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Effects of dilute media on renal hydromineral metabolism in the Baltic sculpins Myoxocephalus scorpius (L.) and M. quadricornis (L.)[1]

AIMO OIKARI

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Renal hydromineral metabolism of two *Myoxocephalus* species captured from Baltic (Gulf of Finland) brackish water (BW) of about 6 ‰ salinity was studied, after catheterization of the urinary bladder, in media more dilute than the natural habitat. The glacial relict *M. quadricornis* differs from the marine species *M. scorpius* in its well-developed mechanisms for renal ion conservation and lower urine flow rate. Results suggest that both species resort, at least occasionally, to tubular water excretion. This may be an important mechanism by which the sculpins are able to resist and become adapted to extremely dilute BW.

Aimo Oikari, Division of Physiology, Department of Zoology, University of Helsinki, Arkadiankatu 7, SF-00100 Helsinki 10, Finland.

1. Introduction

Teleost fish maintain body fluids at a relatively stable composition in varying environmental salinities. They hypo-osmoregulate in sea water (SW) and hyperosmoregulate in fresh water (FW) (CONTE 1969). The salinity range in which different species will survive depends largely on the adaptability of the renal, branchial and intestinal osmoregulatory systems. The balance between these transport organs seems to be mediated by both endocrines and passive external factors (ODULEYE 1976). It is generally agreed that glomerular SW fish reabsorb water from the ultrafiltrate and secrete divalent plasma ions. In FW, a major role of the kidneys is to excrete excess water gained by osmosis and to conserve body salts, principally sodium chloride (HICKMAN & TRUMP 1969).

The hypo-osmotic brackish water (BW) of the inner Baltic Sea harbours fish which, according to their SW or FW ancestry, fall into two major categories. In spite of the relatively stable salinity of their environment (cf. OIKARI 1975), the species, in keeping with their geographical distribution, appear to possess differing degrees of euryhalinity. *Myoxocephalus scorpius* (L.) is a marine teleost whose range includes the Gulf of Finland. Fish from this area do not tolerate FW for longer than 24 h, but can survive a salinity of 2.5 ‰ for at least 2 weeks (OIKARI 1978), whereas specimens from the Irish Sea did not survive for more than 24—48 h in salinities less than iso-osmotic (FOSTER 1969). Evidently the Irish Sea and Baltic Sea populations differ physiologically (RASCHACK 1969, OIKARI 1978). *M. quadricornis* (L.), another sculpin species of the Baltic Sea, is a glacial relict; it tolerates FW for at least one month, but does not survive in hyperosmotic salinities (OIKARI 1978). The present report attempts to evaluate specific differences through the effects of unnaturally dilute water on several parameters of renal hydromineral metabolism.

2. Material and methods

The fish were caught with nets in May-June 1975 in the BW (about 6 ‰ S) area of Tvärminne Zoological Station (Gulf of Finland) and transferred to the laboratory aquaria for adaptation as described previously (OIKARI 1977). An L : D rhythm of 12 : 12 was maintained in the aquarium room.

After at least 2 weeks' recovery at the test temperature (Table 1) sculpins were anaesthetized and catheterized

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Table 1. Data on groups used in experiments.

Species	Group	Experimental medium[2]	Interval between salinity change and urine collection[3]	Urine collection period	Test temperature °C	Weights of fish Mean	Range	Number of fish
M. scorpius	BW[1]	Brackish water (6.1 ‰ S)	Continuously in BW	8–12 h	11.5 ± 0.3	239	180–360	4
	DBW	Diluted BW (1.3 ‰ S)	3–6 h	10–12 h	11.5 ± 0.5	187	110–295	8
M. quadricornis	BW[1]	Brackish water (6.1 ‰ S)	Continuously in BW	8–13 h	12.0 ± 0.3	200	162–270	5
	FW	Fresh water	3–4 h	11–13 h	12.0 ± 0.4	197	125–290	4
	FW	Fresh water	9–10 days	9–13 h	12.0 ± 0.5	194	124–273	8

[1] Control group in natural brackish water.
[2] For ionic composition see OIKARI (1978).
[3] Salinity change lasted 20–30 min.

for urine collection (OIKARI 1977). If, during the subsequent 12- to 24-h period, urine output was adequate (60—70 % of all attempts), the fish was injected intraperitoneally (without anaesthesia) with a 0.5—1.0 ml inulin solution containing 2 mg inulin- ^{14}C-carboxylic acid (2.17 μCi/mg MW 5175 ± 95, Amersham) and 30 mg unlabelled inulin (Merck Art 4733) per ml of 0.9 % NaCl solution (cf. WILLIAMS *et al.* 1974). After a distribution and recovery time of 12—15 h, the plasma inulin concentration remained constant (± 5 %) during the following 24 h (cf. HOLMES & STAINER 1966, OIDE & UTIDA 1968).

Groups investigated are listed in Table 1. Each group comprised both males and females. For urine collection an apparatus was designed and made from grey PVC. Each fish was accommodated in a separate box (8 × 8 × 30 cm) submerged so that the walls were flush with the water surface. Four boxes were joined side by side with two intervening higher boxes (5 × 20 × 30 cm) intended for graduated cylinders. A blood sample was taken at the end of the urine collection period, and plasma was separated immediately. Before sampling fish were immobilized by stunning on the head.

The samples were dissolved in Instagel^R (Packard) scintillation liquid. Carbon-14 activities were counted with a Packard Tri-Carb 2420 liquid scintillation spectrometer, using an external standardization technique. Concentrations of Na^+, K^+, Ca^{2+} and Mg^{2+} were determined by atomic absorption (Perkin Elmer Mod. 305) and Cl^- with a Cotlove chloridometer (Aminco).

Parameters of renal function were calculated as before (OIKARI 1977) except that plasma inulin concentration was assumed to represent the level during the entire period of urine collection. Table 2 shows the proportions of free ions. These were determined according to MILES (1971), using dialysing tubing (A. H. Thomas Co) with approximate pore sizes of 2.4 and 4.8 nm, and a centrifugal force of 400 g for 12 h. As the type of tubing did not appear to influence the value obtained, the results were combined.

The final groups were relatively small, so stress is laid only on the direction of change in an "average fish". The statistical differences presented are based on Student's t test.

Table 2. Mean percentages of free ions, ultrafilterable through 2.4 – 4.8 nm pores, in blood plasma of *M. scorpius* and *M. quadricornis*. In parentheses, the number of samples, each pooled from 2–3 fish of the same sex.

Ion	*M. scorpius* (2)	*M. quadricornis* (3)
Chloride	99.0	98.3
Sodium	94.2	95.2
Calcium	66.2	65.4
Magnesium	87.8	88.8

3. Results

Myoxocephalus scorpius (L.). Exposure to 1.3 ‰ salinity (DBW) caused the rate of urine flow to increase by about 50 % (Table 3). Simultaneously, urine Na^+ and Cl^- concentrations decreased (Fig. 1, Table 6). The fish were divided into two subgroups according to urine/plasma (U/P) ratio of inulin. In those with U/P>1 (mean 1.35), indicating net reabsorption of water (as in natural BW), the glomerular filtration rate (GFR = inulin clearance) increased. The others, with U/P<1 (mean 0.60), showed unchanged GFR associated with net aglomerular water excretion or secretion (Fig. 2). These DBW subgroups will be considered as two successive stages (see Tables 3—5 and Fig. 2). The filtration rates of ions at first increased, but then tended to decrease below the rates seen in BW (Table 4). Similarly, rates of Cl^-, Na^+ and K^+ excretion initially increased but then returned near to the BW

Table 3. Rates of urine flow and glomerular filtration in Baltic *M. scorpius* in natural brackish water (BW) of 6.1 ‰ and after 3–6 h exposure to diluted BW (DBW) of 1.3 ‰ salinity. Means ± SEMs are given with numbers of fish in parentheses.

Test group		Urine flow rate ml/kg h^{-1}	Glomerular filtration rate ml/kg h^{-1}	Inulin U/P
BW	(4)	1.15±0.16	1.26±0.13	1.13±0.08
DBW	(3)[1]	1.82±0.28	2.48±0.46*	1.35±0.07
–»–	(5)[2]	1.81±0.31*	1.12±0.22§	0.60±0.08*§

[1] Individual U/P ratios > 1.
[2] Individual U/P ratios < 1.
* Significantly different from the BW group ($P < 0.05$).
§ DBW groups differ significantly ($P < 0.05$).

control level. In both DBW subgroups rates of Ca^{2+} and Mg^{2+} excretion were slightly elevated. At first reabsorption of Cl^- and Na^+ increased, both absolutely and relatively, but later the process changed to net secretion. For K^+ there was no clear response, some individuals showing net reabsorption and others net secretion, but for both Ca^{2+} and Mg^{2+} secretion was at least as pronounced in DBW as in BW (Table 4, Fig. 2).

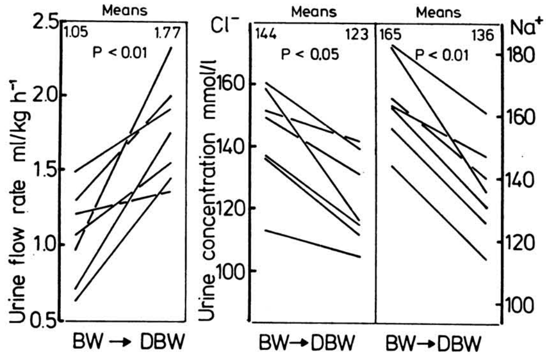

Fig. 1. Changes in urine flow rate, and urinary Cl^- and Na^+ concentrations of *M. scorpius* after transfer from natural brackish water (BW) of 6.1 ‰ to diluted BW (DBW) of 1.3 ‰ slinity. Periods of urine collection lasted 10–12 h, starting 3–6 h after the salinity change. The continuous lines connect values in the two periods for each fish. Means are given in the upper corners of each panel, and P according to Student's t test.

These kidney activities gave rise to the ionic concentrations of urine and plasma listed in Table 5. In dilute media renal loss of electrolytes, particularly Cl^-, Na^+ and Mg^{2+}, was associated with reduced concentrations of plasma ions and aglomerular excretion of water.

Table 4. Filtration and excretion, mean readsorption and secretion of electrolytes in *M. scorpius* in natural brackish water (BW) and in diluted BW (DBW). For further details, see legend to Table 3.

Ion	Test group		Filtration rate µmol/kg h^{-1}	Excretion rate µmol/kg h^{-1}	Net reabsorption rate µmol/kg h^{-1}	Net secretion rate µmol/kg h^{-1}
Cl^-	BW	(4)	221 ± 20	188 ± 26	34.5	Nil
	DBW[1]	(3)	351 ± 63	252 ± 44	99.7	»
	–»–[2]	(5)	146 ± 29	201 ± 15	Nil	54.8
Na^+	BW	(4)	194 ± 19	198 ± 24	12.1 (2)	19.3 (2)
	DBW[1]	(3)	317 ± 62	270 ± 37	47.7	Nil
	–»–[2]	(5)	129 ± 26	222 ± 17	Nil	92.6
K^+	BW	(4)	3.13 ± 0.19	3.36 ± 0.30	0.22 (2)	0.69 (2)
	DBW[1]	(3)	4.49 ± 0.73	4.17 ± 0.58	0.64 (2)	0.34 (1)
	–»–[2]	(5)	2.78 ± 0.71	3.48 ± 0.50	0.68 (2)	1.61 (3)
Ca^{2+}	BW	(4)	1.83 ± 0.17	2.69 ± 0.32	Nil	0.86
	DBW[1]	(3)	3.48 ± 0.82	4.50 ± 1.75	»	1.02
	–»–[2]	(5)	1.63 ± 0.27	4.31 ± 1.47	»	2.69
Mg^{2+}	BW	(4)	0.85 ± 0.17	11.8 ± 3.3	»	10.9
	DBW[1]	(3)	1.05 ± 0.21	12.2 ± 6.1	»	11.2
	–»–[2]	(5)	0.60 ± 0.15	14.3 ± 4.4	»	13.7

[1] Mean inulin U/P ratio 1.35.
[2] Mean inulin U/P ratio 0.60.

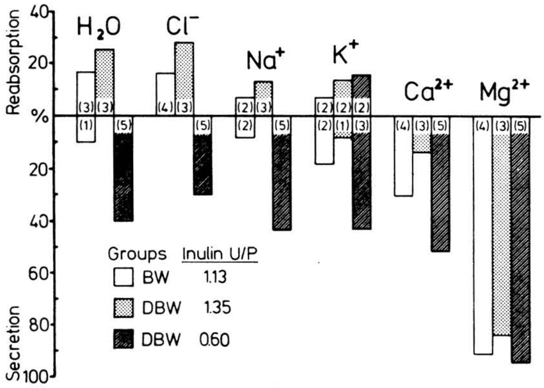

Fig. 2. Mean percentage net reabsorption or secretion of water and electrolytes in kidneys of *M. scorpius*. Three groups are given; see Tables 3—5. Numbers of fish in parentheses.

Table 5. Concentrations of electrolytes (mmol/l) in urine and plasma of *M. scorpius* in natural brackish water (BW) and in diluted BW (DBW). For further details, see legend to Table 3.

Ion	Test group		Urine	Plasma
Cl^-	BW	(4)	164±1.3	174±2.0
	DBW[1]	(3)	138±3.3*	141±2.5*
	—»—[2]	(5)	111±2.1*§	128±2.9*§
Na^+	BW	(4)	174±3.5	174±1.0
	DBW[1]	(3)	149±6.2*	146±3.2*
	—»—[2]	(5)	123±5.2*§	130±3.4*§
K^+	BW	(4)	3.03±0.33	2.99±0.12
	DBW[1]	(3)	2.45±0.53	2.32±0.49
	—»—[2]	(5)	1.91±0.21*	3.11±0.59
Ca^{2+}	BW	(4)	2.36±0.10	2.26±0.11
	DBW[1]	(3)	2.31±0.55	2.26±0.09
	—»—[2]	(5)	2.28±0.68	2.10±0.06
Mg^{2+}	BW	(4)	9.80±1.95	0.78±0.13
	DBW[1]	(3)	6.27±2.29	0.55±0.14
	—»—[2]	(5)	7.68±2.01	0.60±0.05

[1] Mean inulin U/P ratio 1.35.
[2] Mean inulin U/P ratio 0.60.
* Significantly different from the BW group ($P < 0.05$).
§ DBW groups differ significantly ($P < 0.05$).

M. quadricornis (L.). In FW the rate of urine flow at first increased by about 80 %, but on longer exposure returned to normal (Table 6). Similarly, both GFR and filtered loads of ions (Table 7) at least doubled at first, but within 9—10 days returned to a level slightly higher htan in BW. Specimens acclimated to FW for

Table 6. Rates of urine flow and glomerular filtration in Baltic *M. quadricornis* in natural brackish water (BW) of 6.1 ‰ salinity and after 3—4 h and 9—10 d exposure to fresh water (FW). Means ± SEMs are given with numbers of fish in parentheses.

Test group		Urine flow rate ml/kg h^{-1}	Glomerular filtration rate ml/kg h^{-1}	Inulin U/P
BW	(5)	0.79±0.05	0.46±0.08	0.61±0.11
FW 3—4 h	(4)	1.43±0.16*	1.04±0.16*	0.73±0.08
FW 9—10 d	(3)[1]	0.73±0.28	0.61±0.28	0.80±0.12
—»—	(5)[2]	0.74±0.17§	0.90±0.19*	1.29±0.15*§

[1] Individual U/P ratios < 1.
[2] Individual U/P ratios > 1.
* Significantly different from the BW group ($P < 0.05$).
§ FW groups, 3—4 h vs 9—10 d[2], differ significantly ($P < 0.05$).

9—10 days fell into two subgroups according to inulin U/P ratios; in contrast to the norm in BW, some fish showed net reabsorption of water (Fig. 3). Renal loss of ions, especially Cl^- and Na^+, at first increased but later normalized. Percentage reabsorption of Cl^- and Na^+ was high in all FW groups (Fig. 3) but, in absolute terms, was least effective in the FW group showing the most effective secretion of Mg^{2+} and Ca^{2+} (Table 8). For K^+ this species, like *M. scorpius*, showed no clear response; in each group some individuals showed net reabsorption and others net secretion.

In urine, after 9 to 10 days' exposure to FW, ionic concentrations were the same as or slightly higher than in BW (Table 8), but in plasma the concentrations of Cl^-, Na^+ and Mg^{2+} were lower ($P<0.05$). Reduction of plasma Cl^- and Na^+ was smaller in the FW group with net water reabsorption and greater ionic reabsorption than in the other subgroup. Short-term exposure to FW caused no diminution of plasma Cl^-, Na^+ or Mg^{2+} concentration in this species.

4. Discussion

The values for renal function in BW *M. scorpius* and *M. quadricornis* agree fairly well with those previously measured in this environment (Oikari 1977). In *M. scorpius* the GFRs of plasma water and electrolytes were two to three times those in *M. quadricornis*. In *M. quadricornis* there was net aglomerular excretion of fluid and effective reabsorption of Na^+, whereas in *M.*

Table 7. Filtration and excretion, mean reabsorption and secretion of electrolytes of *M. quadricornis* in natural brackish water (BW) and in fresh water (FW). For further details, see legend to Table 6.

Ion	Test group	Filtration rate µmol/kg h^{-1}	Excretion rate µmol/kg h^{-1}	Net reabsorption rate µmol/kg h^{-1}	Net secretion rate µmol/kg h^{-1}
Cl^-	BW (5)	70 ± 13	1.5 ± 0.3	68.7	Nil
	FW 3–4 h (4)	161 ± 29	10.3 ± 5.7	150.6	»
	FW 9–10 d[1] (3)	75 ± 36	1.2 ± 0.3	73.4	»
	–»– [2] (5)	119 ± 28	1.9 ± 0.6	116.8	»
Na^+	BW (5)	68 ± 12	13.9 ± 1.8	54.2	»
	FW 3–4 h (4)	152 ± 26	25.1 ± 6.0	127.0	»
	FW 9–10 d[1] (3)	72 ± 33	17.2 ± 5.3	54.7	»
	–»– [2] (5)	116 ± 27	12.3 ± 2.8	103.5	»
K^+	BW (5)	1.15 ± 0.20	1.06 ± 0.09	0.36 (3)	0.31 (2)
	FW 3–4 h (4)	2.24 ± 0.60	2.04 ± 0.48	0.97 (3)	2.12 (1)
	FW 9–10 d[1] (3)	1.49 ± 0.51	1.52 ± 0.55	0.40 (1)	0.25 (2)
	–»– [2] (5)	2.03 ± 0.30	2.24 ± 0.50	0.38 (2)	0.60 (3)
Ca^{2+}	BW (5)	0.81 ± 0.14	1.22 ± 0.14	Nil	0.41
	FW 3–4 h (4)	1.65 ± 0.28	2.10 ± 0.48	0.20 (1)	0.67 (3)
	FW 9–10 d[1] (3)	0.98 ± 0.39	3.53 ± 1.51	Nil	2.54
	–»– [2] (5)	1.45 ± 0.38	3.21 ± 0.73	»	1.76
Mg^{2+}	BW (5)	0.19 ± 0.03	2.37 ± 0.46	»	2.17
	FW 3–4 h (4)	0.48 ± 0.10	3.17 ± 0.72	»	2.69
	FW 9–10 d[1] (3)	0.10 ± 0.04	4.56 ± 2.15	»	4.46
	–»– [2] (5)	0.22 ± 0.12	2.51 ± 1.01	»	2.29

[1] Mean inulin U/P ratio 0.80.
[2] Mean inulin U/P ratio 1.29.

Table 8. Concentrations of electrolytes (mmol/l) in urine and plasma of *M. quadricornis* in natural brackish water (BW) and in fresh water (FW). For further details, see legend to Table 6.

Ion	Test group		Urine	Plasma
Cl^-	BW	(5)	1.90±0.36	149±3.6
	FW 3–4 h	(4)	6.75±3.50	152±5.2
	FW 9–10 d[1]	(3)	2.20±0.95	120±3.7*
	–»– [2]	(5)	3.20±1.41	129±4.3*§
Na^+	BW	(5)	17.8±2.2	164±4.1
	FW 3–4 h	(4)	16.6±2.9	162±3.9
	FW 9–10 d[1]	(3)	25.9±6.3	132±2.7*
	–»– [2]	(5)	17.3±2.4	141±4.7*§
K^+	BW	(5)	1.38±0.16	2.96±0.21
	FW 3–4 h	(4)	1.38±0.25	2.45±0.37
	FW 9–10 d[1]	(3)	2.15±0.09*	3.24±0.48
	–»– [2]	(5)	3.06±0.39*§	2.87±0.35
Ca^{2+}	BW	(5)	1.56±0.18	2.72±0.08
	FW 3–4 h	(4)	1.41±0.22	2.49±0.07
	FW 9–10 d[1]	(3)	5.06±2.06	2.68±0.25
	–»– [2]	(5)	5.02±1.71	2.47±0.26
Mg^{2+}	BW	(5)	3.13±0.70	0.50±0.04
	FW 3–4 h	(4)	2.34±0.60	0.52±0.04
	FW 9–10 d[1]	(3)	5.97±0.88*	0.20±0.04*
	–»– [2]	(5)	3.90±1.32	0.22±0.08*§

[1] Mean inulin U/P ratio 0.80.
[2] Mean inulin U/P ratio 1.29.
* Significantly different from the BW group ($P < 0.05$).
§ FW groups, 3–4 h vs 9–10 d[2], differ significantly ($P < 0.05$.)

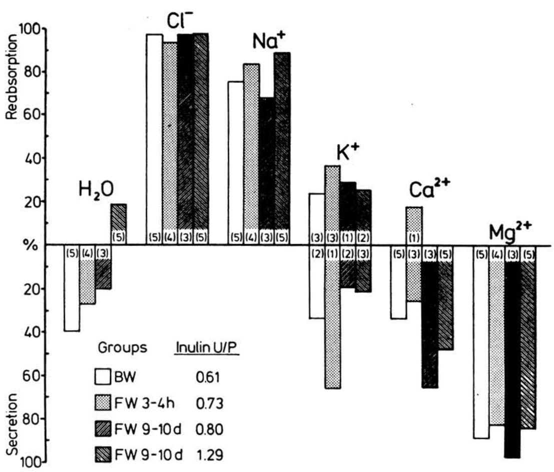

Fig. 3. Mean percentage net reabsorption or secretion of water and electrolytes in kidneys of *M. quadricornis*. Four groups are given; see Tables 6–8. Numbers of fish in parentheses.

scorpius there was net renal reabsorption of water but not of Na^+. Tubular reabsorption of Cl^- seemed to occur in both species, but was clearly more effective in *M. quadricornis* (Figs. 2 and 3). In BW total loss of electrolytes (Cl^-,

Na^+, K^+, Ca^{2+}, Mg^{2+}) through the kidneys of *M. scorpius* was about 20 times that of *M. quadricornis* (Tables 4 and 7), implying compensation by uptake of ions elsewhere, presumably through the gills and intestine. In *M. scorpius*, transfer to dilute BW led to changes in plasma and urine ionic concentrations of the same type as were observed after longer exposure to 2.5 ‰ salinity (Oikari 1978).

Within a few hours after transfer from hypo-osmotic natural BW to a more dilute medium (DBW, FW), both species studied showed a significantly increased urine flow rate (Fig. 1, Tables 3 and 6). Presumably increased osmotic influx of water tends to be compensated by increased elimination of water through the kidneys, as has been demonstrated repeatedly for a number of euryhaline teleosts (Hickman & Trump 1969). After 9—10 days in FW the urine flow rate in *M. quadricornis* did not differ from BW control values, so adaptation seems to occur in this respect. Sculpins exposed to dilute media seem to be capable of both glomerular and aglomerular (tubular) excretion of water. These two different types of water excretion may occur in successive stages, but in which order is uncertain. *M. scorpius*, however, probably maintained an inulin U/P ratio of above 1.0 at first, as it did in BW. In *Anguilla rostrata* renal clearance data were consistent with the hypothesis that fluid is secreted into the renal tubule particularly in FW (Schmidt-Nielsen & Renfro 1975). Of the two sculpins, only *M. quadricornis* seems capable of effectively reabsorbing filtered ions, especially Na^+ and Cl^- (Fig. 3), in a medium as dilute as FW. This is generally considered typical of teleosts in FW (Johnson 1973). In *M. scorpius*, on the other hand, renal loss of electrolytes remains high in DBW and may even increase (Table 4); since branchial uptake of ions is simultaneously reduced (Maetz 1974), the inevitable result will be demineralization of the blood plasma. Probably the huge renal loss of ions is made good by uptake through the gills or intestine, or both, down to a salinity of 2—3 ‰ (cf. Oikari 1978). No such loss occurs in the intertidal teleost *Xiphister atropurpureus* (Evans 1967). The aglomerular water excretion in DBW seems to be accompanied by tubular net secretion of Na^+ and Cl^- in *M. scorpius*, for average ionic loss was smaller than in the fish with greater GFR (Table 4). However, plasma Na^+ and Cl^- concentrations were lowest in these specimens, which may be due to greater loss of ions via the branchial epithelium also. In *M. quadricornis*, after exposure to FW for 9—10 days, some individuals showed increased GFR with simultaneously increased reabsorption rates and higher plasma concentrations of Na^+ and Cl^- (Tables 6—8). In these fish, as in FW teleosts in general (Hickman & Trump 1969), inulin U/P was clearly above 1.0. Even now, however, as in BW (Oikari 1977), some specimens showed inulin U/P less than 1.0. In conclusion, fluid excretion through the tubular wall may be an important mechanism whereby sculpins are able to adapt to extremely dilute brackish water or resist the more or less irregular salinity fluctuations that occur in their natural marginal habitats in the inner Baltic Sea.

Both net reabsorption and net secretion of K^+ were observed in sculpins not only in BW but also in lower salinities (Figs. 2 and 3). This has been observed in northern pike, white sucker and American eel in FW (Hickman 1965, Schmidt-Nielsen & Renfro 1975).

When *M. scorpius* was exposed to DBW and *M. quadricornis* to FW, Ca^{2+} and Mg^{2+} were secreted into and excreted in the urine by these sculpins in quantities the same as or slightly greater than in BW. Urine concentrations also remained high, especially as compared with those of most FW-stenohaline and FW-acclimated fish (Hickman & Trump 1969). Although nothing is known about the pools from which Ca^{2+} and Mg^{2+} are mobilized by starving fish, presumably Ca^{2+} from skeletal and Mg^{2+} from intracellular stores are alternatives to uptake from the exterior (Fleming 1974). In *M. quadricornis*, plasma Mg^{2+} but not Ca^{2+} concentrations decreased during the 9- to 10-day acclimation to FW. The relatively high level of plasma Ca^{2+}, observed before in this species (Oikari 1978), may exert a beneficial effect on the permeability of the gill and kidney epithelia to water and sodium (Cuthbert & Maetz 1972, Fleming *et al.* 1974, Oduleye 1975).

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