



TABLE 3. Unidirectional Na fluxes (microequivalents per gram dry tissue per hour) in pond water acclimated bivalves in 0.5 mM Na₂SO₄

Species	N	Dry tissue weight, g	Influx	Efflux
<i>M. hembeli</i>	10	1.43 ± 0.09 ^a	4.89 ± 0.86	1.36 ± 0.47 ^b
<i>A. grandis</i>	5	6.30 ± 0.79	0.53 ± 0.27	1.87 ± 1.19
<i>C. texasensis</i>	19	1.61 ± 0.13	1.14 ± 0.10	0.99 ± 0.14
	8	0.10 ± 0.00	1.35 ± 0.43	1.54 ± 0.36
<i>L. subrostrata</i>	8	3.07 ± 0.51	1.45 ± 0.31	1.40 ± 0.28
<i>C. manilensis</i>	17	0.21 ± 0.01	8.59 ± 0.74	6.82 ± 0.90
	8	0.07 ± 0.01	9.96 ± 2.35	7.95 ± 1.28
<i>S. transversum</i>	12	0.019 ± 0.002	20.67 ± 2.97	29.91 ± 7.42

^aMean ± SEM.^bSignificantly different from influx, $P < 0.01$.

The differences among the Unionacea are rather small but some are significant.

Sodium transport rates in *C. texasensis* placed in 1 mM NaCl were $J_i = 1.30 \pm 0.20$ and $J_o = 0.99 \pm 0.28$ μ equiv/g dry tissue per hour ($N = 10$). Since J_i is equal to J_o , pond water acclimated animals are capable of maintaining a steady state in dilute NaCl solutions. To observe anion-independent Na transport, the animals were placed in 0.5 mM Na₂SO₄ solutions (Table 3). Sulfate is a nonpenetrating anion (Dietz 1978).

All of the species studied were able to transport Na from Na₂SO₄ solutions, thereby demonstrating anion independence of Na uptake. Sodium transport rates among the Unionacea were similar. The J_i^{Na} in *A. grandis* was slightly lower than the other species. The reduced Na influx may be due to the large size (lower surface area per gram tissue). Sodium influx in *Margaritifera hembeli* was significantly higher than other Unionacea. This may be due to a handling response because similar results have been obtained under a variety of conditions. *Margaritifera* is in a positive Na balance (net uptake) for 6–12 h after placing the animal in the bathing solution to measure flux rates. Similar results have been observed when the experiment was started at the beginning or end of the photoperiod or when the animals were acclimated to constant light. Table 4 presents the net fluxes of Na and Cl when *M. hembeli*, acclimated to constant light, was transferred from pond water to a small container of pond water (100 mL). During the first 6 h the animals accumulated Na then stabilized J_n^{Na} . The animals were in a negative Cl balance.

The Sphaeriacea have significantly higher Na transport rates than the Unionacea (Table 3). The Sphaeriacea are smaller animals and this could be responsible, in part, for the elevated Na turnover. However, the two size classes of *C. texasensis* and *C. manilensis*, differing in weight by an order of

magnitude, indicate Na turnover rate in bivalves is remarkably independent of body size. Sodium transport is significantly greater in *S. transversum* than *C. manilensis*. Again, size may account for some of the difference in fluxes. An alternative explanation is the presence of developing young in the branchial chamber of *S. transversum* (Dietz and Stern 1977). The numerous small bivalves in the gill chamber may be contributing to the high Na metabolism.

Chloride transport is independent of cation fluxes. Chloride is taken up from 1 mM choline chloride; choline is an impenetrable cation. Choline influx in *C. texasensis* is 0.05 ± 0.02 μ equiv/g dry tissue per hour ($N = 8$). A similar rate of choline transport has been measured in *L. subrostrata*. With the exception of *M. hembeli*, all of the species were in a Cl-steady state, $J_i = J_o$ (Table 5). The Cl turnover rate is similar among the Unionacea. Although the Cl transport rate between Sphaeriacea is similar, J_i^{Cl} is six-times higher than found in Unionacea.

Trans epithelial electrical potentials were measured in *C. texasensis* and *C. manilensis*. When the animals were siphoning pond water, the inside (body fluid) was -6 ± 1 mV ($N = 7$) for *C. texasensis* and -12 ± 3 mV ($N = 3$) for *C. manilensis*. Previous studies have shown that trans epithelial electrical potential in bivalves is a Ca-dependent

TABLE 4. Time course of net Na and Cl flux (microequivalents per gram dry tissue per hour) when *M. hembeli* is transferred to pond water ($N = 7$)

Hour interval	J_n^{Na}	J_n^{Cl}
0–6	2.82 ± 0.66	0.00 ± 0.31
6–19	-0.51 ± 0.33	-0.89 ± 0.27
19–24	0.54 ± 0.74	-0.12 ± 0.46
24–32	0.31 ± 0.26	-0.25 ± 0.41
32–42	0.11 ± 0.23	-0.33 ± 0.33

TABLE 5. Unidirectional Cl fluxes (microequivalents per gram dry tissue per hour) in pond water acclimated bivalves in 1.0 mM choline chloride

Species	N	Dry tissue weight, g	Influx	Efflux
<i>M. hembeli</i>	5	2.05 ± 0.15 ^a	1.45 ± 0.20	2.87 ± 0.26 ^b
<i>A. grandis</i>	9	6.48 ± 0.55	0.93 ± 0.20	0.86 ± 0.25
<i>C. texasensis</i>	18	1.26 ± 0.08	1.10 ± 0.10	1.38 ± 0.15
<i>L. subrostrata</i>	10	2.50 ± 0.17	1.03 ± 0.10	1.37 ± 0.12
<i>C. manilensis</i>	10	0.18 ± 0.02	9.13 ± 0.95	8.41 ± 1.53
<i>S. transversum</i>	9	0.018 ± 0.001	8.96 ± 1.15	10.80 ± 1.84

^aMean ± SEM.^bSignificantly different from influx, $P < 0.01$.

diffusion potential (Dietz and Branton 1975). Therefore, the higher blood Ca concentration in *C. manilensis* may be responsible for the difference in voltage.

Discussion

Freshwater bivalves maintain Na and Cl balance by independent ion transport systems. Sodium is transported from 0.5 mM Na₂SO₄ solutions and chloride is taken up from 1 mM choline chloride solutions. Among the Unionacea, the rate of Na or Cl transport is about 1 µequiv/g dry tissue per hour. These transport rates are similar to those reported previously for bivalves exposed to dilute NaCl solutions (Dietz and Branton 1975; Dietz 1977). *Margaritifera hembeli* was unusual in its high rate of Na influx (three to four times the efflux), this transport rate is similar to influxes noted in salt-depleted *C. texasensis* (Murphy and Dietz 1976; Dietz 1978). It is noteworthy that *M. hembeli* were in a negative Cl balance at the same time. These data emphasize the independence of cation and anion transport systems.

The Sphaeriacea are significantly different with regard to the rates of Na and Cl turnover from the Unionacea. Chloride influx in Sphaeriacea was about 10 µequiv/g dry tissue per hour. Sodium influx in *C. manilensis* was about 10 µequiv/g dry tissue per hour; however, values for *S. transversum* were twice as high. These data indicate that size has less influence on transport rates than do the phylogenetic relationships of the species.

Expressing the flux rates on soft tissue weight does not change the relationships between superfamilies noted above. Unionacea J_1 values for Na and Cl are about 0.5–2 µequiv/10 g wet tissue per hour. The J_1^{Na} values for Sphaeriacea are 7–8 µequiv/10 g wet tissue per hour and the J_1^{Cl} values for *C. manilensis* and *S. transversum* are 7 and 4 µequiv/10 g wet tissue per hour, respectively. In comparison, amphibian Na and Cl uptake is about 1–3 µequiv/10 g per hour (Alvarado and Dietz 1970; Alvarado *et al.* 1975); fish Na and Cl uptake is 2–3

µequiv/10 g per hour (Maetz *et al.* 1976; Kerstetter and Kirschner 1970, 1972); and crayfish Na and Cl uptake is 5–7 µequiv/10 g per hour (Maetz *et al.* 1976).

Mussels acclimated to pond water will survive, unfed, for months. Body fluid composition is maintained essentially in a steady state (Dietz and Branton 1975). The electrical potential (–6 to –12 mV) is inadequate to account for the observed flux ratios (Ussing 1949; Dietz and Branton 1975; Dietz 1977). In the absence of convective ion movement (solvent drag) in Unionacea (Dietz 1978), these mussels must be actively transporting Na and Cl into the body fluids. Sphaeriacea also must be actively transporting Na and Cl; however, the contribution of convective salt movement has not been studied.

Although sodium transport in *C. texasensis* is by a Na–H exchange system (Dietz 1978), there is no information available on the mechanism of Na transport in Sphaeriacea. Chloride transport apparently involves a Cl–HCO₃ exchange mechanism in Unionacea (unpublished observation). However, it is apparent that the rate of Cl uptake is independent of body fluid HCO₃ concentration. *Corbicula manilensis* has a high J_1^{Cl} but the lowest blood HCO₃ (4 mM/L). If blood HCO₃ is the source of substrate for a Cl–HCO₃ exchange system, apparently it is not rate limiting since there is no correlation between blood HCO₃ and Cl influx.

The Unionacea and the genus *Sphaerium* have had representatives inhabiting fresh water for the greatest length of time (Purchon 1977), and they display considerable similarity in blood solute composition. However, these animals differ significantly in rates of ion transport. Salt transport rates among the Unionacea are similar to other freshwater animals but *S. transversum* has a high salt turnover, similar to brackish-water animals (Prosser 1973). *Corbicula manilensis* maintains higher blood solute concentrations and transports salt at a higher rate than Unionacea. The tolerance of *C. manilensis* to hyperosmotic conditions and

the presence of other *Corbicula* species living in brackish water suggest that *C. manilensis* is a more recent immigrant into fresh water (Gainey 1978; Sinclair 1971).

The striking net uptake of Na in *M. hembeli* is of some interest. These animals were acclimated to pond water for a week or more, yet J_1^{Na} exceeded J_0^{Na} for several hours after handling the animals. The acclimation conditions may be responsible for this behavior. *Margaritifera hembeli* is the only species used in this study that lives in a fast-flowing stream. Acclimation to still water in an aquarium may sensitize *M. hembeli* to the handling which accompanies the flux measurements. Although no information is available regarding the dissimilarity of Na and Cl transport in these animals, the observed differences support the complete independence of cation and anion transport mechanisms and their control.

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