

POTASSIUM AND RUBIDIUM UPTAKE IN FRESHWATER BIVALVES

BY T. H. DIETZ AND R. A. BYRNE*

Department of Zoology and Physiology, Louisiana State University, Baton Rouge, LA 70803, USA

Accepted 30 January 1990

Summary

Potassium transport characteristics were investigated in three species of freshwater bivalves: a corbiculid, *Corbicula fluminea*, and two unionids, *Carunculina texasensis* and *Ligumia subrostrata*. Using ^{42}K , all three were found to take up potassium from dilute artificial pondwater ($[\text{K}^+]$ about 0.05 mmol l^{-1}). The influx (J_i) was $0.72 \mu\text{equiv g}^{-1} \text{ dry tissue h}^{-1}$ in the corbiculid, significantly higher than the value of about $0.40 \mu\text{equiv g}^{-1} \text{ dry tissue h}^{-1}$ in the unionids. The K^+ uptake displayed saturation kinetics in the range 0.05 – 0.36 mmol l^{-1} : in *Co. fluminea*, there was a J_{max} of $3.56 \mu\text{equiv g}^{-1} \text{ dry tissue h}^{-1}$ and the affinity coefficient (K_m) was 0.27 mmol l^{-1} ; in *Ca. texasensis*, J_{max} had a value of $1.8 \mu\text{equiv g}^{-1} \text{ dry tissue h}^{-1}$ and K_m was 0.16 mmol l^{-1} . Using K^+ -free artificial pondwater containing 0.03 – $0.04 \text{ mmol l}^{-1} \text{ Rb}^+$, the Rb^+ influx was $0.41 \mu\text{equiv g}^{-1} \text{ dry tissue h}^{-1}$ in the corbiculid and $0.28 \mu\text{equiv g}^{-1} \text{ dry tissue h}^{-1}$ in *Ca. texasensis*. All animals lost K^+ during the rubidium flux studies, and since they contained no Rb^+ , the Rb^+ efflux was zero and the net flux was equal to the influx. The J_{max} values for Rb^+ were lower than the corresponding values for potassium: in *Co. fluminea*, J_{max} was $1.4 \mu\text{equiv g}^{-1} \text{ dry tissue h}^{-1}$, significantly higher than in *Ca. texasensis*, which had a J_{max} of $0.84 \mu\text{equiv g}^{-1} \text{ dry tissue h}^{-1}$. The rubidium K_m (approx. 0.05 mmol l^{-1}) values were significantly lower than corresponding values for potassium. Salt depletion increased the rubidium transport rate fourfold for both *Co. fluminea* and *Ca. texasensis*. High rates of net K^+ uptake may account for the bivalves' inability to tolerate elevated environmental potassium.

Introduction

Freshwater bivalves are unusually sensitive to potassium concentration in the bathing medium. Within 12–24 h of exposure to potassium concentrations between 0.6 and 1.0 mmol l^{-1} , mussels display a number of responses, including foot swelling, lack of foot withdrawal in response to mechanical stimulation and shell gaping (Daum *et al.* 1979). We have observed that *Ligumia subrostrata* will

* Present address: Department of Biological Sciences, University of Calgary, Calgary, Alta, Canada T2N 1N4.

Key words: rubidium transport, potassium transport, corbiculid, unionid, bivalve.

not survive 24 h in a 1.0 mmol l^{-1} KCl solution. This sensitivity to potassium has been observed in many bivalve species and even prolonged exposure to 0.25 mmol l^{-1} potassium is toxic to unionid mussels over a 6-month period (Imlay, 1973).

In aquatic animals, the study of potassium transport is less extensive than that of sodium and chloride transport. The vertebrates tend to have limited epithelial potassium influx (Krogh, 1939; Sanders and Kirschner, 1983*a,b*; Zerahn, 1983); however, Krogh noted a substantial uptake of K^+ in the Crustacea. Potassium transport in freshwater bivalves has not been examined.

In this study we have measured the potassium transport characteristics in representative freshwater clams. In addition, we found that the transport characteristics of Rb^+ were significantly different from those for K^+ .

Materials and methods

The unionid mussels *Carunculina texasensis* and *Ligumia subrostrata* were collected from ponds near Baton Rouge, Louisiana, and the corbiculid mussel *Corbicula fluminea* was collected from the Sabine River reservoir area at the Texas-Louisiana border. The animals were acclimated to an artificial pondwater (0.5 NaCl , 0.4 CaCl_2 , 0.2 NaHCO_3 , 0.05 KCl , in mmol l^{-1}) at $22\text{--}25^\circ\text{C}$ for at least a week before use. Some animals were salt-depleted by acclimating the mussels to deionized water for 2 weeks.

The unidirectional influx (J_i) was calculated from the disappearance of isotope from the bathing medium, as previously described (Dietz, 1978; Graves and Dietz, 1982). The animals were rinsed for about 30 min in distilled water and transferred to individual beakers with pondwater containing ^{42}K . When the clams resumed siphoning (5–15 min), samples were removed from the bath at timed intervals and radioactivity was determined with a liquid scintillation counter using a cocktail based on Triton X-114/xylene. We verified that identical results were obtained using Cerenkov radiation detection (eliminating the liquid scintillation cocktail). Decay correction was not necessary as samples from an individual container were counted consecutively within 10 min. The potassium concentration in the samples was determined with a Perkin Elmer 5000 atomic absorption spectrometer in the emission mode, and changes in the ion concentration were used to calculate the net flux (J_{net}). Efflux (J_o) was calculated from the difference: $J_o = J_i - J_{\text{net}}$. The soft tissue was removed from the shell and dried to constant mass (95°C) and the fluxes were normalized to $\mu\text{equiv g}^{-1}$ dry tissue h^{-1} . Potassium transport kinetics were determined by adding KCl to the pondwater bathing solution.

To measure rubidium fluxes, 0.05 mmol l^{-1} RbCl was substituted for potassium in the pondwater. $^{86}\text{Rubidium}$ offers several advantages because it has a longer half-life, sufficient energy to allow Cerenkov counting, and it can serve independently to validate the technique for measuring influx. Since rubidium is not detectable in the body fluids of mussels, there can be no efflux and the influx should equal the net flux. We varied the Rb^+ concentration in the pondwater by

adding RbCl as needed and measured the Rb⁺ concentration using an atomic absorption spectrometer in the emission mode. Other reagents (serotonin, barium) were added to the bathing medium as appropriate.

Data are presented as mean ± s.e.m. The kinetics of ion influx were analyzed by linear regression of double reciprocal plots using the technique of Brooks and Suelter (1986). A one-way analysis of variance (ANOVA) was performed to examine the effects of potassium concentration on J_o and J_{net} . Differences between means were compared with Student's *t*-test and were considered significant if $P < 0.05$.

Results

Potassium uptake

Potassium uptake by many freshwater animals is considered to be small compared with that of other ions, yet a significant influx of K⁺ was found for the mussel species studied (Table 1). The influx and corresponding efflux of K⁺ were significantly different, as each J_{net} was significantly different from zero (Student's *t*-test). *Co. fluminea* were losing K⁺ but the unionids were in a positive ion balance. *Co. fluminea* had significantly higher unidirectional fluxes of K⁺ than the unionid species.

We have previously demonstrated that the transepithelial electrical potential (TEP) in *L. subrostrata* in pondwater is about -15 mV (body fluids negative) and is unchanged when 0.5 mmol l⁻¹ K₂SO₄ is substituted for pondwater (Dietz and Branton, 1975). The electrical potential does not compensate for the 10-fold concentration difference between blood and bathing medium and the K⁺ uptake probably requires the expenditure of energy (Ussing, 1949).

All the bivalves were able to obtain net K⁺ from the environment at higher K⁺ concentrations (Table 2) (*Corbicula* ANOVA, $F=42.078$, $df=2,27$; *Carunculina* ANOVA, $F=42.907$, $df=2,21$). Only the higher fluxes were significantly above

Table 1. Representative K⁺ concentrations in the blood, and average [K⁺] of the pondwater (PW) during unidirectional K⁺ flux measurement in pondwater-acclimated mussels

Species	[K ⁺] (mmol l ⁻¹)			Unidirectional fluxes ($\mu\text{equiv g}^{-1}$ dry tissue h ⁻¹)		
	Blood	PW	N	J_{net}	J_i	J_o
<i>Corbicula fluminea</i>	1.0	0.08	10	-0.41 ± 0.15*, †	0.72 ± 0.03 †	1.12 ± 0.13 †
<i>Carunculina texasensis</i>	0.5	0.05	8	0.22 ± 0.04**	0.40 ± 0.05	0.19 ± 0.03
<i>Ligumia subrostrata</i>	0.6	0.05	9	0.15 ± 0.04**	0.39 ± 0.03	0.24 ± 0.03

Significantly different from zero, * $P < 0.05$; ** $P < 0.01$.

† Significantly different from the unionid mussels, $P < 0.01$.

Table 2. *Potassium uptake in pondwater-acclimated freshwater mussels*

Species	[K ⁺] (mmol l ⁻¹)	N	J _{net} (μequiv g ⁻¹ dry tissue h ⁻¹)
<i>Corbicula fluminea</i> †	0.08	10	-0.41 ± 0.15*
	0.13	10	0.02 ± 0.20
	0.36	10	0.81 ± 0.04**
<i>Carunculina texasensis</i> †	0.05	8	0.22 ± 0.04**
	0.14	8	0.24 ± 0.07**
	0.36	8	0.98 ± 0.08**
<i>Ligumia subrostrata</i>	0.05	9	0.15 ± 0.04**

The [K⁺] is the average bath concentration during the flux study.
Significantly different from J_{net}=0, *P<0.05; **P<0.01.
† Significant one-way ANOVA, P<0.01.

zero for *Co. fluminea*, indicating a net uptake of K⁺, but the unionids gained K⁺ at all concentrations tested.

There appears to be no significant exchange diffusion or 'trans effect' since changes of bathing medium K⁺ concentration did not significantly alter the efflux of K⁺ for either *Co. fluminea* or *Ca. texasensis* (Fig. 1). The regression equation for the scatterplot for *Co. fluminea* was $J_o = (-0.11 \pm 0.48)[K^+] + (1.15 \pm 0.33)$ and for *Ca. texasensis* it was $J_o = (0.16 \pm 0.36)[K^+] + (0.25 \pm 0.22)$. There was no significant difference between the slopes of the equations for the two species;

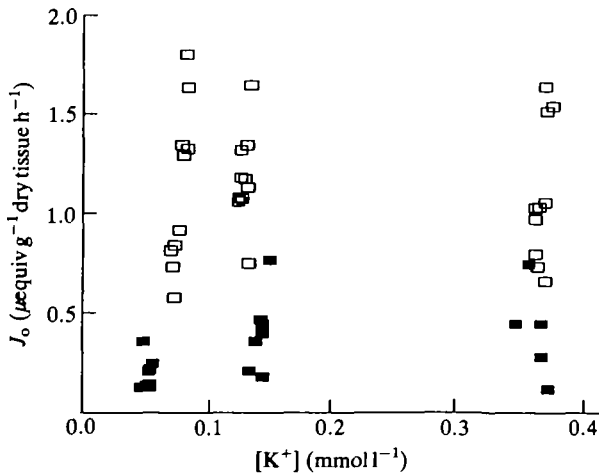


Fig. 1. The effect of bathing medium KCl concentration on the efflux (J_o) of potassium in pondwater-acclimated mussels. There is no significant slope to a linear regression analysis for either species (see text). An analysis of variance was not significant for either species (*Corbicula fluminea*, open squares; *Carunculina texasensis*, filled squares).

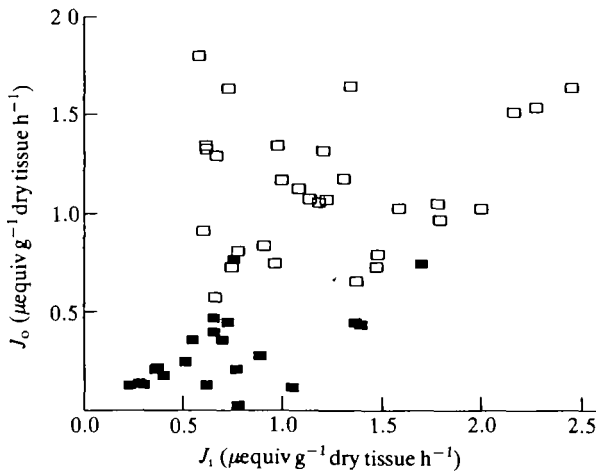


Fig. 2. The relationship between influx (J_i) and the efflux (J_o) of potassium over the range of KCl concentrations used in Fig. 1. There is no significant slope to a linear regression analysis for *Corbicula fluminea* (open squares), but there is for *Carunculina texasensis* (filled squares) (see text).

however, the intercepts were significantly different, reflecting the higher renal efflux or epithelial permeability in *Co. fluminea*.

There was a significant relationship between the influx and efflux of potassium only in *Ca. texasensis* (Fig. 2). The linear regression equation relating J_o and J_i in the scatterplot for *Co. fluminea* is $J_o = (0.10 \pm 0.11)J_i + (1.00 \pm 0.33)$, and for *Ca. texasensis* it is $J_o = (0.37 \pm 0.08)J_i + (0.02 \pm 0.22)$. The intercepts are significantly different because of the higher K⁺ fluxes in *Co. fluminea*. The slopes of the equations are not significantly different between species; however, there was a statistically significant slope for *Ca. texasensis*. It should be noted that there is a significant efflux of potassium (renal and/or epithelial) in the absence of external potassium ($J_i = 0$) in these whole-animal studies. The potassium J_o when J_i is zero was not measured for this data set, and is not shown in Fig. 2 (see below for J_o in K⁺-free pondwater).

The kinetics for inward K⁺ transport was examined by varying the concentration of KCl in the pondwater bathing medium (Fig. 3). The influx was saturable, with the K⁺ influx in *Co. fluminea* having significantly higher J_{max} and K_m values (Table 3).

Rubidium uptake

As predicted, in *Co. fluminea* and *Ca. texasensis* the J_{net} and J_i values for ⁸⁶Rb were not significantly different from each other and J_o was not significantly different from zero (Table 4). There were no differences in the rubidium flux between the species at pondwater Rb⁺ concentrations (approx. 0.05 mmol l⁻¹). Although we used ⁸⁶Rb and measured J_i for the data presented below, we noted that J_{net} gave essentially the same results. During the flux study, K⁺ was lost from

the mussels and the potassium J_{net} in $\mu\text{equiv g}^{-1}$ dry tissue h^{-1} for *Co. fluminea* was -0.46 ± 0.10 ($N=15$) and for *Ca. texasensis* was -0.35 ± 0.07 ($N=8$).

Rb^+ influx kinetics was studied in *Co. fluminea* in K^+ -free pondwater containing variable concentrations of RbCl (Fig. 4). The kinetics was qualitatively similar to that for K^+ transport but differs quantitatively. The Rb^+ transport in K^+ -free

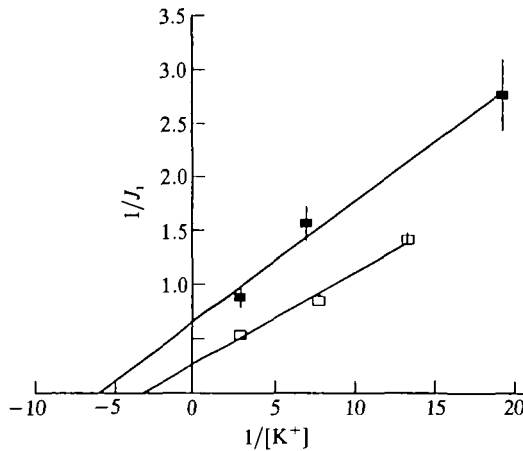


Fig. 3. A Lineweaver-Burke double reciprocal plot of KCl concentration (in mol l^{-1}) and K^+ influx (in $\mu\text{equiv g}^{-1}$ dry tissue h^{-1}) in pondwater-acclimated mussels exposed to the range of KCl concentration indicated in Fig. 1. The filled squares represent *Carunculina texasensis* and the open squares represent *Corbicula fluminea*. Vertical lines represent \pm s.e.m. and are present where they exceed the size of the symbol.

Table 3. Potassium influx kinetic coefficients for pondwater-acclimated mussels using Lineweaver-Burke analyses of double reciprocal plots

Species	N	J_{max} ($\mu\text{equiv g}^{-1}$ dry tissue h^{-1})	K_m (mmol l^{-1})
<i>Corbicula fluminea</i>	29	$3.56 \pm 0.09^{**}$	$0.27 \pm 0.01^{**}$
<i>Carunculina texasensis</i>	21	1.78 ± 0.08	0.16 ± 0.01

** Significantly different from *Ca. texasensis*, $P < 0.01$.

Table 4. Unidirectional rubidium fluxes in pondwater-acclimated mussels incubated in K^+ -free rubidium pondwater

Species	Bath [Rb^+]	N	Unidirectional fluxes ($\mu\text{equiv g}^{-1}$ dry tissue h^{-1})		
			J_{net}	J_i	J_o
<i>Corbicula fluminea</i>	0.04	16	0.37 ± 0.07	0.41 ± 0.06	0.03 ± 0.04
<i>Carunculina texasensis</i>	0.03	8	0.28 ± 0.02	0.28 ± 0.03	0.00 ± 0.01

The [Rb^+] was the average value during the flux study.

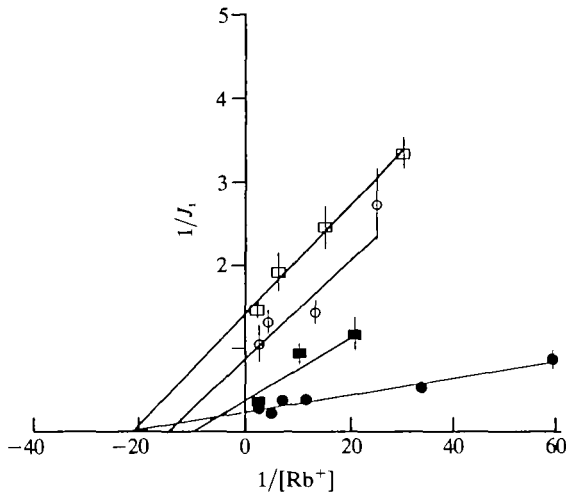


Fig. 4. Lineweaver-Burke double reciprocal plot of Rb^+ concentration (in mol l^{-1}) and Rb^+ influx (in $\mu\text{equiv g}^{-1}$ dry tissue h^{-1}) in pondwater-acclimated (open symbols) or salt-depleted (filled symbols) mussels. The animals were incubated in K^+ -free rubidium pondwater containing a range of $RbCl$ concentrations. Vertical lines are \pm S.E.M. (*Corbicula fluminea*, circles; *Carunculina texasensis*, squares).

pondwater was saturable, but the J_{max} for pondwater-acclimated mussels was significantly less ($P < 0.01$) than that for K^+ influx (Tables 3 and 5). It is interesting that the apparent affinity is significantly higher (lower K_m) for rubidium transport than for K^+ transport. Salt depletion of *Co. fluminea* stimulated Rb^+ uptake significantly and J_{max} was higher than that observed in pondwater-acclimated *Co. fluminea*; moreover, it was higher than the J_{max} for K^+ transport in pondwater-acclimated *Co. fluminea*. Salt depletion did not alter the apparent affinity for Rb^+ influx.

The same pattern was observed for Rb^+ influx kinetics in *Ca. texasensis* exposed to a range of $RbCl$ concentrations in K^+ -free pondwater (Fig. 4). There was a substantial reduction in the maximal influx of Rb^+ and it was about 56 % of the

Table 5. Rubidium influx kinetic coefficients for pondwater-acclimated (PW) or salt-depleted (SD) mussels in K^+ -free rubidium artificial pondwater using Lineweaver-Burke analyses of double reciprocal plots

Species	N	Acclimation medium	J_{max} ($\mu\text{equiv g}^{-1}$ dry tissue h^{-1})	K_m (mmol l^{-1})
<i>Corbicula fluminea</i>	40	PW	1.41 ± 0.02	0.058 ± 0.002
	33	SD	$5.87 \pm 0.10^{**}$	0.061 ± 0.002
<i>Carunculina texasensis</i>	29	PW	0.84 ± 0.12	0.051 ± 0.002
	11	SD	$3.34 \pm 0.24^{**}$	$0.102 \pm 0.014^{**}$

** Significantly different from pondwater-acclimated animals, $P < 0.01$.

J_{\max} for potassium (Tables 3 and 5). Rubidium uptake in *Ca. texasensis* was significantly less than in *Co. fluminea*, a characteristic that was noted also for K^+ transport. The K_m for Rb^+ uptake in *Ca. texasensis* was significantly lower than for K^+ influx, suggesting that the transport mechanism has a higher apparent affinity for Rb^+ (Tables 3 and 5; $P < 0.01$). Salt depletion significantly elevated the kinetic coefficients for Rb^+ in *Ca. texasensis* compared to those in pondwater-acclimated animals (Table 5).

Serotonin stimulates sodium transport in freshwater mussels (Dietz *et al.* 1982). To determine if serotonin affects Rb^+ transport, we placed *Co. fluminea* in K^+ -free Rb^+ pondwater with 0.1 mmol l^{-1} serotonin. Serotonin had no significant effect on Rb^+ uptake [Rb^+ J_i : control, 0.67 ± 0.14 ($N=6$); serotonin, $0.82 \pm 0.06 \mu\text{equiv g}^{-1} \text{ dry tissue h}^{-1}$ ($N=6$)]. However, the animals did respond to serotonin with increased foot movement, valve gaping, elevated sodium J_{net} and, in separate studies, they had an elevated J_i for sodium: control, 9.29 ± 2.97 ($N=4$); serotonin, $18.84 \pm 1.37 \mu\text{equiv g}^{-1} \text{ dry tissue h}^{-1}$ ($N=5$).

Barium is an effective channel blocker for basolateral K^+ channels and we examined the apical effects of Ba^{2+} on Rb^+ influx. Barium interfered with Rb^+ determination using the atomic absorption spectrometer in the emission mode, and we calculated the specific activity of Rb^+ in the initially K^+ -free Rb^+ pondwater bathing medium and monitored the disappearance of ^{86}Rb from the bath. We calculated the influx from the reduction in radioactivity of the bathing medium during the 1 h incubation, assuming a constant specific activity for Rb^+ . J_i for Rb^+ in control *Co. fluminea* was $0.79 \pm 0.03 \mu\text{equiv g}^{-1} \text{ dry tissue h}^{-1}$ ($N=6$) and J_i was not significantly changed in the presence of either 0.05 or 0.1 mmol l^{-1} Ba^{2+} [0.66 ± 0.06 ($N=4$); 0.73 ± 0.13 ($N=3$) $\mu\text{equiv g}^{-1} \text{ dry tissue h}^{-1}$, respectively].

Discussion

Maximal potassium influx into pondwater-acclimated unionid mussels is $1.8 \mu\text{equiv g}^{-1} \text{ dry tissue h}^{-1}$ and is equal to the maximal rate of sodium transport (Dietz, 1978). Potassium uptake by *Corbicula fluminea* is about twice as fast as in the unionids. However, the K^+ influx observed in *Co. fluminea* is significantly slower than the Na^+ transport (this study; McCorkle-Shirley and Dietz, 1980). In both bivalve species, the apparent affinities for K^+ are high, with similar values to those observed for Na^+ and Cl^- transport ($0.1\text{--}0.2 \text{ mmol l}^{-1}$) (Dietz, 1985; Prosser, 1973). High-affinity transport of K^+ would be physiologically appropriate as the K^+ concentration in natural pondwater is typically about 0.05 mmol l^{-1} . These data indicate that unfed freshwater mussels are capable of transporting K^+ across their epithelia in amounts sufficient to maintain a steady state or a net accumulation. Preliminary data suggest the site of K^+ transport is the gill tissue (T. H. Dietz, unpublished observations).

The transepithelial electrical potential in the unionid *L. subrostrata* in pondwater is about -15 mV (body fluids negative) and it is -7 mV in *Co. fluminea* in

0.5 mmol l⁻¹ Na₂SO₄ (Dietz and Branton, 1975; McCorkle-Shirley and Dietz, 1980). Coimbra *et al.* (1988) measured the TEP in outer mantle epithelia in an Ussing chamber as -23 to -41 mV (with the rather high [K⁺] of 7 mmol l⁻¹ in the saline solution). For the range of TEP from -15 to -41 mV, the flux ratio equation (Ussing, 1949) suggests that J_o should be 2–6 times greater than J_i in *Ca. texasensis* and *L. subrostrata* if fluxes are all passive. For *Co. fluminea*, with a TEP ranging from -7 to -41 mV, passive J_o should be 4–14 times greater than J_i . Yet, we observed that the mussels could take up K⁺ from dilute potassium solutions. These data indicate that active epithelial K⁺ transport makes a significant contribution to bivalve potassium balance.

Rubidium is not a 'perfect' substitute for potassium in freshwater mussels. The Rb⁺ fluxes are nearly equivalent to the K⁺ fluxes only at the low concentrations present in artificial pondwater. They are about 44–60% less than K⁺ influx at higher Rb⁺ concentrations in pondwater-acclimated animals, as noted previously (Grubb *et al.* 1988; Sanders and Kirschner, 1983a). In addition to the lower influxes, the K_m values for Rb⁺ influx are statistically less than the K_m for potassium influx, suggesting a higher transport affinity for Rb⁺. However, a K_m value of 0.05 mmol l⁻¹ is reasonably consistent with transport affinities noted for a variety of freshwater animals (Prosser, 1973). Although Rb⁺ is not an exact substitute for K⁺, it is useful considering the practical limitations of ⁴²K isotope studies. It is important that investigators be aware of the potential limitations that this study illustrates, and perhaps it would be better to substitute Rb⁺ for K⁺, and not to use ⁸⁶Rb in a K⁺ medium and assume that rubidium is 'behaving' as a tracer for elemental K⁺ (see Grubb *et al.* 1988).

Rubidium transport was stimulated by salt depletion in both *Co. fluminea* and *Ca. texasensis*, suggesting that an endogenous control mechanism for regulating K⁺ transport is present. We do not know what factors may be involved in regulating K⁺/Rb⁺ fluxes, but serotonin does not change Rb⁺ uptake rates. We have found that serotonin stimulates only Na⁺ transport in freshwater bivalves (Dietz *et al.* 1982). As mussels will live for months in deionized water, with little change in intracellular [K⁺], they must have the ability to regulate and preserve K⁺, as well as other ions, in order to survive these conditions (Murphy and Dietz, 1976). Compared with other freshwater animals, freshwater mussels seem to be unique in their adaptation to low levels of ionic constituents in their body fluids (Krogh, 1939; Prosser, 1973; Dietz, 1985).

The turnover of K⁺ in freshwater clams is very high. Our estimate of the K⁺ content in *L. subrostrata* is 57 μ equiv g⁻¹ dry tissue (Murphy and Dietz, 1976). The influx of K⁺ of 0.4 μ equiv g⁻¹ dry tissue h⁻¹ would indicate that 17% of the animal's potassium is exchanged daily. The ability to accumulate K⁺ by epithelial transport is probably important in bivalve mineral balance. In the laboratory, when mussels are stored unfed, the epithelial uptake is their only means of maintaining ionic balance. The importance of epithelial transport mechanisms is further emphasized by the observation that many of the bivalve species can be maintained in aquaria for over a year without feeding.

The basis for the difference in K^+/Rb^+ transport rates observed between the unionids and *Corbicula fluminea* is unknown. However, *Corbicula* is a more recent invader of fresh water and members of this genus are found in estuarine habitats. It has been noted that brackish-water animals usually have higher ionic turnover rates than their freshwater relatives (Prosser, 1973).

The presence of an epithelial transport system and perhaps passive epithelial permeability to K^+ may be the reason for the freshwater mussel's inability to survive when $[K^+]$ approaches 1 mmol l^{-1} in the environment. The sensitivity to even low concentrations of K^+ in these bivalves is unusual, since fish, amphibians and other freshwater invertebrates can be acclimated to KCl solutions (approx. 1 mmol l^{-1}) for prolonged periods (Krogh, 1939). Krogh noted that some invertebrates (e.g. crustaceans) were also capable of accumulating K^+ at rates nearly equal to Na^+ transport. This feature is notably different from the freshwater vertebrates, in which K^+ transport is usually slower than Na^+ transport.

The magnitude of net flux of potassium in the freshwater clams bathed in solutions having the moderately elevated $[K^+]$ of 0.36 mmol l^{-1} is substantial. In both *Co. fluminea* and *Ca. texasensis* the average net uptake of K^+ was $0.8\text{--}1.0 \mu\text{equiv g}^{-1} \text{ dry tissue h}^{-1}$. In 24 h, the animals would increase their tissue content by 34–38% if the net flux remained constant. One possible consequence of an imbalance between intracellular and extracellular $[K^+]$, if it occurred, would be depolarization of excitable tissues. This would explain the inability of the mussels to withdraw their foot or close the valves when stimulated (Daum *et al.* 1979). Moreover, the apparently swollen condition of the soft tissues suggests impaired kidney function. The heart is responsible for forming the ultrafiltrate in the pericardial chamber that drains into the kidney (Florey and Cahill, 1977), and high $[K^+]$ probably impairs cardiac contractility.

The results from this and other studies suggest that KCl may be an effective agent for controlling bivalve populations. *Corbicula fluminea* is a prolific breeder and has invaded many of the water-ways in the United States since its introduction in the 1920s (Britton and Morton, 1979; McMahan, 1982). It is possible that short-term treatment with KCl may be an effective mechanism for reducing mussel populations, with limited impact on other freshwater animals.

We want to thank Janice Horohov and Jewel Crockett for their technical assistance. We thank R. F. McMahan and the reviewers for their suggestions. This study was supported by NSF grant DCB87-01504.

References

- BRITTON, J. C. AND MORTON, B. (1979). *Corbicula* in North America: The evidence reviewed and evaluated. In *Proceedings, First International Corbicula Symposium* (ed. J. C. Britton), pp. 249–287. Fort Worth: Texas Christian University Research Foundation.
- BROOKS, S. P. J. AND SUELTER, C. H. (1986). Estimating enzyme kinetic parameters: A computer program for linear regression and non-parametric analysis. *Int. J. bio-med. Computing*, **19**, 89–99.

- COIMBRA, J., MACHADO, J., FERNANDES, P. L., FERREIRA, H. G. AND FERREIRA, K. G. (1988). Electrophysiology of the mantle of *Anodonta cygnea*. *J. exp. Biol.* **140**, 65–88.
- DAUM, K. A., NEWLAND, L. W., BRITTON, J. C., CHAMPAGNE, L. AND HAGEN, J. (1979). Responses of *Corbicula* to potassium. In *Proceedings, First International Corbicula Symposium* (ed. J. C. Britton), pp. 215–225. Fort Worth: Texas Christian University Research Foundation.
- DIETZ, T. H. (1978). Sodium transport in the freshwater mussel, *Carunculina texasensis* (Lea). *Am. J. Physiol.* **235**, R35–R40.
- DIETZ, T. H. (1985). Ionic regulation in freshwater mussels: a brief review. *Am. Malacol. Bull.* **3**, 233–242.
- DIETZ, T. H. AND BRANTON, W. D. (1975). Ionic regulation in the freshwater mussel, *Ligumia subrostrata* (Say). *J. comp. Physiol.* **104**, 19–26.
- DIETZ, T. H., SCHEIDE, J. I. AND SAINTSING, D. G. (1982). Monoamine transmitters and cAMP stimulation of Na transport in freshwater mussels. *Can. J. Zool.* **60**, 1408–1411.
- FLOREY, E. AND CAHILL, M. A. (1977). Hemodynamics in lamellibranch molluscs, Confirmation of constant-volume mechanism of auricular and ventricular filling. Remarks on the heart as site of ultrafiltration. *Comp. Biochem. Physiol.* **57A**, 47–52.
- GRAVES, S. Y. AND DIETZ, T. H. (1982). Cyclic AMP stimulation and prostaglandin inhibition of Na transport in freshwater mussels. *Comp. Biochem. Physiol.* **71A**, 65–70.
- GRUBB, B. R., BROWN, H. V. AND BENTLEY, P. J. (1988). Anomalous behaviour of ^{86}Rb as a tracer for transintestinal potassium transport in the fowl, *Gallus domesticus*. *J. exp. Biol.* **135**, 487–490.
- IMLAY, M. J. (1973). Effects of potassium on survival and distribution of freshwater mussels. *Malacologia* **12**, 97–113.
- KROGH, A. (1939). *Osmotic Regulation in Aquatic Animals*. Cambridge: Cambridge University Press.
- MCCORKLE-SHIRLEY, S. AND DIETZ, T. H. (1980). Sodium transport in the freshwater Asiatic clam *Corbicula fluminea*. *Biol. Bull. mar. biol. Lab., Woods Hole* **159**, 325–336.
- MCMAHON, R. W. (1982). The occurrence and spread of the introduced Asiatic freshwater bivalve, *Corbicula fluminea* (Müller), in North America, 1924–1982. *Nautilus* **97**, 56–58.
- MURPHY, W. A. AND DIETZ, T. H. (1976). The effects of salt depletion on blood and tissue ion concentrations in the freshwater mussel, *Ligumia subrostrata*. *J. comp. Physiol.* **108**, 233–242.
- PROSSER, C. L. (1973). *Comparative Animal Physiology*. Philadelphia: Saunders.
- SANDERS, M. J. AND KIRSCHNER, L. B. (1983a). Potassium metabolism in seawater teleosts. I. The use of ^{86}Rb as a tracer for potassium. *J. exp. Biol.* **104**, 15–28.
- SANDERS, M. J. AND KIRSCHNER, L. B. (1983b). Potassium metabolism in seawater teleosts. II. Evidence for active potassium extrusion across the gill. *J. exp. Biol.* **104**, 29–40.
- USSING, H. H. (1949). The distinction by means of tracers between active transport and diffusion. *Acta physiol. scand.* **19**, 43–56.
- ZERAHN, K. (1983). Comparison between active transport of Tl^+ , K^+ and Rb^+ across the isolated short-circuited frog skin. *J. exp. Biol.* **107**, 65–72.