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PRELIMINARY OBSERVATIONS ON THE IONIC REGULATION OF THE ARCTIC CHAR *SALVELINUS ALPINUS*

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INTRODUCTION

The char, *Salvelinus alpinus*, family Salmonidae, is a cold-water species showing circum-polar distribution (Wheeler, 1969). In the arctic part of its range the species is anadromous, differing, however, from typical salmonids in that the fresh-water breeding periods of the adult are long compared to the periods spent in sea water (Gordon, 1957).

S. alpinus is also represented in the Northern Hemisphere by resident fresh-water populations which have completely eliminated sea-water migration. These lacustrine populations are relics of migratory stock which invaded fresh water following glacial regression at the end of the Ice Age and subsequently became isolated with the warming of the surrounding sea water and unfavourable conditions for migration.

Within the British Isles char are restricted to a number of cold-water lakes in the Lake District, Scotland and North Wales and loughs throughout Ireland. The systematic position of British char is far from clear, populations from different localities having been accorded in the past specific status based on morphological characteristics which, to a large extent, may depend on the growth rates as influenced by local conditions, e.g. Windermere char, *S. willughbii*; Hawswater char, *S. londalli*; Irish char, *S. obtusus* and *colii*. Many authorities regard these different forms as subspecies or races of the single species *S. alpinus*.

Although salmonid species may have been the focal point of many investigations on osmotic physiology (Parry, 1958, 1961; Gordon, 1957, 1959, 1963; Conte & Wagner, 1965, 1966; Potts, Foster & Stather, 1970) the char, probably due to its being difficult to obtain has received little attention (Gordon 1957), and osmotic regulation in resident fresh-water populations has not been studied.

Anadromous salmonids are typically fresh-water stenohaline forms during the juvenile phase of the life cycle, but develop the ability for hypo-osmotic regulation prior to their entry into sea water. The development of hypo-osmotic regulation has been related to the parr–smolt transformation in the Atlantic salmon (Houston, 1959) but precedes smoltification by 6–7 months in the coho salmon and rainbow trout (Conte & Wagner, 1965; Conte, Wagner *et al.* 1966). There is evidence in *Oncorhynchus nerka*, the sockeye salmon, and in *Salmo gairdneri*, the rainbow trout, that after hypo-osmotic regulation has been activated it may be de-activated again. The significance of this de-activation is not clear, but it may serve to prevent migration during unfavourable conditions. The presence of non-migratory fresh-water popula-

tions in certain species which show this regression in the regulatory mechanism, a[illegible] the absence of non-migratory forms in those species not showing this regression, suggests that de-activation of the salt-water regulatory mechanisms may partly be responsible for stream residualism and 'land-locked' forms (Conte *et al.* 1966).

The present investigation was undertaken to determine the regulatory ability of 'land-locked' arctic char when they are in their natural environment of fresh water and when exposed to increased external salinities. This investigation to a large extent is exploratory.

MATERIALS AND METHODS

The specimens of char used in this investigation were obtained from Hawswater in the English Lake District and supplied by the Freshwater Biological Association, Ambleside. Experiments were undertaken between the months of January and May, 1970. Animals weighed between 50 and 100 g. Within the laboratory animals were maintained in constant-temperature rooms at 10 °C. Fresh water was de-chlorinated Lancashire tap water containing sodium 0·26 mM/l and chloride 0·32 mM/l, and sea water was either Morecambe Bay water or artificial sea water (Pantin, 1959), both containing sodium 420 mM/l and chloride 535 mM/l.

Animals were transferred directly from fresh water to one-third sea water and then to one-half, two-thirds and three-quarters sea water, and finally to full-strength sea water. Animals remained in each salinity for 7 days, the transfer from fresh water to sea water taking 4 weeks.

Blood analysis

Blood was taken in a heparinized hypodermic syringe from the caudal artery, repetitive sampling of each fish being possible using this method without any apparent ill effect to the animal. Plasma and corpuscles were separated by centrifugation and the plasma was analysed for sodium and potassium using the E.E.L. flame photometer and for chloride by means of an Aminco chloride titrator. All analyses were made in triplicate where sample size permitted.

Total body sodium and water

For total body-water estimation the wet weight was first determined and then the fish was dried to constant weight at 100 °C.

The dried fish was digested in Analar concentrated nitric acid, and after the appropriate dilution with glass-distilled water the sodium concentration of this solution was determined by flame photometry.

Samples of muscle from the dorsal muscles mass were treated in a similar fashion for the estimation of whole-tissue concentrations of sodium and potassium.

Measurement of sodium fluxes

(i) *Sodium efflux*

The rate of sodium efflux in fish acclimatized to various external salinities was measured using the radio-active isotope sodium-22. Each fish was injected intraperitoneally with *c.* 0·5 μC of sodium-22 in isotonic saline in an injection volume of 0·1 ml. Animals were transferred after injection to 40 litres of experimental medium. This volume was assumed to be sufficient to prevent re-cycling of tracer during the

flux period. Two hours were allowed for absorption of the injected sodium into the blood and equilibration through the blood space (Mayer & Nibelle, 1969) before an initial count of the animal was taken. Radio-active sodium remaining in the fish was recorded over a period of 24–28 h.

Sodium-22 was monitored by means of a Nuclear Enterprises 'whole-arm counter', type NE 8111, this detector allowing the whole live fish to be counted. The rate of efflux, K_E (h^{-1}), was calculated from the formula

$$K_E = 1/T \times 2{\cdot}303 \log_{10} C_i/C_t,$$

where C_i is the initial count of the animal and C_t the count after an efflux period of T hours. Results are expressed as percentage of the total sodium exchanged per hour.

(ii) *Sodium influx*

Single animals were placed in two litres of experimental medium labelled with sodium-24 for an influx period of 5 h in animals acclimatized to sea water and 20 h for fresh water. After the designated period the animals were removed and washed for 5 min in a large volume of inactive medium to remove labelled sodium from the body surface and buccal cavity. The activity of the fish was monitored in the 'arm counter'. All counts were corrected for decay by reference to a standard sodium-24 source. The influx K_I (h^{-1}) was calculated from the formula

$$K_I = 1/T \times 2{\cdot}303 \log_{10} \frac{C_\infty}{C_\infty - C_t}$$

where, C_t is the count of the fish after an influx period of T hours and C_∞ the count of the fish at equilibrium with the medium, when the specific activities of the sodium in the fish and the medium are equal. C_∞ was calculated from the specific activity of the medium and the total sodium content of the fish.

In fresh water where the sodium content of the fish is much higher than that of the loading medium there is a significant decline in the specific activity of the loading medium during the period of influx measurements. In this case the mean of the initial and final specific activities of the loading medium was used in calculating the sodium influx.

Chloride efflux to fresh water

Chloride-36 was injected as isotonic sodium chloride to give an activity of 1 μC/fish. After 2 h for equilibration of the injected chloride with the blood an initial blood sample was taken from the caudal artery. This was transferred to a planchet, weighed and then heated to dryness beneath an infra-red lamp. Planchets were counted with an E.K.C.O. N620 thin-window Geiger–Müller tube in connexion with an E.K.C.O. N610B automatic decatron scaler.

A further sample was taken after 20 h and treated similarly. Counting time was selected to give 10000 counts. There was no self-absorption of chloride-36 in the 0·1–0·2 g of blood used here.

Sample counts were calculated for a blood sample of 1 g, and the rate of chloride efflux was calculated as for sodium efflux, where C_i is the initial count of 1 g of blood and C_t the count of 1 g of blood after an efflux period of T hours.

RESULTS

Salinity tolerance

Animals transferred directly from fresh water to sea water were moribund after 24–48 h and none survived after 72 h. Survival in sea water was improved by prior acclimization to dilutions of sea water.

Survival in a given salinity as a percentage of the animals initially transferred from fresh water is given in Table 1. Control animals maintained in fresh water showed complete survival during this 4-week experimental period.

Table 1. *Percentage survival of* Salvelinus alpinus (*post-spawning individuals*) *in increasing salinities*

	Fresh water	Sea water (%)				
Salinity...		33	50	66	80	100
Survival (%)	100	100	100	100	54	25

Table 2. *Blood sodium, potassium and chloride concentrations in various salinities*

Medium	Blood concentration (mM/l)		
	Sodium	Potassium	Chloride
Fresh water	151 ± 1·06 (10)	2·75 (3)	130 ± 3·8 (9)
50% sea water	172 ± 1·06 (6)	—	144 ± 1·05 (5)
66% sea water	181 ± 3·4 (6)	—	158 (3)
80% sea water	200 (4)	6·8 (1)	170·5 (1)
100% sea water	233 ± 7·3 (9)	4·1 (3)	213·5 (3)

Mean values given ± S.E. Figures in parentheses are the number of samples. 100% sea water has a composition: sodium, 420 mM/l; chloride, 535 mM/l; potassium, 10 mM/l.

In salinities of 33, 50 and 66% sea water survival was 100%, but in more hypertonic salines mortality increased. Only 50% of animals transferred to 80% sea water were alive after 7 days and of these only a half survived the transfer to full-strength sea water.

Total body-sodium analyses of fish which failed in 80 and 100% sea water showed a sodium content much higher than survivors in full-strength sea water, indicating that mortality was probably the result of a failure of the osmoregulatory system and not due to entraneous factors. Animals which survived the transfer to full-strength sea water appeared normal and healthy after 7–14 days in this medium.

The blood sodium, potassium and chloride concentrations in various media

Variation in blood concentration with medium concentration is summarized in Fig. 1, and statistical analysis of the data is given in Table 2.

Salvelinus shows a good capacity to regulate plasma ionic levels within the salinity range fresh water to two-thirds sea water. Blood sodium and blood chloride concentrations are maintained only 20% higher in two-thirds sea water compared to fresh water, although the external ion concentration is increased by a factor of 1000. Individual variability is small, suggesting regulation within this salinity range is a characteristic of the whole population. This agrees with survival results given above.

Animals in sea water show a further increase in plasma sodium and plasma chloride concentrations, these being approximately 30% higher than in animals maintained in two-thirds sea water, although the medium concentration is increased by less than a factor of 2. Variability is also increased.

Total body sodium

The sodium content of fish acclimatized to fresh water and to sea water is given in Table 3. There are large increases in total body sodium in animals acclimatized to sea water, this being over twice the value of animals in fresh water.

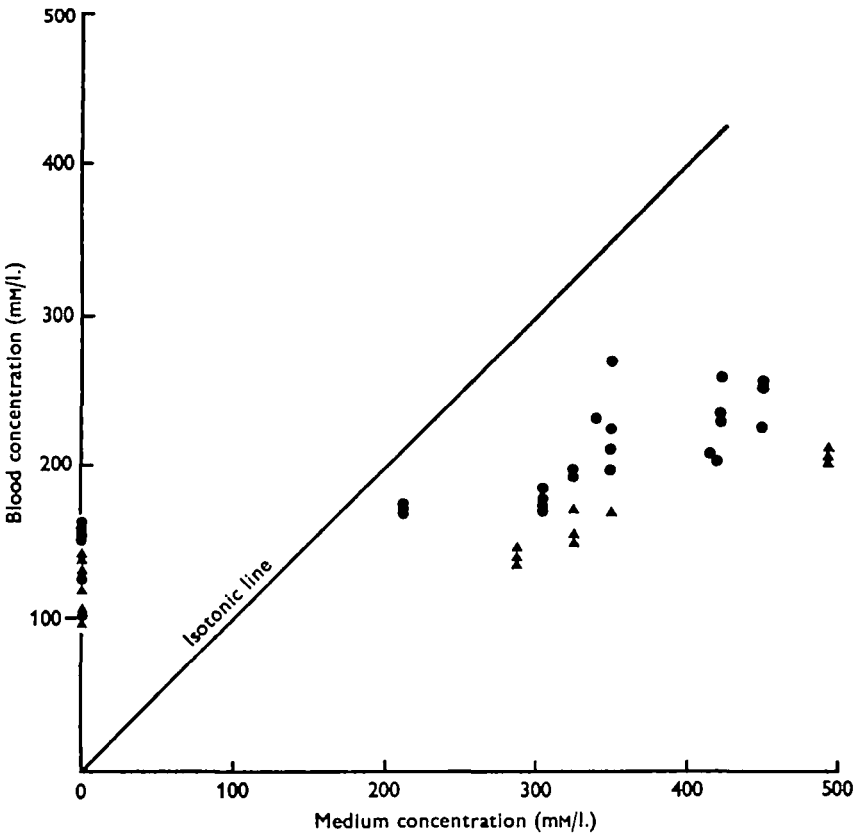

Fig. 1. The relation between the sodium and chloride concentrations of the blood and those of the medium. Each point represents a sample from a single animal. The diagonal represents equality of concentration. ● sodium, ▲ chloride.

Muscle analysis

Sodium and potassium concentrations of fresh-water-adapted and sea-water-adapted fish are given in Table 4. Intracellular potassium concentration is only slightly higher in sea water than fresh water. Sodium concentration, however, shows a large increase.

Sodium fluxes

The rate constants of efflux of sodium in various salinities, together with the rates of influx in animals in fresh water and sea water, is given in Table 5. Both influx and

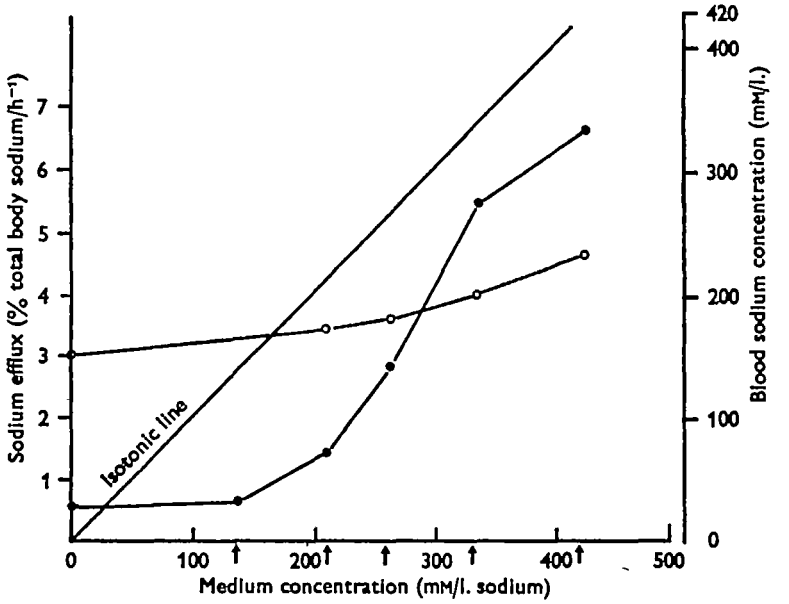

Fig. 2. The relation between sodium efflux and external concentration. Each solid circle, ●, represents the mean of several determinations. The dotted line and open circles, – – ○ – –, represents the blood sodium concentration maintained in each salinity, the diagonal represents equality of concentration.

Table 3. *Total body water and sodium in animals acclimatized to fresh water and sea water*

Medium	Body water (%)	Sodium concentration (mM/kg body water)
Fresh water	74·0 ± 0·77 (7)	32·18 ± 2·4 (5)
Sea water	69·2 ± 0·85 (10)	76·70 ± 6·3 (5)

Table 4. *Water content, and potassium and sodium concentrations in muscle*

Medium	Muscle water (%)	Muscle sodium (mM/kg muscle water)	Muscle potassium (mM/kg muscle water)
Fresh water	76·8 ± 0·22 (6)	13·5 ± 0·4 (6)	140 ± 5·5 (6)
100% sea water	74 ± 0·42 (20)	36·8 ± 1·63 (16)	160 ± 13·7 (16)

Table 5. *Rate of efflux (K_E) and influx (K_I) of sodium and efflux of chloride (K_{ECl}) in* Salvelinus *acclimatized to various salinities expressed as percentage of the total body ions h^{-1}*

Medium	K_E	K_I
Fresh water	0·56 ± 0·047 (20)	0·436 ± 0·0375 (16)
33% sea water	0·68 ± 0·047 (10)	—
50% sea water	1·41 ± 0·140 (16)	—
66% sea water	2·80 ± 0·004 (22)	—
80% sea water	5·45 ± 0·032 (18)	—
100% sea water	6·59 (4)	6·15 ± 0·16 (6)
	K_{ECl}	
Fresh water	0·483 ± 0·086 (8)	

flux show an increase with increasing salinity, sodium turnover in fresh water is less than one-tenth of that occurring in sea water. Fairly good agreement is seen between the rates of influx and efflux in both media.

A plot of sodium efflux against medium concentration is shown in Fig. 2.

Chloride efflux

The rate of chloride efflux determined in fish acclimatized to fresh water only is given in Table 5. Mean chloride efflux is slightly lower than sodium efflux, but the difference is not significant at the 1% level by '*t*' test.

DISCUSSION

The specimens of *Salvelinus* used in this investigation were all adult (sexually mature) individuals, and may therefore from the viewpoint of osmotic physiology be compared to anadromous species that have undergone seaward migration and in which hypo-osmotic regulation is developed.

Hawswater char show a good degree of euryhalinity characteristic of their ancestral stock, although they have been isolated in fresh water for *c.* 10000–12000 years. Euryhalinity, however, is not developed to the same extent in all individuals. Whereas all specimens tolerate the salinity range 0–66% sea water, only one-quarter of these were alive after 7 days in full-strength sea water. Extraneous factors other than salinity may have been responsible for some of the observed mortality; cannabalism was prominent, but the very high sodium content of failing fish suggests that death was the result of osmotic failure.

Gordon (1959) has tentatively proposed that euryhalinity in the brown trout is correlated with the ability to regulate intracellular sodium concentration. Brown trout tolerating the full transfer from fresh water to sea water, via one-half sea water, show an almost constant intracellular (muscle) sodium concentration in spite of an elevated plasma concentration, whereas those failing show invasion of the cells by sodium. In contrast, char in sea water show a large increase in muscle sodium, this being 36·8 mM/kg muscle water in sea water compared to 13·5 mM/kg in fresh water. This increase is the result of net ion gain as the dehydration in sea water is small (Table 4). In this respect char may be compared to salmon smolts (Parry, 1961), where a large increase in sodium of the muscle occurs following seaward migration. It is possible that part of the large increase in muscle sodium may be attributed to extracellular sodium trapped between individual muscle fibres. Muscle segments were thoroughly blotted dry prior to analysis but some extracellular fluid may remain. However, only a 50% increase would be expected from this source assuming the same volume of fluid was trapped in each case.

Muscle potassium is regulated to a finer degree. Nearly half of the increased concentration (10%) seen in sea water may be attributed to cellular dehydration.

The total sodium content in fresh water is 32·18 mM/kg wet weight. Potts *et al.* (1970) give a value of 30 mM/kg in salmon smolts, and work in this laboratory (unpublished) has shown a similar value at 37·5 mM/kg for the brown trout. The two-fold increase in sea water reflects the increase in the intracellular compartment discussed above and also an increase in extracellular sodium. Ingested sodium may also contri-

bute to this increase. Marine teleosts and euryhaline species in sea water must continually drink sea water to replace water lost by exosmosis. Although drinking rates were not determined in these specimens, rates of 0·25–0·5% of the total body weight per hour are to be expected from analysis of fish of comparable size (Motais & Maetz, 1965; Potts *et al.* 1970; Hickman, 1968). This would form an additional 1·05–2·1 mM/kg of fish.

Plasma ionic concentrations in fresh-water fish (sodium 150 mM/l; potassium 2·7 mM/l; chloride 130 mM/l) are in good agreement with published data on other salmonid species. Gordon (1959) lists mean sodium concentrations of 150 and 141 mM/l for the brown trout and sea trout in fresh water, and chloride concentrations of 133 and 123 mM/l respectively, and Conte *et al.* (1966) give a sodium concentration of 143 mM/l and a chloride concentration of 132 mM/l for the coho salmon.

Hawswater char in sea water have a plasma sodium and chloride concentration 50–60% higher than that maintained in fresh water. This increase is large compared to the 0–25% change in the blood concentration observed in anadromous salmonids following transfer between sea water and fresh water and vice versa. In this respect these 'land-locked' forms differ significantly from anadromous char, as reported by Gordon (1957). Transfer from sea water to fresh water results in a decline in plasma concentration by only 25% to the steady-state fresh-water level after 20 h. In the reverse transfer steady-state sea-water levels were attained after 15 h, although the significance of this latter result is doubtful as the fish were dying at the time of sampling.

The high electrolyte level of the plasma and muscle in sea water would indicate a reduced ability to regulate body electrolytes when under osmotic stress, compared to anadromous species. It is worth noting, however, that although anadromous forms regulate plasma sodium and chloride within narrow limits when fully acclimatized to fresh water and sea water, the concentration differences may be quite large in non-steady-state fish following abrupt transfer between the two media. Two phases of response may be distinguished. Immediately following transfer there is an 'acute adaptive' phase when there is a large increase in muscle and plasma ionic concentrations above the steady-state sea water level, followed by a 'chronic regulatory phase' which result ultimately in the establishment of the new steady-state electrolyte levels. These two phases of response may be distinguished in most euryhaline species, species differences being in the time period for the onset of the regulatory phase and the establishment of steady-state levels. It is possible that the high plasma and muscle concentrations noted in these char are due to the fact that the animals are still within the 'regulatory phase'. This, however, would appear doubtful as the 7-day period allowed for the fish to equilibrate within each salinity is longer than that required by most salmonid species to establish ionic equilibrium. Sodium flux data would also suggest that ionic equilibrium is established by the end of this period. The data of Gordon (1959) is of interest in this respect as sea trout and brown trout, following gradual acclimatization to sea water, both showed lower plasma sodium and chloride concentrations after 64 days than after 1–10 days.

Typical of euryhaline species, *Salvelinus* demonstrates a higher rate of sodium turnover in sea water (6·6% total body sodium/h) than in fresh water (0·56%). The mean rate for animals adapted to sea water is considerably lower than that recorded for most teleosts of a comparable size in this medium and for the salmon smolt (Potts

al. 1970). The significance of this low flux value is difficult to assess without the knowledge of the part played by 'ion exchange diffusion', which unfortunately was beyond the scope of this investigation owing to the shortage of available specimens. Exchange diffusion may constitute up to 90% of the observed sodium flux in the euryhaline flounder (Motais, Garcia Romeu & Maetz, 1966) and 50% of the flux in brown trout in sea water (Roberts & Potts, unpublished). Gross fluxes in these char approach the value of other teleosts after the subtraction of the 'ion exchange diffusion' component of the observed flux, but part of the observed 6·6% may be attributed to exchange diffusion.

From values of total body sodium and rates of sodium flux, it is possible to construct a picture of sodium balance in char acclimatized to fresh water and to sea water, although without measurements of drinking rates in the two media values must be regarded as approximate values only.

In fresh-water sodium exchange is 0·18 mM/kg fish/h. This increases to 5·06 mM/kg/h in sea water. Assuming a drinking rate of 0·5% of the body weight/h, based on available data of animals of a similar size, ingested sodium will be 2·1 mM/kg fish/h. This will leave a residual influx of 2·96 mM/kg, which will represent passive inward diffusion across the permeable region of the body surface, predominantly the gills. Sodium influx is balanced by a concomitant efflux. Ingested sodium and sodium diffusing into the animal will be excreted across the branchial epithelium; urinary loss is likely to be small.

In the absence of a potential difference across the branchial epithelium the rate of sodium efflux in fresh water may be predicted to be one-third of the influx in sea water, as the blood concentration maintained in fresh water is approximately one-third sea water. The observed flux, however, is much lower than this value. This may indicate a reduction in permeability of the branchial epithelium to sodium movement in fresh-water animals. Two other possibilities must be borne in mind. First, part of the exchange seen in sea water may be the result of ion exchange diffusion, the rate of sodium movement measured with isotope exceeding the net gain or loss of sodium. Secondly, a potential difference developed across the diffusion pathway will modify the passive movements of ions. Few measurements have been made of potential differences existing across teleostean gills (House, 1963; Maetz & Campanini, 1966; Evans, 1968) but the limited data shows that from a positive potential of 10–20 mV in sea water the potential changes to a few millivolts negative in fresh water. The effect of this potential difference would be to enhance passive sodium diffusion in sea water whilst retarding outward diffusion in fresh water.

The role of each of these three possibilities is at present being studied.

In conclusion it may be stated that although these fresh-water char populations have been isolated since the end of the Ice Age they still retain a certain degree of euryhalinity characteristic of their ancestoral stock. In certain ways they depart from typical anadromous salmonids. Because little is known about regulation in anadromous char, it is difficult to assess whether this is a character of the species or solely of this fresh-water population.

SUMMARY

1. The degree of euryhalinity in a fresh-water resident population of the arctic char, *Salvelinus alpinus*, has been determined.

2. Although isolated in fresh water for *c.* 10000–12000 years these fish still show a high degree of salinity tolerance characteristic of their ancestral stock, but this is variably developed in individuals.

3. In fresh water, blood sodium concentration is regulated at 150 mM/l and chloride at 130 mM/l. These increase to 233 and 218 mM/l respectively in sea water.

4. Fish in sea water show a large increase in muscle sodium, although the potassium concentration is only slightly higher than that maintained in fresh water. The total sodium content of the fish reflects the increase observed in the intracellular and extracellular compartments.

5. The rate of sodium turnover in sea-water-adapted fish is some ten times higher than in fresh-water-adapted fish, although it is significantly lower than that observed in most sea-water-adapted teleosts.

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