

FURTHER STUDIES ON THE KINETICS OF OSMOSIS IN LIVING CELLS

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In a series of papers (1-5) it has been shown that a study of the kinetics of osmotic swelling and shrinking of the *Arbacia* egg may yield information concerning an important property of the cell—*viz.*, the ease with which water can enter or leave it, under the influence of osmotic forces. This permeability of the cell to water has been shown to be affected by many factors, such as temperature, specificity and valence of ion, etc.

The earliest study of the kinetics of osmotic swelling of cells was made by Lillie (6). He showed that the course of the process may be described by the equation which governs the course of a unimolecular chemical reaction. The velocity constant of the process, given by this equation, was used in our earlier papers as a measure of the permeability of the cell to water. It was found that the "permeability," measured in this way, depended, among other factors, upon the salt concentration of the solution in which the cells were swelling or shrinking (3). Northrop (7), in an investigation of the theory of osmotic swelling, showed that the unimolecular equation was, in this case, devoid of any particular physical significance, and developed an equation which satisfactorily described the course of osmotic swelling in the *Arbacia* egg. Using the data published by us, he investigated the effect of concentration upon permeability (now differently defined) according to his theoretical treatment. This new permeability constant proved to be much less affected by concentration, although, with the data available to him, there was still an appreciable effect.

This reopened the question of effect of salt concentration, and we wished to inquire whether the data indicate a true change in the per-

meability of the cell with changing concentration of the external medium. To this end we have made a more extensive series of experiments. As our attention had been called to the empirical nature of the Lillie equation prior to the appearance of Northrop's paper, and as we had already developed and applied an equation whose derivation differs somewhat from that of Northrop's, we shall include in this paper our theoretical treatment, and apply it, together with Northrop's, to the new data.

Theory

That the *Arbacia* egg constitutes an osmotic system is suggested by the simple observation of its swelling or shrinking when placed in a medium whose osmotic pressure differs from that of sea water. To account for the experimental data quantitatively in terms of the known laws governing osmotic processes, it is necessary to make certain assumptions concerning the cell and its surroundings:

1. The *Arbacia* egg consists of a solution of osmotically active substances, surrounded by a semipermeable membrane.

The fact that a fraction of cell volume is occupied by osmotically inactive material is neglected for the moment for the sake of simplicity, but will be introduced later as a correction.

2. The aqueous systems concerned obey the laws of ideal dilute solutions.

3. Only osmotic forces are concerned in the passage of water across the surface of the egg.

Assumptions 1 to 3 have been discussed in a previous communication (8).

4. The resistance to the diffusion of water is confined to the surface of the egg.

This neglects the time required to equalize concentration differences within the egg itself, as compared with that required for the water to diffuse across the membrane. It is made in the interests of simplicity of mathematical treatment.

5. The resistance to the diffusion of water, per unit area of cell surface, is constant.

This assumption in effect neglects any change in the properties of the membrane as the cell swells or shrinks. In the absence of defi-

nite knowledge concerning the structure of the membrane, this seems to be the most general method of treatment. Northrop (7), however, has dealt with this problem differently; a comparison of the resulting theories will be made in the present paper.

These assumptions permit the development of a theory which shall attempt to account, quantitatively, for the experimental facts of swelling and shrinking. It is evident that when an *Arbacia* egg is placed in a solution the osmotic pressure of which is not equal to that of the interior of the egg, water will be transported across the membrane under the influence of the outstanding difference in pressure on the two sides. This transfer takes place, according to the laws governing such processes, in such a direction as to tend to equalize the difference in pressure—*i.e.*, from the more dilute to the more concentrated medium. The egg, being a closed system, will consequently gain or lose water, and will finally come into a condition of equilibrium, when the osmotic pressure of the interior equals that of the surrounding medium. This gain or loss of water is equal to, and may be directly measured by, the change in volume of the egg.

When in equilibrium with the external solution, we have already shown (8) that the product of pressure and volume of these cells is, as a first approximation, constant, and that

$$P_{ex} V_e = P_o V_o \quad (I)$$

Here, P_{ex} is the osmotic pressure of a solution with which the cell is in equilibrium, and therefore is also the pressure inside the egg; V_e is the cell volume at equilibrium; P_o and V_o are pressure and volume of the egg in ordinary sea water.

In the present paper we are dealing chiefly with cells not in equilibrium with the external solution and must therefore assume that the pressure-volume product is constant also under this condition. We write,

$$PV = P_o V_o \quad (I a)$$

where P and V are pressure and volume of the cell at any time.

When the egg is not in equilibrium with the external medium, we observe the process of swelling or of shrinking. According to assumption 5 the rate of transfer of water across unit area of membrane de-

pends only on the available pressure difference, and is proportional to it. Consequently the rate of transfer of water into or out of the egg will be proportional to the area of its surface, and to the difference in osmotic pressure between the interior and the external medium. This rate of transfer of water for the entire egg is measured directly by its rate of change of volume, and we write

$$\frac{dV}{dt} = k \cdot S \cdot (P - P_{ex}) \quad (\text{II})$$

Here $\frac{dV}{dt}$ is the rate of change of volume of the egg; S is the area of the surface, P is the osmotic pressure of the interior of the egg, P_{ex} that of the surrounding medium, k is a factor of proportionality, which we shall term the *permeability of the cell to water*.*

It is seen that the equation holds equally for swelling ($\frac{dV}{dt} > 0$) or shrinking ($\frac{dV}{dt} < 0$), and is so written that k is always a positive number. Moreover, it satisfies the condition for equilibrium ($\frac{dV}{dt} = 0$), that the internal pressure equal that of the external medium.

Equation II cannot be integrated as it stands. However, Equation Ia furnishes the necessary relation between the internal osmotic pressure, P , and the volume of the egg. P_{ex} is a constant in the integration; for the sake of symmetry we shall, however, introduce the constant V_0 given by Equation I. S is readily expressed in terms of V , and we have:

$$\frac{dV}{dt} = k (36 \pi)^{\frac{1}{3}} \cdot P_0 V_0 \cdot V^{\frac{2}{3}} \left(\frac{1}{V} - \frac{1}{V_0} \right) \quad (\text{II } a)$$

* This definition of permeability is seen to possess a definite physical meaning *viz.*, the number of cubic micra of water entering the cell per minute per unit area of membrane, per atmosphere of difference in osmotic pressure between interior and external medium. This definition of permeability has been used in our more recent papers (4, 5); its value may be computed directly from the graph of the swelling or shrinking processes.

In this differential equation the variables are the time, t , and the volume of the egg, V ; all other terms are constant. On integration we obtain the equation governing the expected course of swelling or shrinking:

$$k(36 \pi)^{\frac{1}{3}} \cdot P_o V_o \cdot t = V_o \left[V_o^{\frac{1}{3}} \left(\frac{1}{2} \ln \frac{V_o^{\frac{2}{3}} + (V_o V)^{\frac{1}{3}} + V^{\frac{2}{3}}}{(V_o^{\frac{1}{3}} - V^{\frac{1}{3}})^2} + \sqrt{3} \tan^{-1} \frac{2 V^{\frac{1}{3}} + V_o^{\frac{1}{3}}}{\sqrt{3} V_o^{\frac{1}{3}}} \right) - 3 V^{\frac{1}{3}} \right]_{V_{t=0}}^V \quad \text{(III)}$$

where V is the volume of the eggs at time t . As indicated by the conventional notation, the term in the square brackets is to be taken between the limits V and $V_{t=0}$.*

The treatment given by Northrop is somewhat different. He considers two cases: (a) the membrane contains pores whose diameter

* We shall find it convenient subsequently to refer to the entire right hand side of this equation (without regard to limits) as $f(V, V_o)$, it being understood that in any one experiment of swelling or shrinking V_o is a constant, given by Equation I. We therefore write III simply

$$k(36 \pi)^{\frac{1}{3}} \cdot P_o V_o \cdot t = f(V, V_o) \Big|_{V_{t=0}}^V \quad \text{(III a)}$$

For purposes of computation, it is helpful to note that $f(V, V_o)$ is homogeneous in V and V_o and of degree $\frac{2}{3}$. We therefore have the identity

$$f(V, V_o) = (V_o)^{\frac{2}{3}} \cdot f\left(\frac{V}{V_o}, 1\right)$$

This has the distinct advantage that $f(\frac{V}{V_o}, 1)$ may be computed once for all for a number of values $\frac{V}{V_o}$; these values of f are then plotted against those of $\frac{V}{V_o}$ as a conversion chart. The computation of $f(V, V_o)$ is thus reduced to three steps:

1. Computation of $\frac{V}{V_o}$.
2. Finding, by means of the conversion chart, $f(\frac{V}{V_o}, 1)$.
3. Computation of $f(V, V_o)$ by the identity given above. The construction of the conversion charts—one for swelling ($\frac{V}{V_o} < 1$) and one for shrinking ($\frac{V}{V_o} > 1$)—forms the only laborious part of the work.

increases as the cell membrane is stretched in the swelling process; (b) the membrane, as it is stretched, does not alter in volume—its area increasing and its thickness decreasing. He then shows that both these assumptions lead to the same differential equation:

$$\frac{dV}{dt} = C_2 \cdot (36\pi)^{\frac{1}{2}} \cdot P_o V_o \cdot V^{\frac{1}{2}} \left(\frac{1}{V} - \frac{1}{V_o} \right) \quad \text{II} \quad (N)$$

from which he writes

$$C_2 (36\pi)^{\frac{1}{2}} P_o V_o \cdot t = V_o^{\frac{1}{2}} \left[\frac{1}{2} \ln \frac{V_o^{\frac{3}{2}} + (V_o V)^{\frac{1}{2}} + V^{\frac{1}{2}}}{(V_o^{\frac{3}{2}} - V^{\frac{1}{2}})^2} - \sqrt{3} \tan^{-1} \frac{2V^{\frac{1}{2}} + V_o^{\frac{1}{2}}}{\sqrt{3} V_o^{\frac{1}{2}}} \right]_{V_t=0}^V \quad \text{III} \quad (N)$$

where the notation is as in III.* It is to be noted that Northrop's "C₂" is different from the *k* of II and III.

EXPERIMENTS

The method employed in the present study is the same as has been previously described. Briefly stated, unfertilized eggs from a single specimen of *Arbacia punctulata* are placed in sea water which has been diluted with sufficient distilled water to give a solution having the desired osmotic pressure. Temperature control is accurate to $\pm 0.5^\circ\text{C}$. With an ocular micrometer and low power objective, the diameter of an egg is measured at minute intervals. Since the cells are spherical, volume can be calculated from diameter. Each volume recorded in this paper represents the mean value of six cells.

The first group of experiments here reported were designed to answer the question, Is the permeability of the cell affected by the salt concentration of the medium? Cells were taken from undiluted (100 per cent) sea water and placed in 20, 40, and 60 per cent sea water,

* We have converted Northrop's notation to the form used in this paper.

We note once more that the right hand side is homogeneous in *V* and *V_o*: we may, therefore, use the same method of computation by a conversion chart. Indeed, the presence of so many terms which are common to both Equations III and III_N makes it possible to construct charts for both equations with very little additional labor.

respectively.* The course of swelling was followed for a number of minutes. Data obtained from three experiments of this character are given in Table I. The same data have been used in Fig. 1, where

$$\frac{1}{(36\pi)^{\frac{1}{2}} \cdot P_o V_o} \cdot f(V, V_o)$$

has been plotted against time. The resulting graphs are, in general, straight lines, showing that Equation III fits the data.**

Moreover, these straight lines are approximately parallel, showing that there is no effect of salt concentration of the medium on permeability, at least under these conditions. Values of permeability factor k are given in Table I; these values show no drift with concentration.

In seven other experiments, in which various concentrations of sea water—20, 30, 40, 50, 60, 70 and 80 per cent—were used in different combinations, and at temperatures ranging from 15 to 21°C., the permeability factor was not found to vary in any definite way with the osmotic pressure of the medium.

Similar results are obtained by applying Northrop's equation. This is found to fit the data quite as well as Equation III. Constants calculated by means of Northrop's equation are given in Table I as values of C_2 . These values also, it is seen, show no drift with change in concentration.

It is, therefore, concluded that under these conditions—that is, when cells previously in 100 per cent sea water are made to swell in various hypotonic dilutions of sea water, permeability as now defined is not affected by the osmotic pressure of the medium. The “velocity constant” of the unimolecular equation used in earlier papers has been shown to possess no physical significance, and the “concentra-

* By 20 per cent sea water, for example, is meant a solution consisting of 20 parts of sea water and 80 parts of distilled water.

** More accurately stated, the equation fits the data over the first few minutes of the experiment. The later points in the 20 per cent experiments are seen to rise above the straight line, indicating increase in permeability, which is probably due to injury, as cytolysis occurs a few minutes later. In contrast to this the later points in 60 per cent sea water (and especially in 70 and 80 per cent, as shown by unpublished experiments) tend to lie below the line, indicating that in these concentrations the equation does not fit the later part of the course of swelling.

tion effect" on this velocity constant is seen to be due to the empirical nature of the equation.

TABLE I

Data from three experiments (A, B, C) on the effect of salt concentration of the medium on permeability of the cell to water. The temperature was 15°C. The figures in the table must be multiplied by 100 to give the actual volumes in cubic micra. Each figure represents the mean volume of six cells. Volumes at times zero (0) have been obtained by extrapolation. In the bottom rows are given the values of the permeability factors obtained by the equation developed in this paper (k), and by Northrop's equation (C_2). The values of k indicate the number of cubic micra of water that pass through one square micron of cell surface per minute per atmosphere of pressure. The values of Northrop's constant are expressed in different units. It is seen that neither of these constants is affected by the salt concentration of the medium.

Experiment:	A			B			C		
Per cent sea water:	20	40	60	20	40	60	20	40	60
Time Min.									
0	(2294)	(2294)	(2294)	(1960)	(2105)	(2045)	(2300)	(2300)	(2310)
1	2368	2377	2344	2135	2240	2139	2447		2405
2	2543	2523	2447	2298	2358	2223	2666	2494	2494
3	2716	2606	2523	2471	2494	2289	2819	2646	2548
4	2850	2742	2582	2582	2591	2363	2914	2742	2616
5	2967	2845	2646	2742	2666	2428	3092	2887	2656
6		2914	2691	2903	2767	2480	3313	2962	2721
7	3233			3092			3538		
8	3348	3114	2809	3279	2914	2557	3894	3114	2845
9	3520			3556					
10	3629	3290	2898		3065	2646		3389	2940
11	3798								
12	3965	3440	2962		3216	2731		3642	2994
14		3580	3048		3348	2757			3059
k	0.051	0.052	0.051	0.058	0.055	0.055	0.050	0.049	0.050
$C_2 \times 10^6$	2.50	2.56	2.55	3.13	2.79	2.94	2.62	2.58	2.60

We have furthermore noted that Northrop's treatment, based on different assumptions of membrane structure, is also satisfactory for describing the experimental data. Moreover, his differently defined "permeability," C_2 , is also seen to be independent of the concentra-

tion of the external medium. Indeed, the equation $k = C_2 S$, which expresses the relation between Northrop's permeability and ours, assures us that, if the constants be determined (graphically) always for the same volume of the egg, they will be proportional to one another. We conclude that the small effect of concentration noted

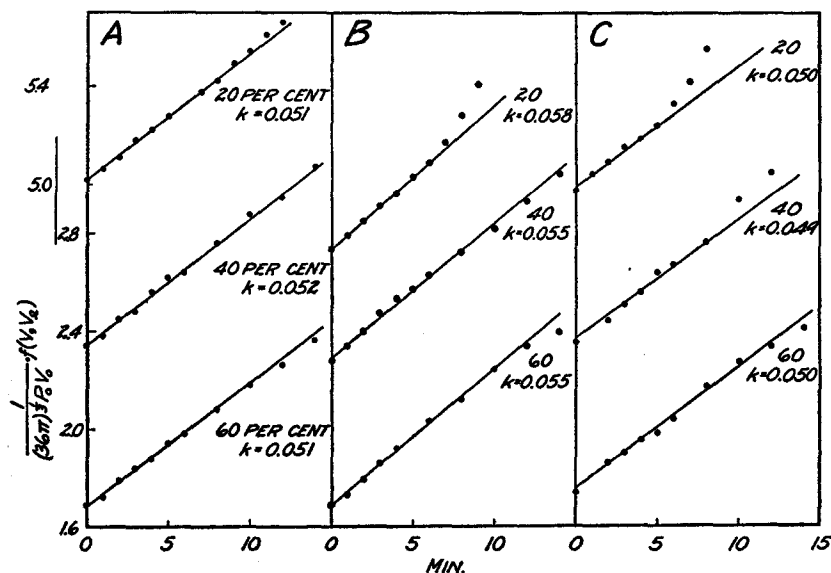


FIG. 1. The effect of salt concentration of the medium on the permeability of the cell to water. Data from three experiments (A, B, C) given in Table I, have been calculated by Equation III. When $\frac{1}{(36\pi)^{\frac{1}{2}} P_0 V_0} \cdot f(V, V_0)$ is plotted against time the resulting graphs are, in general, approximately parallel straight lines, the slopes of which are the values of the permeability factor. It is seen that the equation fits the data over the first several minutes; the deviations at later minutes are discussed in the text.

by Northrop was due to the fact that the scanty data available to him at that time were less reliable than the present.

That the two equations should agree so closely is explained when a numerical comparison of the two is made. It is then seen that the difference between the two becomes appreciable only in extremes of concentration which cannot be employed with this material, or at

volumes so close to equilibrium that the experimental errors mask any real differences.* In short, at the present time, it is impossible to choose between the two treatments on the basis of kinetics alone. In the absence of definite knowledge of membrane structure it is consequently a matter of indifference which is chosen.

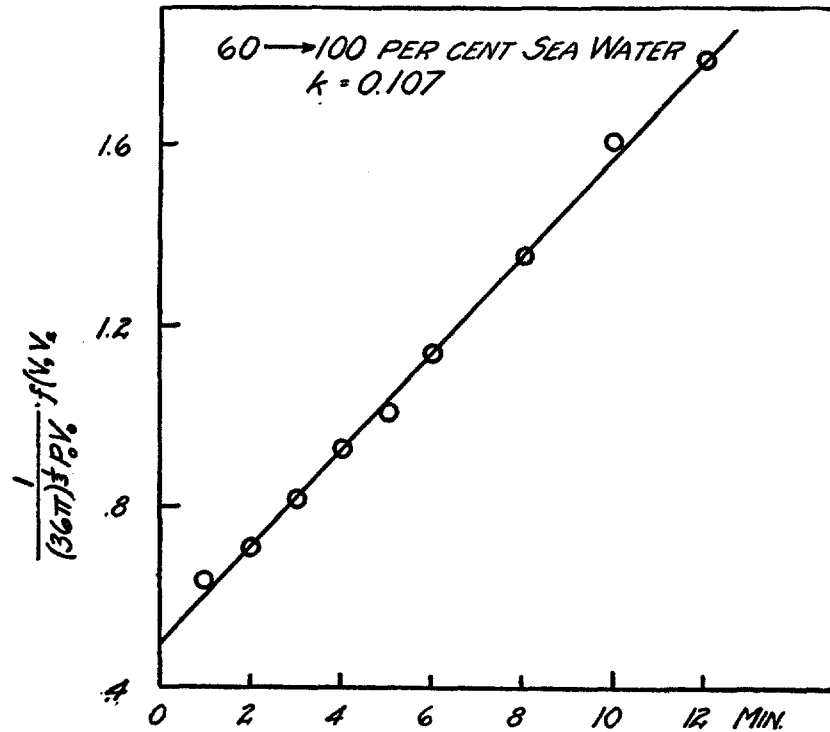


FIG. 2. The course of shrinking computed by Equation III. Cells previously swollen in 60 per cent sea water were returned to ordinary sea water in which they were measured during shrinking. The temperature was 15°C.

It is seen that a linear graph is obtained, showing that the equation fits the data.

As has been remarked, there is nothing in the derivation of the equation which in any way limits the treatment to swelling alone;

* This is largely due to the presence, in both equations, of the term $\ln(V_0^{\frac{1}{3}} - V^{\frac{1}{3}})$ which predominates over all the rest.

indeed it is found adequately to describe the shrinking process as well. This is shown to be the case in Fig. 2, which is typical of a large number of experiments. The cells, previously swollen in 60 per cent sea water, are returned to 100 per cent sea water and the course of shrinking measured. The plot of $\frac{1}{(36\pi)^{\frac{1}{3}} P_o V_o} \cdot f(V, V_o)$ against time is seen to be linear, indicating that the equation fits the data for shrinking. Northrop's equation describes the data equally well.

It is observed, however, that the value of k for shrinking is much greater than the values for swelling given in the preceding experiments. This difference has been found invariably in a large number of experiments in which swelling and shrinking have been compared.

A representative experiment is given in Table II. Cells have been measured while swelling in 60 per cent sea water at several temperatures. Other cells from the same animal, previously swollen in 60 per cent solution, have subsequently been measured while shrinking in ordinary sea water. Values of k , as determined by Equation III are given at the bottom of the table. It is seen that at corresponding temperatures, the value for shrinking is always greater than for swelling. The average ratio of shrinking to swelling in this experiment is 1.4.

Thus we reach the surprising conclusion that permeability, as defined by Equation III, is greater in shrinking than in swelling.

This at once suggests that Equation III may require modification. Indeed, one correction is already available. It was mentioned under assumption 1 that a fraction of cell volume is occupied by osmotically inactive material. Hence Equation Ia, heretofore used on account of its simplicity must be corrected for this fraction, which has been computed at 11 or 12 volume per cent (8). We now write for Ia

$$P(V - b) = P_o(V_o - b)$$

in which b is the volume occupied by osmotically inactive material.

Making the necessary substitutions in Equation IIa and integrating, we obtain

$$k(36\pi)^{\frac{1}{3}} \cdot P_o(V_o - b)t = (V_e - b) \left[\left(1 - \frac{b}{V_e}\right) \cdot V_e^{\frac{1}{3}} \left(\frac{1}{2} \ln \frac{V_e^{\frac{2}{3}} + (V_e V)^{\frac{1}{3}} + V^{\frac{1}{3}}}{(V_e^{\frac{1}{3}} - V^{\frac{1}{3}})^2} \right) + \sqrt{3} \tan^{-1} \frac{2V^{\frac{1}{3}} + V_e^{\frac{1}{3}}}{\sqrt{3}V_e^{\frac{1}{3}}} - 3V^{\frac{1}{3}} \right]_{V_t=0}^V \quad (IV)$$

TABLE II

Permeability to water during swelling compared with that during shrinking at several temperatures. The upper half of the table represents the course of swelling in 60 per cent sea water, the lower half, the course of shrinking of cells returned from 60 per cent sea water to ordinary sea water. Permeability has been computed by Equation III (k_3) and by Equation IV (k_4), b has been taken as 12 per cent of the volume of cells in ordinary sea water. It is seen that there is less difference in the values of k_4 in swelling and shrinking than in the values of k_3 .

Each figure represents the mean volume of six cells. The figures must be multiplied by 100 to obtain volumes in cubic micra. The mean volume of 20 control cells in ordinary sea water was $2033 \times 10^2 \mu^3$.

	Time	12°	15°	18°	21°	24°
Course of swelling	<i>min.</i>					
	1	2276	2187	2317	2331	2313
	2	2368	2253	2428	2447	2471
	3	2400	2322	2504	2557	2577
	4	2447	2381	2548	2631	2691
	5	2485	2437	2606	2696	2778
	6	2509	2494	2651	2731	2834
	8	2596	2572	2757	2819	2903
	10	2646	2681	2834	2850	2978
	12	2716	2721	2887	2914	
	14	2783	2778	2967	2967	
	16	2834	2809	3016	3000	
	18	2850	2809	3026	3037	
	20	2898	2876	3070	3081	
	22	2919	2898			
	24	2940				
	k_3	0.043	0.051	0.071	0.107	0.135
	k_4	0.047	0.059	0.079	0.111	0.156
Course of shrinking	1	2871	2819	2861	2757	2606
	2	2772	2716	2778	2596	2428
	3	2691	2666	2606	2485	2344
	4	2631	2562	2523	2381	2209
	5	2562	2494	2461	2326	2179
	6	2499	2447	2400	2244	2152
	8	2442	2353	2313	2165	2101
	10	2395	2285	2262	2109	2092
	12	2335	2227	2240	2092	2079
	14	2335	2218	2205		
	16	2298				
	k_3	0.067	0.074	0.098	0.142	0.175
	k_4	0.059	0.067	0.086	0.128	0.157

Equation IV has been found to fit the data, if anything, a little better than Equation III.* Applying it to the data of Table II, we obtain the values for permeability given in the bottom row. It is seen that k for swelling is slightly increased while k for shrinking is distinctly reduced. The average ratio of shrinking to swelling now becomes slightly greater than 1.1.**

TABLE III

Permeability to water during swelling in 60 per cent sea water compared with that during shrinking in cells returned from 60 per cent sea water to ordinary sea water. Permeability has been computed in several experiments by Equation III (k_3) and Equation IV (k_4). b has been taken as 12 per cent of the volume of cells in ordinary sea water. The mean ratio of shrinking to swelling is, for k_3 , 1.51; for k_4 , 1.25.

Temp.	Swelling	Shrinking	Ratio	Swelling	Shrinking	Ratio
°C.	k_3	k_3		k_4	k_4	
20	0.081	0.155	1.91	0.087	0.141	1.62
12	0.043	0.067	1.56	0.047	0.059	1.26
15	0.051	0.074	1.45	0.059	0.067	1.14
18	0.071	0.098	1.38	0.079	0.086	1.09
21	0.107	0.142	1.33	0.111	0.128	1.15
24	0.135	0.175	1.30	0.156	0.157	1.01
12	0.041	0.090	2.19	0.045	0.076	1.69
15	0.051	0.086	1.69	0.057	0.076	1.33
18	0.079	0.119	1.51	0.083	0.106	1.28
21	0.098	0.125	1.28	0.104	0.106	1.02
24	0.133	0.200	1.50	0.136	0.184	1.35
18	0.085	0.118	1.39	0.084	0.105	1.24
18	0.077	0.091	1.18	0.081	0.082	1.01

However, this ratio varies considerably in different experiments. In Table III, values of k_3 and k_4 are given for a number of experiments,

* A similar correction can of course be applied to Northrop's equation.

** While Equation IV describes the course of osmosis more accurately, it is relatively unwieldy. Therefore Equations II and III are to be preferred when no serious error is introduced by their use; this is the case in experiments in which cells from ordinary sea water are swelled in hypotonic dilutions.

together with the ratios of these permeability factors for shrinking and swelling. The mean ratio of shrinking to swelling when computed by Equation III is 1.51; by Equation IV is 1.25.

Thus Equation IV reduces the difference between shrinking and swelling by one-half, on the average. There still remains a significant difference between the two processes; water leaves the cell more readily than it enters. Consideration of the forces, such as elasticity and surface tension, and of mechanisms within the cell which might bring about this result will be made the subject of a future paper.

DISCUSSION

In the present paper a theoretical treatment of osmosis has been developed which we believe marks a step in advance. Permeability has been defined in terms having definite physical meaning. So defined, permeability is found no longer to be dependent on the osmotic pressure of the medium, and so we have simplified our conception of the mechanism by which the flow of water across the cell surface is regulated. Our working hypothesis in its present form has already been found useful in measuring changes in permeability brought about by various environmental factors. That the hypothesis is subject to further modification is suggested by the observations that permeability, as we have defined it, is not constant after the first few minutes of the swelling and shrinking processes, and that its numerical value is greater in shrinking than in swelling.

SUMMARY

Using unfertilized eggs of *Arbacia punctulata* as natural osmometers an attempt has been made to account for the course of swelling and shrinking of these cells in anisotonic solutions by means of the laws governing osmosis and diffusion. The method employed has been to compute permeability of the cell to water, as measured by the rate of volume change per unit of cell surface per unit of osmotic pressure outstanding between the cell and its medium.

Permeability to water as here defined and as somewhat differently defined by Northrop is approximately constant during swelling and shrinking, at least for the first several minutes of these processes.

Permeability is found to be independent of the osmotic pressure of the solution in which cells are swelling.

Water is found to leave cells more readily than it enters, that is, permeability is greater during exosmosis than during endosmosis.

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