The rate of efflux of sodium and chloride from salmon smolts is similar to that from other fresh-water fish (Table 3). The data for six fish in fresh

water is published in full (Table 4) to illustrate the general correlation between sodium and chloride effluxes. The average drinking rate in seven smolts adapted to fresh water was only 0·0013 ml./g./hr.

Sea-water-adapted smolts. Salt fluxes in sea-water-adapted smolts are much higher than in fresh-water-adapted fish (Table 2). In the seven animals shown in detail in

Table 1. *Content of sodium, chloride and water of smolting salmon adapted to fresh water and to sea water*

Results given as $X \pm$ S.E.(N)

	Fresh water
Na	30·3 ± 1·20 (15) m-equiv./kg. (wet wt.)
Cl	29·2 ± 2·42 (7) m-equiv./kg. (wet wt.)
H_2O	81·1 ± 0·37 (8) % of wet weight
	Sea water
Na	44·8 ± 1·93 (12) m-equiv./kg. (wet wt.)
Cl	46·0 ± 3·45 (5) m-equiv./kg. (wet wt.)
H_2O	80·2 ± 0·33 (6) % of wet weight

Table 2. *Fluxes of sodium, chloride and water in the smolting salmon*

All values measured as K_{efflux} $X \pm$ S.E. (N)

	Fresh-water-adapted
Na	0·0221 ± 0·0031 (16)
Cl	0·0260 ± 0·0034 (16)
H_2O	0·475 ± 0·028 (6)
	Sea-water-adapted
Na	0·120 ± 0·007 (19)
Cl	0·168 ± 0·014 (11)
H_2O	0·325 ± 0·058 (13)

Table 3. *Fluxes of total sodium, chloride and water in fresh-water-adapted and sea-water-adapted animals*

	Fresh-water-adapted
Na	16·0 m-equiv./kg. fish/day
Cl	18·2 m-equiv./kg. fish/day
Water	9245 g./kg. fish/day
	Sea-water-adapted
Na	129·0 m-equiv./kg. fish/day
Cl	194·6 m-equiv./kg. fish/day
Water	6256 g./kg. fish/day

Drinking rate in sea water 0·29 %/hr. (av. of 4)
= 69·6 g./kg. fish/day
= 29·2 m-equiv. Na/kg. fish/day

Table 4 the mean rate constant of the sodium efflux is only 0·12 hr.$^{-1}$, rather lower than that found in most sea-water-adapted fish (Motais & Maetz, 1965; Potts & Evans, 1967). However, the mean rate constant of sodium efflux in smolts from the River Lune in May 1967 was 0·23 hr.$^{-1}$ and in May 1969, 0·25 hr.$^{-1}$. All three groups had been adapted to sea water for 1 week, and the difference between the years

suggests that the 1968 fish were in a less advanced stage of smoltification at the time of the experiment. In marked contrast the rate of efflux for salmon parr in sea water averaged 0·035 hr.$^{-1}$ in those fish which managed to survive as long as 2 days, and they contained 56·7 mM-Na/kg. (N = 4. range 53·9–58·8).

The rate of drinking in a small number of 1968 smolts averaged 0·29% body weight/hr.: range 0·18–0·40%/hr. (N = 4). In a larger batch of sea trout smolts which were very similar in terms of water fluxes and salt fluxes the rate of drinking averaged 0·43%/hr. (N = 9).

Table 4. *Fluxes of sodium, chloride and water in individual animals adapted to fresh water*

K_{efflux} hr.$^{-1}$		
Na	Cl	H_2O
0·018	0·026	0·55
0·024	0·031	0·42
0·013	0·018	0·39
0·022	0·030	0·45
0·016	0·019	0·50
0·026	0·029	0·54

Fluxes of sodium, chloride and water in individual animals adapted to sea water

K_{efflux} hr.$^{-1}$		
Na	Cl	H_2O
0·11	0·15	0·33
0·16	0·26	0·35
0·12	0·15	0·21
0·11	0·19	0·26
0·12	0·17	0·40
0·09	0·12	0·30
0·10	0·15	0·41

Table 5. *Sodium and chloride balance in the smolt mM/kg./hr.*

	Total flux	Influx by drinking	Influx through body wall	Urine loss	Extra renal loss
			In sea water		
Na	5·4	1·6	3·8	< 0·01	5·4
Cl	7·7	1·9	5·8	< 0·01	7·7
			In fresh water		
Na	0·68	—	0·68	0·02	0·66
Cl	0·76	—	0·76	0·02	0·74

Salt balance in smolts

The rate of exosmosis can be calculated from the diffusional water flux (Table 3) and the mole fraction difference in concentration between the blood and sea water on the assumption that the diffusional and osmotic permeabilities are similar. Sea water containing 420 mM-Na/l. has a freezing-point depression of 1·65° C., equivalent to 0·88 M/l. The blood plasma of salmon smolts has a freezing-point depression of 0·66° C., 0·35 M/l. (Parry, 1960). Hence the osmotic flux should be equivalent to the

fraction (0·88–0·35)/55·4 of the total water flux, that is 0·31% of the body water/hr. or 0·25% of the body weight/hr. The drinking rate must exceed the osmotic efflux somewhat to allow for renal and rectal losses. The observed drinking rate is of the right order of magnitude, but perhaps 0·4% is nearer the true average. Shehedeh & Gordon (1969) found that *Salmo gairdneri* drank 0·54% of the body weight/hr. at 17° C., of which 79% was absorbed. An approximate balance sheet can be drawn up in order to illustrate salt balance in the smolt on the assumption that the animals are in equilibrium, i.e. efflux = influx (Table 5). Salt losses in the urine, when in sea water, can be neglected as the rate of urine production of the rainbow trout adapted to sea water is only 0·5–1·0 ml./kg./day (Holmes, 1961). The rate of urine production in smolting rainbow trout in fresh water was 2·07 ml./kg./hr. and the urine contained 12·1 mM/l. Na and 12·1 mM/l. Cl (Holmes & Stanier, 1966) corresponding to a renal loss of 0·02 mM-NaCl/kg./hr. The renal loss in smolting salmon is likely to be of the same order.

Time course of adaptation

On transfer from sea water to fresh water or fresh water to sea water the salt fluxes change dramatically. In sea water the greater part of the sodium influx takes place through the body wall. On transfer to fresh water the rate of influx will drop instantaneously to a much lower level as the external source is removed, but detailed analysis shows that the permeability of the body wall also changes.

When transferred from fresh water to sea water the rate of sodium efflux remains almost constant at around 0·03 $hr.^{-1}$ for about 6 hr. and then rises slowly, reaching 0·1 after a further 20 hr. (Fig. 1). The chloride flux rises more rapidly, doubling in the first hour and reaching 0·1 in under 7 hr. (Fig. 1). Complete adaptation takes several days. On transfer back to fresh water the fluxes of both sodium and chloride fall very rapidly in the first hour. Chloride flux falls from 0·16 to 0·07 $hr.^{-1}$ and sodium flux from 0·13 to 0·05 $hr.^{-1}$ and both soon reached the fresh-water level of 0·02 $hr.^{-1}$.

The more detailed analysis of the adaptation during the first half hour or so was made by the continuous-flow method described earlier. These experiments were carried out on a different batch of smolts from those described above. The results are expressed in terms of the percentage of the sodium flux in sea water. On transfer to fresh water there was a reduction of the rate of efflux of sodium to 50% of the sea-water rate in the period 2–15 min. after transfer to fresh water. A further decline to about 35% of the sea-water flux follows some time later. This decline is apparent in some fish during the first hour (Fig. 2). Unfortunately, it was not possible to follow the effects of rapid changes of medium on the fluxes of chloride because of the low efficiency of chloride-counting techniques available, but by the end of the first hour in fresh water the chloride flux has declined in proportion to the sodium flux (Fig. 1).

The effect of various dilutions of sea water on the sodium fluxes

Although transfer to fresh water results in a rapid decline in the rate of sodium efflux, placing the smolts in intermediate concentrations of sea water has little immediate effect on the sodium flux. The effects of even a short immersion in a dilute medium on the fluxes is prolonged and this complicates both the experiments and their interpretation. Occasionally, the reductions in efflux following a short period in

fresh water were seen to disappear during the next period in sea water. More often the efflux remained low for long periods in sea water, after a 10 or 15 min. period in dilute sea water or fresh water. Most of the data in Fig. 3 were based on experiments

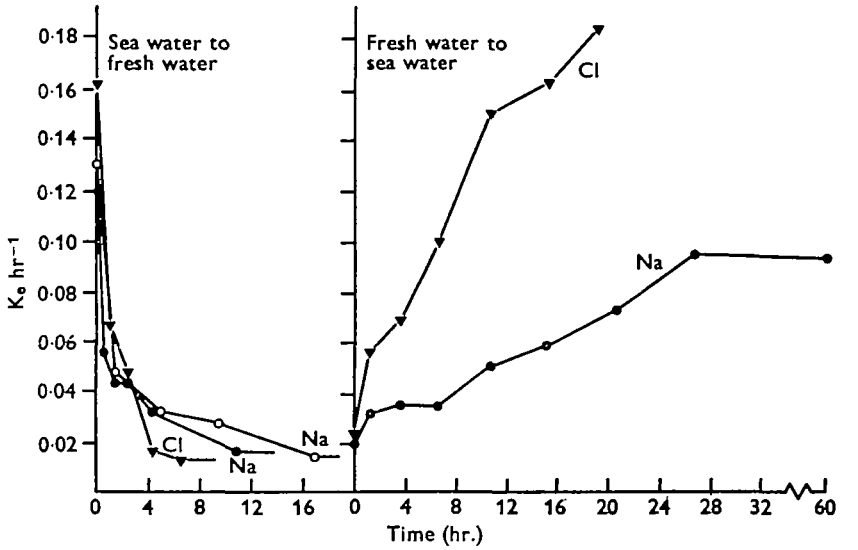

Fig. 1. Rate of loss of sodium ions from salmon smolts after transfer from sea water to fresh water, and from fresh water to sea water. (Early May, 10° C.)

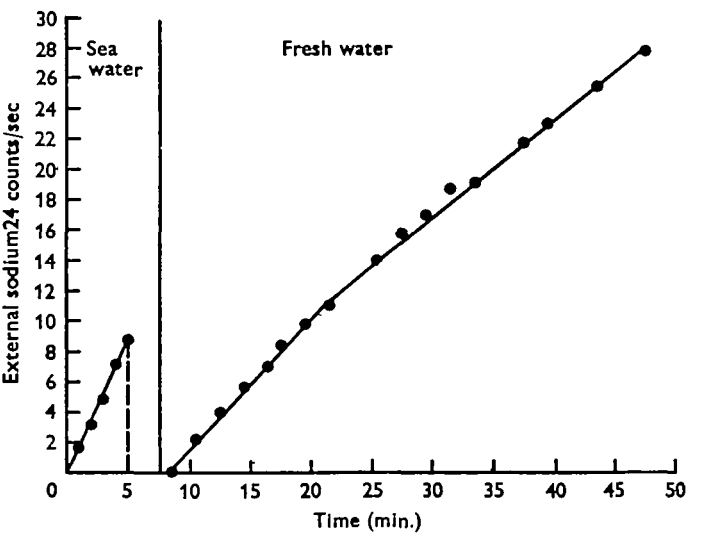

Fig. 2. Rate of loss of sodium ions from salmon smolts after transfer from sea water to fresh water. (Late May, 10° C.)

in which the effluxes were measured in progressively more dilute media, 100, 25, 5, 2 or 100, 50, 10%, F.W. It is possible that the last results were depressed by the earlier periods in more concentrated but not full-strength sea water.

DISCUSSION

The sodium and chloride content of salmon smolts in fresh water is about 30 mM/kg. This is similar to the value reported by Houston & Threadgold (1963) for the chloride content of muscle in fresh-water-adapted smolts. In sea water the salt content increases about 30%. Part of this increase must be attributed to an increase in blood concentration. Parry (1960) reported that the blood concentration of *Salmo salar*

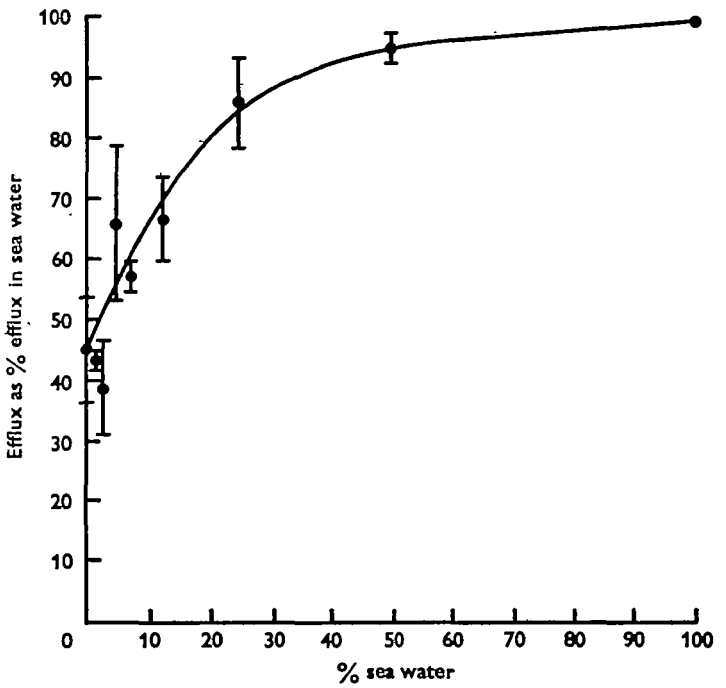

Fig. 3. Relative loss of sodium ions from salmon smolts after transfer to various dilutions of sea water expressed as percentage of loss in sea water. (Late May, 10° C.)

increased by about 10% on adaptation to sea water, but this is insufficient to account for the total increase even if it is assumed that the tissue salt rises in proportion. Part of the increase may be attributed to sea water in the gut. If the fish contain sea water equivalent to 1% of their body weight this would increase the total salt by 4 mM of sodium and 5 mM of chloride, an increase of 13 and 17% respectively. Although the fish were washed briefly with fresh water before analysis some additional salt was probably present on the body surface, gills, etc.

The mean rate constant for sea-water-adapted smolts was considerably higher in 1967 and 1969 than in 1968. In 1967 and 1969 the rate constant for sodium was similar to that reported for a variety of other marine fish. The 1967 and 1969 fish were collected in late May and early June while the 1968 fish were collected in early May, and it is probable that smoltification was not fully developed in the latter fish; these included some specimens with faint parr markings, which had the lowest rates of efflux even though they survived in sea water. The 1968 smolts survived direct transfer to sea water very well, of the twenty-two animals transferred nineteen

remained alive, but the 1967 smolts did not survive transfer well, about 40% dying in the first 2 days. The survival results are at first sight contradictory to the suggestion that the early smolts are less fully adapted to sea water, but the poor survival of the late smolts may be attributed to the sensitivity of smolts to any form of treatment. The ability of a few early smolts or late parr to survive in sea water while maintaining low fluxes raises some interesting fundamental questions. A similar ability to live in sea water while maintaining low salt fluxes has been observed in large parr at other times of the year. Altogether the following stages may be tentatively distinguished:

(1) Early parr unable to survive in sea water (Parry, 1960).

(2) Late parr, a few able to survive in sea water for several days but maintaining low salt fluxes with rate constants of the order 0·03 hr.$^{-1}$.

(3) Early smolts surviving well in sea water, with moderate salt fluxes, K *c.* 0·11 hr.$^{-1}$.

(4) Late smolts, very sensitive to handling but with high salt fluxes, K *c.* 0·24 hr.$^{-1}$.

Salt and water balance in parr and in early and late smolts

From the fluxes, body composition and drinking rates it is possible to construct a table of the salt balance in the 1968 smolts (Table 5). Drinking accounts for only one-fifth of the sodium influx and one-sixth of the chloride influx in sea water. In late smolts it would account for only one-tenth of the total salt input. The rest of the influx must take place through the body wall, most probably through the gills. In contrast, salt balance in those parr which can survive in sea water shows some very peculiar features. Regulation is poor and the total body sodium is much higher (57 mM/kg.) than in the smolts (45 mM/kg.). Parry (1960) found that in some parr the blood concentration doubled on transfer to sea water. The total rate of sodium efflux was 2·0 mM/kg./hr., and as the animals survived for at least 3 days they must have been close to equilibrium. As the blood concentration was closer to sea water their drinking rate was probably lower than in the smolts, but it is clear that the passive influx must also be lower than in the smolts and cannot be much more than 1·0 mM/kg./hr. In contrast, the passive loss in fresh water, in both parr and smolts, was about 0·6 mM/kg./hr. although the sodium gradient was only one-third as large. Sea-water-adapted parr evidently maintain the low permeability characteristic of fresh-water fish. In this respect they resemble other euryhaline fish including smolts in the hours immediately following transfer to sea water.

In transfer experiments with smolts from sea water to fresh water and back again the salt fluxes change dramatically. On transfer to fresh water the salt influx declines immediately to a very low level. The analysis of the changes in efflux following transfer is difficult. The rapid decline in efflux that follows transfer to fresh water has some of the attributes of exchange diffusion (Motais *et al.* 1966). On the other hand a complete restoration of the efflux on return to sea water, after a short period in fresh water, was rarely observed, and the decline might be attributed instead to the cessation of the active output of sodium by the gills. The exchange-diffusion hypothesis may be examined first. In this case efflux in sea water may be attributed in part to exchange diffusion, in part to the active output of sodium, in part to passive outward diffusion and in small part to losses in the urine. If it is assumed that 50% of the efflux is exchange diffusion, the average reduction of loss in the first 15 min. following transfer, then influxes can be analysed into exchange diffusion 2·7 mM-Na/kg./hr.,

drinking 1·6 mM/kg./hr., passive influx 1·1 mM/kg./hr. The passive influx, I_p and the passive efflux, O_p across the gill will be related to the sodium concentrations in the sea water $(Na)_{SW}$ and blood $(Na)_B$ and the potential across the gill (E) by the relation

$$\frac{O_p}{I_p} = \frac{(Na)_B}{(Na)_{SW}} \exp\left(\frac{EF}{RT}\right),$$

where F is the Faraday, R the gas constant and T temperature in degrees absolute. The sodium content of the sea water was 420 mM-Na/l. The freezing-point depression of the blood of smolts in sea water is 0·66° C. (Parry, 1960), equivalent to a sodium content of about 170 mM-Na/l. Few measurements of potentials across fish gills are available but these few agree that the blood is electropositive to sea water by about 20 mV. (*Blennius pholis* + 23 mV., House, 1963; *Anguilla* + 18 mV., Maetz and Campanini, 1966; *Pholis gunnellus* + 18 mV., Evans, 1969). A positive potential inside will increase the ratio of the passive efflux to the passive influx of sodium ions. If the passive sodium influx were 1·1 mM/kg./hr. and the potential across the gills were 20 mV., blood positive, then the passive sodium efflux (O_p) can be calculated from the relationship

$$\frac{O_p}{1{\cdot}1} = \frac{170}{420} \exp\left(\frac{EF}{RT}\right).$$

Whence O_p = 1·0 mM/kg./hr. The sodium efflux can then be broken down into 2·7 mM-Na/kg./hr. exchange diffusion, 1·0 mM/kg./hr. passive diffusion, 1·7 mM-Na/kg./hr. active output. Urine loss may be neglected. If the sodium efflux is partly passive the chloride efflux must be nearly all active as the positive potential will reduce the passive efflux of chloride. In the absence of any estimate of the exchange-diffusion component detailed analysis of the chloride fluxes is impossible. The further decline in sodium efflux which follows between 30 min. and 1 hr. after transfer to fresh water (Figs. 1, 2) must be due either to the reduction of the active efflux or to a decline in the permeability of the body wall. It is clear from the very low efflux in fresh-water-adapted animals that the passive loss is reduced far below the passive loss in sea water (*c.* 1·0 mM/kg./hr.) even when allowance is made for possible changes in potential However, if the later decline is due to a reduction in permeability it follows that the sodium pump must continue unchecked for an hour or more after transfer. If the later decline is due to the reduction of active sodium outflux then the pump must still continue for between 30 min. and an hour after transfer, during the linear period of sodium outflux (Fig. 2). It seems *a priori* unlikely that the fish will continue to push out sodium in fresh water at the same rate as in sea water for so long. This is a weakness of the exchange-diffusion hypothesis.

As an alternative the hypothesis that the rapid decline on transfer is due to the turning off of the active sodium pump may now be considered. In this case influx may be analysed into drinking 1·6 mM/kg./hr., passive influx 3·8 mM/kg./hr. Hence, as before,

$$\frac{O_p}{3{\cdot}8} = \frac{170}{420} \exp\left(\frac{EF}{RT}\right), \quad \text{whence} \quad O_p = 3{\cdot}4 \text{ mM/kg./hr.}$$

Only 2·0 mM-Na/kg./hr. is actively extruded. If the potential were as high as 30 mV. no sodium pump would be required. Again, if the sodium efflux is largely passive the

chloride efflux must be nearly all active, for the positive potential of the fish will reduce the passive efflux of chloride to a low level. If the two pumps are turned off in the first few minutes in fresh water the sodium efflux will drop to the level of passive loss in the absence of any marked potential. Efforts to measure the potentials of smolts under these conditions were not successful, but the turning off of the powerful chloride pump is likely to make the fish more negative, the condition found in fish adapted to fresh water. A decline in potential of 20 mV. will reduce the passive sodium efflux by about 30%, giving a total passive efflux of about 2·5 mM/kg./hr. The somewhat variable results of the transfer experiments may be due to some variation in the potentials following transfer. The further decline that takes place later may then be attributed to a reduction in the permeability of the body surface. The reduction of the efflux by one-half following transfer may be accounted for by a combination of the cessation of active output and the potential change.

It is possible that the full explanation lies somewhere between these alternative hypotheses. Unpublished experiments in the laboratory with *Tilapia mossambica* suggest that there is a linkage between influx and the active output of sodium in sea-water-adapted fish. It is possible that the pump is 'leaky' in a manner similar to that of the input pump in *Astacus* which therefore also produces a spurious exchange-diffusion effect when it is stopped (Bryan, 1960*a*, *b*). In the case of salmon smolts a part of the 'passive' influx may only occur when the output pump is in operation.

After a period of 2 hr. in fresh water the fluxes have dropped to such a low level that a real decline in permeability must be postulated since the rates of efflux are then below the level of the passive effluxes alone when in sea water. After any prolonged period in fresh water the fluxes remain low for many hours after transfer back to sea water. It is impossible to suggest any convincing reason why marine teleosts should be more permeable to salts than fresh-water teleosts, but if the leaky pump hypothesis is correct then the influx should remain low until the sodium pump comes into operation, when both influx and efflux should increase. The changes which take place in the blood concentration on the transfer of parr and smolts from fresh water to sea water suggest that the initial rate of influx in sea water is of the order 5%/hr. and that the sodium pump begins to be active within an hour or two in smolts but not in parr (Parry, 1960). If part of the increase in blood concentration is due to the loss of water rather than the gain of salt then the initial rate of influx must be rather less than 5%/hr.

The most fundamental difference between the smolt and the parr is the ability of the smolt to osmoregulate in sea water. Little is known of the mechanisms underlying smoltification, but hormones such as cortisol and arginine vasotocin (Review Potts 1968), which are known to affect salt balance in teleost fishes, may be involved. The occurrence of regulating and non-regulating forms in different stages of the life history of the same species provides a convenient tool for the analysis of effect of hormones and other agents on salt balance in teleosts.

SUMMARY

1. Salmon smolts adapted to sea water maintain a high rate of turnover of both sodium and chloride, but when adapted to fresh water the rate of turnover is low.

2. Only a small part of the influx takes place through the gut.

3. On immediate transfer from sea water to dilute sea water or to fresh water the influxes decline rapidly, but on transfer from fresh water to sea water the restoration of the fluxes takes place slowly.

4. The alternative hypotheses that the rapid changes are due to exchange diffusion or to rapid adjustments of the sodium pump are discussed.

This work was supported by N.E.R.C. grant GR/3/105. We are very grateful to Mr L. Stewart and the Lancashire River Authority for supplying the smolts.

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