

When  $P_i^{18O}$  and  $H_2^{16O}$  are present, the following approximates total exchange from average values of excess  $^{18O}$  in the  $P_i$ :

$$\frac{P_o^{18O_1}}{P + P_o} - 18O_2 = \text{atom \% excess } ^{18O} \text{ lost by exchange} \quad (1)$$

$$\frac{\text{atom \% excess } ^{18O} \text{ lost by exchange}}{^{18O_1}} = \text{fraction of exchange } (F_{ex}) \quad (2)$$

$$4 \text{ (average } P_i \text{ concentration) } \ln (1 - F_{ex}) = \text{mM } P_i \rightleftharpoons \text{HOH} \quad (3)$$

$$\text{(mM } P_i \rightleftharpoons \text{HOH exchange) (ml volume) = } \mu\text{atoms O exchange} \quad (4)$$

When  $P_i^{16O}$  and  $H_2^{18O}$  are present, the atom % excess  $^{18O}$  of the final  $P_i$  introduced by exchange is given by

$$^{18}O_2 - P \frac{^{18}O_w}{4(P_o + P)} = \text{atom \% excess introduced by exchange} \quad (5)$$

$$\frac{\text{atom \% excess introduced by exchange}}{^{18}O_w} = \text{fraction exchange } (F_{ex}) \quad (6)$$

Millimolarity of  $P_i \rightleftharpoons \text{HOH}$  exchange and  $\mu$ atoms total exchange may be calculated according to equations 3 and 4.

Determination of the  $P_i \rightleftharpoons \text{ATP}$  and  $\text{ATP} \rightleftharpoons \text{HOH}$  Exchanges. The  $P_i \rightleftharpoons \text{ATP}$  exchange was determined by use of  $^{32}P$  with separation of  $P_i$  from adenine nucleotides by extraction of the phosphomolybdate complex (19).  $^{18O}$  in the ATP was determined by adsorption of nucleotides on charcoal followed by acid hydrolysis to liberate the  $\beta$ - and  $\gamma$ -phosphoryl groups and measurement of the  $^{18O}$  in the  $P_i$  formed (20).

## II. RESULTS

Effects of  $Na^+$  and  $K^+$  on the  $P_i \rightleftharpoons \text{HOH}$  Exchange. In the absence of added ADP or ATP and in the presence of  $K^+$  and  $Mg^{2+}$ , the membrane-bound