THE EFFECTS OF HYPOPHYSECTOMY, PROLACTIN THERAPY AND ENVIRONMENTAL CALCIUM ON ELECTROLYTE BALANCE OF THE BROWN TROUT *SALMO TRUTTA*, L.

BY S. O. ODULEYE*

Department of Biological Sciences, University of Lancaster, Lancaster, England

SUMMARY

Adaptation of the brown trout to fresh water containing increasing concentrations of calcium resulted in a decrease in plasma electrolyte level and total electrolyte excretion. The electrolyte excretion rate was higher at the beginning than at the end of the urine collection periods.

Hypophysectomized fish had a lower plasma electrolyte concentration than the controls. This deficiency was partially corrected by prolactin therapy. High environmental calcium was only effective to a limited extent. There was no difference in the normal renal sodium output between hypophysectomized and intact fish in fresh water. Environmental calcium did not have any significant effect on renal electrolyte output of hypophysectomized fish.

INTRODUCTION

Migratory teleosts such as the sea trout pass a stage of their life cycle in fresh water and another in sea water. The difference between the two media is so drastic as to require the regulatory organs of the fish to be able to vary their function or even reverse it in order to maintain that constancy of the '*milieu interieur*' which is essential for survival. To various degrees, all euryhaline teleosts have organs of regulation and exchange which are capable of modulating their functional activities. It has become apparent that adaptive changes of this nature are under hormonal control, despite the fact that some confusion has arisen from attempts to equate teleost and tetrapod hormones.

The possibility of the pituitary involvement in teleostean osmoregulation was first proposed by Fontaine, Callamand & Olivereau (1949). Since then, a great deal of evidence has accumulated showing the importance of pituitary hormones in hydro-mineral regulation.

The physiological role of prolactin differs in various vertebrate groups, from the fish to the mammal (Bern, 1967). Unlike other pituitary hormones, prolactin has been shown to affect a variety of target organs including the gills, mammary glands, mucous cells, brood patches, crop sac, the kidney and even the nervous system.

* Present address: Department of Zoology, University of Ibadan, Ibadan, Nigeria.

S. O. ODULEYE

Table 1. *Effect of calcium, season and temperature on plasma electrolytes*

All electrolyte values given in m-equiv/l ± S.E.M.
Osmotic pressure given in m-osmoles ± S.E.M.
Normal fresh water (FW) contained approximately 0·3 mM Ca²⁺. n = number of fish.

Medium	Season	Temperature (°C)	Na⁺	K⁺	Cl⁻	Osmotic pressure
FW (0·3 mM Ca²⁺) $n = 6$	Winter	4	187 ± 2·2	3·5 ± 0·19	143 ± 0·72	329 ± 3·7
FW (5 mM Ca²⁺) $n = 5$	Winter	4	163 ± 3·8	3·7 ± 0·31	130 ± 5·8	315 ± 2·1
FW (10 mM Ca²⁺) $n = 6$	Winter	4	152 ± 4·7	3·24 ± 0·22	127 ± 3·9	309 ± 3·2
FW (0·3 mM Ca²⁺) $n = 7$	Summer	15	110 ± 3·2	3·26 ± 0·14	119 ± 3·8	293 ± 4·1
FW (0·3 mM Ca²⁺) $n = 6$	Winter	15	161 ± 1·1	3·75 ± 0·2	142 ± 3·2	317 ± 1·9

This investigation was carried out to assess the relative roles of calcium and the pituitary on water and electrolyte regulation in the brown trout. This paper describes the effect of calcium and prolactin on electrolyte balance and renal function of the fish.

MATERIALS AND METHODS

The source of fish, maintenance of fish stock and the composition of media have been described elsewhere (Oduleye, 1975 a). All experiments were performed at 15 ± 1 °C except where specified otherwise. The techniques of hypophysectomy and prolactin therapy have also been described in detail (Oduleye, 1975 b).

Urine was collected by cannulation, and flow rate determined by connecting the cannula to a LKB UltroRac Fraction Collector. Urine was collected over a minimum period of 48 h (the first 24 h were for recovery from handling stress and anaesthetics).

Blood samples were obtained from the caudal vein with a hypodermic syringe. The syringe and needle were moistened with heparin and dried before blood was withdrawn. Samples were centrifuged immediately and the plasma withdrawn. The procedure for the analysis of plasma and urine electrolytes has been described elsewhere (Oduleye, 1975 c).

RESULTS

Effect of calcium, season and temperature on plasma electrolytes

In an attempt to find the best temperature for maintaining fish stock in the laboratory prior to use in experiments, a group of fish was kept at 4 °C and another at 15 °C. Plasma samples obtained from the two groups were found to differ in electrolyte composition. Plasma samples obtained from the two groups in winter differed from each other and also from those obtained in the summer. Even at the same temperature, trout maintained in fresh water containing 5 and 10 mM calcium chloride had a lower level of sodium and chloride ions and lower osmotic pressure compared with those in normal fresh water. The effect of temperature, season and environmental calcium on plasma electrolytes is given in Table 1.
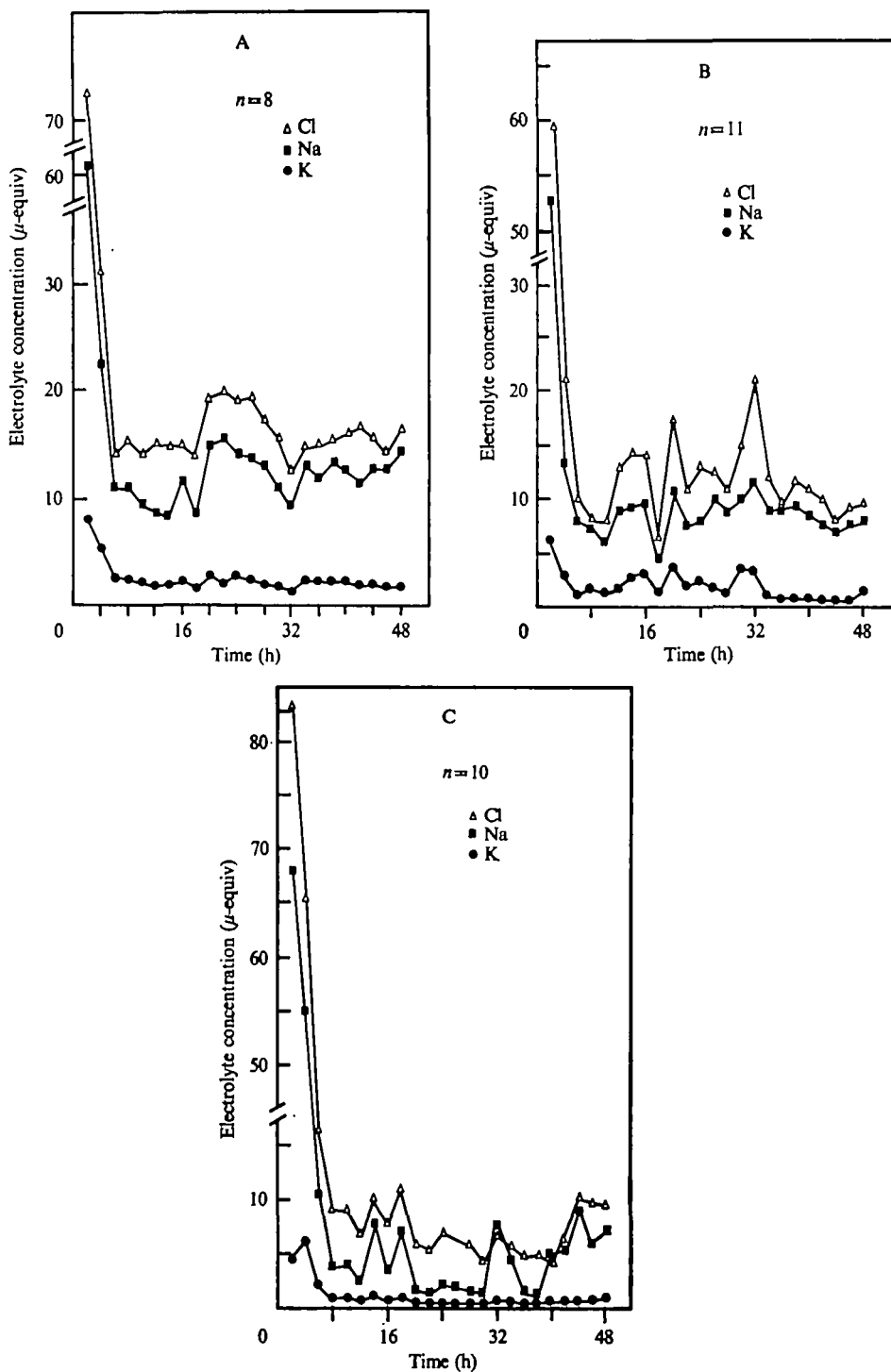
Fig. 1. Effect of calcium on renal electrolyte output in intact brown trout. Consecutive hourly urine samples were pooled for electrolyte analysis. Total renal electrolyte output was obtained from the urine volume and electrolyte concentration and summarized in Table 2. A, fresh water (0.3 mM Ca^{2+}); B, fresh water (5.0 mM Ca^{2+}); C, fresh water (10 mM Ca^{2+}). *n* = number of replicates.

Table 2. *Analysis of renal electrolyte excretion*

Consecutive hourly urine samples were pooled for electrolyte analysis. First and second day urine electrolyte content are presented separately to show diuretic response consequent upon handling and anaesthetization. Renal electrolyte excretion rate is given in μ-equiv/kg/h$\pm$s.e.m. n = number of individual fish; FW = fresh water.

Medium	Na+		K+		Cl-	
	1st day	2nd day	1st day	2nd day	1st day	2nd day
FW (0·3 mM Ca²⁺) n = 8	32·56±8·35	24·43±0·79	6·07±1·03	4·01±0·18	43·69±9·55	31·02±0·99
FW (5 mM Ca²⁺) n = 11	27·68±8·55	20·39±0·85	6·09±0·91	3·55±0·69	37·1±9·41	26·78±2·28
FW (10 mM Ca²⁺) n = 10	46·02±21·72	13·83±2·71	4·83±1·83	1·16±0·16	65·5±25·11	21·5±2·06

Table 3. *Relative tubular electrolyte reabsorption at the beginning and end of urine collection in fresh water*

The average urine electrolyte concentrations in the first and last 8 h of urine collection are given. It was assumed that plasma electrolyte concentration remained unchanged throughout the duration of the experiment. Plasma and urine electrolyte values are given in m-equiv/l.

Electrolyte	Plasma	Urine (beginning)	Urine (end)	Urine/Plasma (beginning)	Urine/Plasma (end)
Na+	110·4	11·4	7·2	0·1	0·07
K+	3·3	1·9	0·95	0·58	0·29
Cl-	118·7	14·2	8·2	0·12	0·07

Table 4. *The effect of hypophysectomy and prolactin therapy on plasma electrolytes*

Electrolytes are given in m-equiv/l$\pm$s.e.m. and osmotic pressure in m-osmoles$\pm$s.e.m. n = number of individuals.

Group	Na+	K+	Cl-	Osmotic pressure
Unoperated control n = 5	153±2·4	3·75±0·03	150±1·9	318±1·9
Operated (prolactin injected) n = 6	141±0·85	3·3±0·01	146±1·6	304±0·7
Operated (saline injected) n = 9	117±1·07	3·3±0·01	107±1·2	290±1·5

Effect of calcium on renal electrolyte output

Renal electrolyte output in three groups of trout maintained in fresh water containing increasing amounts of calcium is shown in Fig. 1 and summarized in Table 2. In the three groups, there was a maximum electrolyte output in the first 8 h after cannulation. Output dropped and settled down after about 16 h. Comparison of total electrolyte output in the first and second days after operation showed that normal electrolyte output was more than double during diuresis (Table 2).

Table 3 shows the urine/plasma ratio for electrolytes at the beginning and end of urine collection periods. This ratio is sometimes used, in the absence of renal clearance studies, to indicate the level of reabsorptive function of the kidney with respect to

Table 5. *Effect of calcium on plasma electrolytes of hypophysectomized brown trout*

Groups of fish were kept in fresh water (FW) containing the indicated calcium concentrations for two days before blood sampling. They had however been previously acclimated for two weeks to 33 % sea water containing the appropriate calcium level before transfer into fresh water. Electrolytes are given in m-equiv/l±s.e.m. and osmotic pressure in m-osmoles±s.e.m. n = number of fish.

Group	Na+	K+	Cl−	Osmotic pressure
Intact control (FW; 0·3 mM Ca²⁺) $n = 5$	153±2·4	3·75±0·03	150±1·9	318±1·8
Sham operated (FW; 0·3 mM Ca²⁺) $n = 6$	155±1·7	3·9±0·02	151±1·1	320±2·1
Operated (FW; 0·3 mM Ca²⁺) $n = 7$	*112±1·4	*3·1±0·02	*104±0·7	*279±1·1
Operated (FW; 5·0 mM Ca²⁺) $n = 9$	*†132±0·9	3·5±0·01	*†126±1·3	*†298±0·8
Operated (FW; 10 mM Ca²⁺) $n = 9$	*†131±1·0	3·7±0·02	*†130±0·9	*†301±1·2

* Significantly different from the corresponding intact and sham-operated control groups ($P < 0.05$).
† Significantly different from the corresponding 0·3 mM Ca⁺⁺ group ($P < 0.05$).

electrolytes (Fromm, 1963; Hunn & Willford, 1970). The ratio was higher at the beginning than at the end of urine collection periods.

Hypophysectomy and prolactin therapy

Table 4 shows the effect of hypophysectomy and prolactin therapy on plasma electrolytes and osmotic pressure. Hypophysectomy resulted in the lowering of plasma sodium and chloride ion levels. Total osmotic pressure was also depressed. Prolactin therapy enabled hypophysectomized trout in fresh water to maintain a higher sodium, chloride and osmotic pressure; even then, however, these were still lower than those of the unoperated control fish. Thus in the brown trout, the hypophysectomy-induced lowering of plasma electrolyte in fresh water was not completely corrected by prolactin therapy at the dose provided.

Table 5 shows the effect of environmental calcium on plasma electrolytes of hypophysectomized fish. Sham-operated and unoperated control groups did not show significant differences in any of the parameters. All the other groups, irrespective of the calcium concentration, showed a significant drop in plasma sodium, chloride and osmotic pressure compared with the control groups. Hypophysectomized fish maintained in 5 and 10 mM calcium had a higher level of sodium and chloride ions and higher osmotic pressure compared with the group in normal fresh water containing 0·3 mM calcium. This indicates that calcium was effectual in partially preventing the drop in plasma electrolytes resulting from hypophysectomy.

A comparison of Tables 4 and 5 shows that even at 10 mM calcium, the action of calcium in mitigating the fall in plasma electrolytes did not compare with that of prolactin.
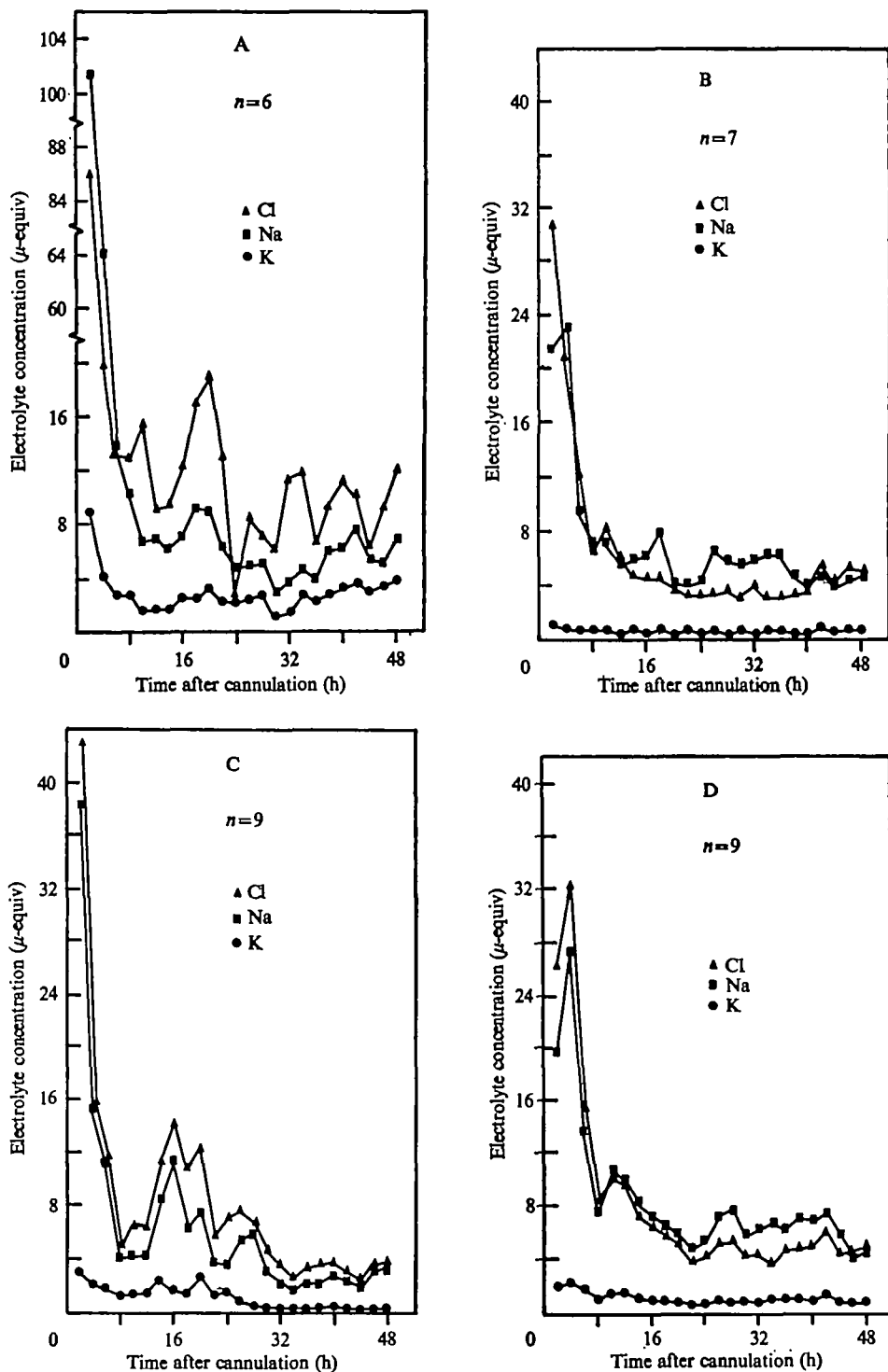
Fig. 2. Effect of calcium on urine electrolyte output in hypophysectomized brown trout. A, Sham operated (FW; 0·3 mM Ca²⁺); B, operated (FW; 0·3 mM Ca²⁺); C, operated (FW; 5·0 mM Ca²⁺); D, operated (FW; 10 mM Ca²⁺). n = number of fish.

Table 6. *Analysis of renal electrolyte excretion in hypophysectomized
brown trout*

Average total electrolyte output (in μ-equiv/kg/h) are given and were obtained from the electrolyte
output/h and weight of fish. n = number of fish.

	Na+		K+		Cl⁻	
Group	1st day	2nd day	1st day	2nd day	1st day	2nd day
Sham operated (FW;	65·98	17·24	10·21	9·46	61·89	29·78
0·3 mM Ca²⁺) n = 6	±27·98	±1·27	±1·84	±0·77	±20·01	±2·11
Operated (FW; 0·3 mM Ca²⁺)	29·87	15·33	1·89	1·83	29·59	13·13
n = 7	±5·89	±0·48	±0·16	±0·06	±7·89	±0·82
Operated (FW; 5·0 mM Ca²⁺)	42·78	13·33	7·98	1·40	54·28	17·66
n = 9	±12·07	±1·69	±0·76	±0·2	±12·75	±2·00
Operated (FW; 10 mM Ca²⁺)	27·14	16·34	3·22	2·54	28·68	12·33
n = 9	±5·0	±0·78	±0·38	±0·12	±6·76	±0·48

Table 7. *Effect of hypophysectomy and calcium on relative tubular
electrolyte reabsorption*

Urine electrolytes were averaged for the first and last 8 h of urine collection periods. Urine and plasma
electrolytes are given in m-equiv/l. U/P = urine/plasma electrolyte ratio which measures the relative
efficiency of tubular electrolyte reabsorption. The higher the ratio the lower the efficiency of reabsorption.

Group	Electrolyte	Plasma	Urine (beginning)	Urine (end)	U/P (beginning)	U/P (end)
Sham operated	Na	155	39·8	5·3	0·26	0·03
(FW; 0·3 mM Ca²⁺)	K	3·9	3·2	3·4	0·82	0·87
	Cl	151	25·4	9·4	0·17	0·06
Operated	Na	112	55·04	14·0	0·49	0·13
(FW; 0·3 mM Ca²⁺)	K	3·1	2·3	1·69	0·74	0·55
	Cl	104	63·8	16·0	0·61	0·15
Operated	Na	132	33·1	7·4	0·25	0·06
(FW; 5 mM Ca²⁺)	K	3·5	3·3	0·41	0·94	0·12
	Cl	126	36·0	8·0	0·29	0·06
Operated	Na	131	32·4	8·5	0·25	0·06
(FW; 10 mM Ca²⁺)	K	3·7	2·95	1·6	0·8	0·43
	Cl	130	40·8	8·9	0·31	0·07

Hypophysectomy and renal function

Fig. 2 shows the effect of hypophysectomy and environmental calcium concentration on urine electrolyte output. In the sham-operated control group, both sodium and chloride outputs were very high in the first 2 h after cannulation. Relative stability of both ions was established after 24 h. The average electrolyte output in the first 24 h after cannulation was higher than that of the next 24 h period. This indicates that diuresis was also accompanied by decreased renal electrolyte reabsorption. The analysis of renal electrolyte filtration during the first and second days of urine collection is shown in Table 6. Hypophysectomized fish in fresh water containing the normal level of calcium (0·3 mM) showed a reduction in the amount of electrolyte output during the first 24 h period compared with sham-operated control fish. Similar reductions were also shown by the experimental groups in 5 and 10 mM calcium. 'Normal' electrolyte output, as indicated by the second day electrolyte output, was

steadier in the four groups. 'Normal' chloride output was lower in all the three experimental groups compared with the sham-operated controls.

Table 6 shows that hypophysectomy did not have any significant effect on renal sodium output although chloride output was decreased, while Table 7 indicates that there was only very slight disturbance to tubular function following hypophysectomy. The efficiency of renal electrolyte reabsorption was slightly reduced following hypophysectomy in fresh water, and this was almost completely rectified at high calcium concentrations.

DISCUSSION

Plasma electrolytes

The brown trout exhibits a seasonal variation in plasma electrolyte level similar to that observed by Gordon (1959) for the American variety. The summer estimates in that case are higher and the winter estimates lower than those obtained in this work for the same electrolytes. Differences in acclimation temperature and also intrinsic differences between the two varieties could account for the disparities.

Since adults of 2–3 years old were used in all these experiments, seasonal variations observed in the plasma electrolytes could not have been due to age. Size-related differences are common in the steelhead trout of the same age, even in the same season (Houston, 1959). In the rainbow trout, *Salmo gairdneri*, winter fish are characterized by higher plasma sodium and chloride levels and lower potassium levels compared with the summer fish (Houston *et al.* 1968).

The reasons for these seasonal variations are yet to be established directly, although they are generally believed to be linked with seasonal changes in endocrine function.

The result of the effect of temperature on plasma electrolyte obtained in this work is not consistent with that of Gordon (1959) who obtained only a slight difference between 10 °C and 20 °C. Similarly, Houston *et al.* (1968) observed a high degree of thermal compensation associated with the operation of the plasma ionic regulatory system in the rainbow trout. It is, however, in agreement with the suggestion by Hickman *et al.* (1964) that the concentration of sodium and chloride ions in the plasma varies inversely with temperature.

The effect of high calcium was to lower the serum electrolyte level in intact fish. This looks curious at first, especially since the same treatment produces a decrease in total body water, low urine volume (Oduleye, 1975*a*) and low renal electrolyte loss (Table 2). These should, other factors remaining constant, result in increased electrolyte concentration. Eels adapted to sea water and then exposed to calcium-free artificial sea water for 15 h show an increase in plasma sodium concentration compared with the controls (Bornancin *et al.* 1972). Calcium has been shown to control the permeability of fish gills to water (Potts & Fleming, 1970; Oduleye, 1975*a*) and monovalent cations (Potts & Fleming, 1971; Cuthbert & Maetz, 1972). Changes in fluxes of monovalent cations, particularly sodium and chloride ions, have been shown to cause changes in gill potentials which is negative in low calcium media and positive in media containing high calcium (Eddy, 1975). It is probable that these changes will also affect the magnitude of intracellular and extracellular spaces and consequently plasma electrolyte concentrations. In the goldfish, *Carassius auratus*, although it remained positive, net sodium flux is higher in low calcium media than in high calcium media

(Cuthbert & Maetz, 1972). This difference, if applicable to the brown trout, should result in higher plasma sodium in low calcium media as has indeed been observed. High environmental calcium inhibits both influx and outflux of sodium (Potts & Fleming, 1971; Cuthbert & Maetz, 1972; Eddy, 1975); the effect on outflux being more drastic than on influx.

The effect of hypophysectomy in lowering plasma electrolyte level and osmotic pressure in the brown trout was similar to that observed in *Poecilia latipinna* by Ball & Ensor (1967) and in *Oryzias latipes* by Utida *et al.* (1971).

The fall in plasma electrolytes of the brown trout was almost completely restored by prolactin therapy. A similar effect has been established for *Poecilia latipinna* where a single injection of the hormone prevents the fall in plasma sodium that occurs when the fish is hypophysectomized in fresh water (Ball & Ensor, 1965).

In fresh water there is a net loss of electrolytes following hypophysectomy of most teleosts (Maetz *et al.* 1967*b*; Lahlou & Sawyer, 1969). The low plasma sodium following hypophysectomy is expectedly a result of this negative sodium balance. The enhanced sodium outflux following hypophysectomy in fresh water has been shown to be reduced by prolactin injection in *Fundulus heteroclitus* (Maetz *et al.* 1967*a*) although influx still remained low. This may explain the incomplete restoration of plasma electrolyte levels of the hypophysectomized trout even after prolactin therapy.

The effect of increased environmental calcium, in slightly elevating the plasma electrolyte level of hypophysectomized trout, is similar to that of *Fundulus kansae* (Pickford *et al.* 1966). In seawater-adapted eel, *Anguilla anguilla*, calcium causes a reversible decrease in sodium outflux rate (Bornancin *et al.* 1972). In the freshwater goldfish, *Carassius auratus*, no significant effect is produced on the sodium efflux rate, but influx is decreased by the addition of calcium to the external medium (Cuthbert & Maetz, 1972). Calcium has the general property of rendering membranes impermeable. The ion could thus be acting in limiting the rate of electrolyte outflux from the plasma. Subsequent freshwater failure will however be inevitable as the electrolytes lost are not replenished as a result of the very low influx in hypophysectomized fish.

Renal electrolyte loss

Despite the reduction in urine volume following hypophysectomy of the brown trout (Oduleye, 1975*b*), there was no marked change in total renal sodium output, although chloride output was reduced. Sodium loss following hypophysectomy of *Fundulus kansae* has been attributed to renal loss (Stanley & Fleming, 1966). In *Anguilla anguilla* and *Fundulus heteroclitus* the effect of hypophysectomy on sodium balance is largely extra-renal (Potts & Evans, 1966; Maetz *et al.* 1967*a*, *b*); and probably so too in most teleosts. Prolactin has been shown to reduce this extra-renal loss. Thus, while at the kidney prolactin is apparently a water conservation hormone, at the gills it is both a water and electrolyte conservation hormone. It is likely that some aspect of prolactin action with respect to freshwater survival involves the interrenals. There is very little direct evidence to prove this. It is noteworthy that in Gambusia sp., which cannot survive in fresh water after hypophysectomy, adrenocorticotrophic hormone (ACTH) as well as prolactin injections are able to promote survival (Chambolle, 1966, 1967). The fact that in most hypophysectomized teleosts in fresh water prolactin is not able to completely restore normal plasma electrolyte composition, and

is not able to increase sodium influx, suggests that another hypophysial hormone, possibly ACTH, is involved in the observed effects of prolactin. Injection of ACTH is able to restore sodium turnover rate to normal in hypophysectomized eel and to increase it in intact fish (Maetz *et al.* 1967*b*; Mayer & Maetz, 1967). This suggests that in normal fish both ACTH and prolactin function together; the production of ACTH being induced in the presence of prolactin.

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