SYMPOSIA
OF THE SOCIETY FOR EXPERIMENTAL BIOLOGY

NUMBER XIX

THE STATE AND MOVEMENT OF WATER IN LIVING ORGANISMS

CAMBRIDGE UNIVERSITY PRESS

SYMPOSIA OF THE SOCIETY FOR EXPERIMENTAL BIOLOGY

NUMBER XIX

THE STATE AND MOVEMENT OF WATER IN LIVING ORGANISMS

Published for The Company of Biologists
on behalf of the Society for Experimental Biology

CAMBRIDGE: AT THE UNIVERSITY PRESS
1965

PUBLISHED BY
THE SYNDICS OF THE CAMBRIDGE UNIVERSITY PRESS
Bentley House, 200 Euston Road, London, N.W.1
West African Office: P.O. Box 33, Ibadan, Nigeria

Printed in Great Britain at the University Printing House, Cambridge
(Brooke Crutchley, University Printer)

PREFACE

As long ago as 1913 L. J. Henderson, in his classic *The Fitness of the Environment*, drew attention to the unique physical properties of water and their profound biological significance. Later biologists, while accepting Henderson's view of the importance of water, have done comparatively little to amplify it, or to examine critically their concepts of the physical state of water in cells and of the mechanisms by which it is transported. The nineteenth Symposium of the Society for Experimental Biology was organized in the belief that discussion of these topics between biologists and physicists was overdue. One indication of the unsatisfactory state of the subject that was evident at the meeting was that different terminology for the forces which bring about water movement was used by soil scientists, plant physiologists and zoologists, and even by specialists of the same sort. The time does not seem ripe yet for an attempt to impose uniformity but the reader may be directed to the excellent exposition of these matters by Drs R. O. Slatyer and W. R. Gardner on pp. 113–15.

The Symposium was held in Swansea from 8 to 12 September 1964, by kind invitation of the University College of Swansea. The Society is indebted to the University College for its hospitality and for the provision of facilities and to members of its academic and technical staffs for their generous help in organizing the meeting.

Professor J. Edelman acted as Symposium Secretary, Professor J. Dainty, Dr P. Tuft and Professor P. E. Weatherley gave invaluable help in arranging the programme and Dr Helgi Öpik was Local Secretary. The indexes were prepared by Miss Phoebe Northcroft. To these and to the Cambridge University Press for its assistance in the preparation of this volume the Editor wishes to express his deep appreciation and thanks.

G. E. FOGG

Editor of the nineteenth Symposium of the Society for Experimental Biology

CONTENTS

I THE PHYSICAL BACKGROUND

II WATER IN THE PLANT

III WATER IN THE ANIMAL

PART I

THE PHYSICAL BACKGROUND

TABLES OF SOME PHYSICAL AND CHEMICAL PROPERTIES OF WATER

COMPILED BY PETER G. KOHN
School of Biological Sciences, University of East Anglia

The following data represent only a very small part of the total work on the properties of water. The most recent comprehensive review of the properties of ordinary water (H_2O) is that of Dorsey (1940). For data on heavy water (D_2O) the reviews of Kirshenbaum (1951) and Dirian (1962) are particularly useful. In addition, much information about water can be found in the standard reference works such as the *Handbook of Chemistry and Physics* (1962).

It must be emphasized that the majority of these tables are for pure water and the parameters listed are often substantially altered by the presence of dissolved solutes. This will usually be due not only to the properties of the solute itself but also to the change in the structure of water produced by that solute. Good discussions of the effects of dissolved electrolytes can be found in such texts as Harned & Owen (1957) and Robinson & Stokes (1959). More detailed analyses of the changes in structure have been made by Frank & Quist (1961) and by Némethy & Scheraga (1962*a*, *b*, *c*, 1964). For information about the chemical and physical properties of natural waters see Hutchinson (1957) for fresh waters and Sverdrup, Johnson & Fleming (1942) and Hill (1962) for sea waters.

GENERAL REFERENCES

DIRIAN, J. (1962). *Constantes Physiques des Variétés Isotopiques de l'Eau* (*^{17}O—^{18}O—D—T*), Bibliographie no. 15, Service de Documentation, Commissariat à l'Énergie Atomique, Centre d'Études Nucléaires de Saclay, B. P. no. 2, Gif-sur-Yvette (S.-et-O.).

DORSEY, N. E. (1940). *Properties of Ordinary Water Substance*, American Chemical Society Monograph no. 81. New York: Reinhold.

FRANK, H. S. & QUIST, A. S. (1961). *J. chem. Phys.* **34**, 604.

Handbook of Chemistry and Physics (1962). 44th ed. Cleveland: Chemical Rubber Publishing Co.

HARNED, H. S. & OWEN, B. B. (1957). *The Physical Chemistry of Electrolytic Solutions*, American Chemical Society Monograph no. 137, 3rd ed. New York: Reinhold.

HILL, M. N. (ed.) (1962). *The Seas*, vol. 1. New York and London: Wiley.

HUTCHINSON, G. E. (1957). *A Treatise on Limnology*, vol. 1. New York: Wiley.

KIRSHENBAUM, I. (1951). *Physical Properties and Analysis of Heavy Water*, National Nuclear Energy Series, Manhattan Project Technical Section, Division III–4A. New York: McGraw-Hill.

NÉMETHY, G. & SCHERAGA, H. A. (1962*a*). *J. chem. Phys.* **36**, 3382.
NÉMETHY, G. & SCHERAGA, H. A. (1962*b*). *J. chem. Phys.* **36**, 3401.
NÉMETHY, G. & SCHERAGA, H. A. (1962*c*). *J. phys. Chem.* **66**, 1773.
NÉMETHY, G. & SCHERAGA, H. A. (1964). *J. chem. Phys.* **41**, 680.
ROBINSON, R. A. & STOKES, R. H. (1959). *Electrolytic Solutions*, 2nd ed. London: Butterworths.
SVERDRUP, H. U., JOHNSON, M. W. & FLEMING, R. H. (1942). *The Oceans*. Englewood Cliffs, N.J.: Prentice Hall.

Thanks are due to Professor J. Dainty, Dr G. Wyllie and Dr F. Franks both for suggestions of sources of data and for a great deal of most helpful discussion.

MOLECULAR WEIGHT OF H_2O = 18·0160 (O = 16·0000)
MOLECULAR WEIGHT OF D_2O = 20·0338

The ratio of H to D in naturally occurring water is usually of the order of 6500 to 1, and no more accurate figure can usefully be given since this ratio is not a constant: considerable changes may result from naturally occurring fractionation processes.

VISCOSITY OF H_2O (η) IN CENTIPOISE (g. cm.$^{-1}$ sec.$^{-1} \times 10^{-2}$)

The standard reference value is normally taken as 1·002 at 20° C. (Swindells, Coe & Godfrey, 1952) and the temperature variation in the following table is based on the results of Coe & Godfrey (1944) and of Weber (1955).

T (° C.)	0	5	10	15	18	20	25	30	35	40	50	60	80
η	1·787	1·516	1·306	1·138	1·053	1·002	0·890	0·798	0·719	0·653	0·547	0·434	0·355

COE, J. R. & GODFREY, T. B. (1944). *J. appl. Phys.* **15**, 625.
SWINDELLS, J. F., COE, J. R. & GODFREY, T. B. (1952). *J. Res. nat. Bur. Stand.* **48**, 1.
WEBER, W. (1955). *Z. angew. Phys.* **7**, 96.

VISCOSITY OF D_2O (η) IN CENTIPOISE (g. cm.$^{-1}$ sec.$^{-1} \times 10^{-2}$)

There are fairly wide discrepancies between the values found by different authors. The values quoted are those of Hardy & Cottington (1949) but see also Timrot & Chynskaya, who give values about 2·5 % higher.

T (° C.)	5	20	40	60	80
η	1·974	1·243	0·782	0·547	0·411

HARDY, R. C. & COTTINGTON, R. L. (1949). *J. Res. nat. Bur. Stand.* **42**, 573.
TIMROT, D. L. & CHYNSKAYA, K. F. (1959). *Atomn. Energ.* **7**, 459.

DENSITY OF H_2O (g. ml.$^{-1}$)

These data are certainly reliable to the number of figures quoted.

T (° C.)	0° C.	2° C.	4° C.	6° C.	8° C.
0	0·99987	0·99997	1·00000	0·99997	0·99988
10	0·99973	0·99953	0·99927	0·99897	0·99862
20	0·99823	0·99780	0·99733	0·99681	0·99626
30	0·99568	0·99506	0·99440	0·99372	0·99300
40	0·99225	—	—	—	—

Owen, B. B., White, J. R. & Smith, J. S. (1956). *J. Amer. chem. Soc.* **78**, 3561.
Stott, V. & Bigg, P. H. (1928). *Int. crit. Tables*, **3**, 24.
Tilton, L. W. & Taylor, J. K. (1937). *J. Res. nat. Bur. Stand.* **18**, 205.

DENSITY (ρ) OF D_2O (g. ml.$^{-1}$)

The agreement between different authors is poor. The following data are taken from Chang & Chien (1941) but see also Costello & Bowden (1957) and Heiks *et al.* (1954).

T (° C.)	3·8	5	10	15	20	25	30	35	40
ρ	1·1053	1·1055	1·1059	1·1058	1·1053	1·1044	1·1032	1·1017	1·0995

Chang, T.-L. & Chien, J.-Y. (1941). *J. Amer. chem. Soc.* **63**, 1709.
Costello, J. M. & Bowden, S. T. (1957). *Research*, **10**, 320.
Heiks, J. R. *et al.* (1954). *J. phys. Chem.* **58**, 488.

MAXIMUM DENSITY OF H_2O OCCURS AT 3·98° C. (International Hydrogen Scale)

MAXIMUM DENSITY OF D_2O OCCURS AT 11·23° C.

THE MAXIMUM DIFFERENCE BETWEEN THE DENSITIES OF H_2O AND D_2O OCCURS AT 40° C.

EFFECT OF SOLUTES ON TEMPERATURE OF MAXIMUM DENSITY

Although most solutes lower the temperature of maximum density, it is raised by certain alcohols in low concentrations.

Wada, G. & Umeda, S. (1962). *Bull. chem. Soc. Japan*, **35**, 646.

DENSITY OF ICE = 0·917 g. cm.$^{-3}$ at 0° C. and 1 atm. pressure

N.B. This figure is for Ice-I. Other crystalline forms of ice occur at higher pressures and/or lower temperatures. All other forms of ice are more dense than liquid water. For a further discussion of the ices see, for instance:

Bridgman, P. W. (1935). *J. chem. Phys.* **3**, 597.
Bridgman, P. W. (1937). *J. chem. Phys.* **5**, 964.

COMPRESSIBILITY (κ) OF H_2O (atm.$^{-1}$)

The following data are from Diaz-Peña & McGlashan (1959), and are based on sound absorption data, i.e. are for adiabatic compressibility. See also Hall (1948), and, for the most recent discussion of the subject, Hayward (1964).

T (° C.)	5	15	25	35	40	50
$10^6 \times \kappa$	50·4	47·8	46·2	45·0	44·8	44·7

DIAZ-PEÑA, M. & MCGLASHAN, M. L. (1959). *Trans. Faraday Soc.* **55**, 2018.
HALL, L. (1948). *Phys. Rev.* **73**, 775.
HAYWARD, A. J. T. (1964). *Acta Imeko* (Proc. Int. Measurements Conference), p. 249.

SURFACE TENSION OF H_2O (dyn. cm.$^{-1}$)

The results obtained are liable to variation according to the method of determination. Moreover, very small amounts of surface-active substances can cause very major changes in the surface tension. The following values are from Young & Harkins (1929), who took as their primary standard 72·75 (± 0·05) dyn. cm.$^{-1}$ at 20° C. Their results should only be applied to biological systems with the very greatest caution. The values for 0°, 5°, and 80° are accurate to (± 0·1) and the remaining values to (± 0·05).

T (° C.)	0° C.	2° C.	4° C.	5° C.	6° C.	8° C.
0	75·64	—	—	74·92	—	—
10	74·22	73·95	73·64	—	73·34	73·05
20	72·75	72·44	72·13	—	71·82	71·50
30	71·18	—	—	70·38	—	—

40° 69·56 60° 66·18 80° 62·61

YOUNG, T. F. & HARKINS, W. (1929). *Int. crit. Tables*, **4**, 447.

SURFACE TENSION OF D_2O

The surface tension of D_2O is almost identical with that of H_2O to within 1 part in 2000.

JONES, G. & WRAY, W. A. (1937). *J. chem. Phys.* **5**, 505.

THERMAL CONDUCTIVITY (k) OF LIQUID H_2O AND D_2O (J cm. cm.$^{-2}$ sec.$^{-1}$ deg C.$^{-1}$)

There is some variation between the results of different authors and the third figure of each value should be treated with caution. The tabulated data are from Powell & Challoner (1959), and for a review of work up to 1963 see Jamieson & Tudhope (1964).

T (° C.)	0	20	40
k (H_2O)	5·61	6·04	6·32
k (D_2O)	5·54	5·79	6·00

JAMIESON, D. T. & TUDHOPE, J. S. (1964). *N.E.L. Rep.* p. 137.
POWELL, R. W. & CHALLONER, A. R. (1959). *Phil. Mag.* **4**, 1183.

THERMAL CONDUCTIVITY OF ICE $= 2{\cdot}2\times 10^{-2}$ J cm. cm.$^{-2}$ sec.$^{-1}$ deg C.$^{-1}$ at $-5°$ C.

RATCLIFFE, E. H. (1962). *Phil. Mag.* **4**, 1197.

To calculate the VOLUME EXPANSION OF WATER see TABLES OF DENSITY.

COEFFICIENT OF LINEAR EXPANSION (α) FOR ICE AND SOLID D_2O (degC.$^{-1}$)

Ice (H_2O), $\alpha = (56{\cdot}5 + 0{\cdot}250\theta)$;
solid D_2O, $\alpha = (55{\cdot}5 + 0{\cdot}248\theta)$;

where θ is the temperature in degC.

POWELL, R. W. (1948). *Proc. roy. Soc.* A, **247**, 464.

SPECIFIC HEAT OF WATER (abs. J g.$^{-1}$ degC.$^{-1}$)

T (° C.)	0° C.	2° C.	4° C.	6° C.	8° C.
0	4·2177	4·2107	4·2048	4·1999	4·1957
10	4·1922	4·1893	4·1869	4·1849	4·1832
20	4·1819	4·1808	4·1800	4·1793	4·1788
30	4·1785	4·1783	4·1782	4·1783	4·1784
40°	4·1786	60°	4·1844	80°	4·1964

OSBORNE, N. S., STIMSON, H. F. & GINNINGS, D. C. (1939). *J. Res. nat. Bur. Stand.* **23**, 197.

SPECIFIC HEAT OF LIQUID D_2O

The values reported differ markedly. Those of Cockett & Ferguson (1940) show a minimum at about 40° (cf. H_2O) whilst the work of Eucken & Eigen (1951) shows a much greater temperature dependence and no minimum. The results of Ribkin & Egorov (1959) are intermediate between those of the earlier authors and there is an implied point of inflexion somewhere around 50°, although their data are not very precise.

COCKETT, A. H. & FERGUSON, A. (1940). *Phil. Mag.* **29**, 185.
EUCKEN, A. & EIGEN, M. (1951). *Z. Electrochem.* **55**, 343.
RIBKIN, C. L. & EGOROV, B. N. (1959). *Atomn. Energ.* **7**, 462.

SPECIFIC HEAT OF ICE AT 0° C. = 2·115 J $g.^{-1}$ $degC.^{-1}$

DICKINSON, H. C. & OSBORNE, N. S. (1915). *Bull. Bur. Stand.* **12**, 49.

REFRACTIVE INDEX OF WATER

Visible spectrum. There is a very large volume of data. Those of Tilton & Taylor (1938) are particularly comprehensive.

STOKLAND, K. (1937). *K. norkse Vidensk. Selsk. Skr.* **10**, 145.
TILTON, L. W. & TAYLOR, J. K. (1938). *J. Res. nat. Bur. Stand.* **20**, 419.

Ultra-violet

DUCLAUX, J. & JEANTET, P. (1921). *J. Phys. Radium, Paris,* **2**, 346.
DUCLAUX, J. & JEANTET, P. (1925). *J. Phys. Radium, Paris,* **5**, 92.

Infra-red

RUBENS, H. (1892). *Ann. Phys.* **45**, 238.

REFRACTIVE INDEX OF ICE: 1·305–1·315 in the visible spectrum

MERWIN, H. E. (1930). *Int. crit. Tables,* **7**, 17.

ABSORPTION OF RADIATION BY WATER

Infra-red and Raman spectra. A very useful introduction to the subject will be found in Herzberg (1945). The following are the three principal characteristic I–R absorption frequencies (as wave numbers in $cm.^{-1}$):

Gas	3652	1595	3756
Liquid	3450	1640	3615 (±50)

HERZBERG, G. (1945). *Infra-red and Raman Spectra* (see p. 280). Princeton, N.J.: Van Nostrand.
STANEVICH, A. E. & YAROSLAVSKI, N. G. (1961). *Opt. Spectrosc.* **10**, 278.
WALRAFEN, G. E. (1964). *J. chem. Phys.* **40**, 3249.

Nuclear magnetic resonance. Pople, Schneider & Bernstein (1959) provides a good general reference on n.m.r. The paper of Shcherbakov

(1961) deals in particular with the hydration of ions. The work of Meiboom and his collaborators is concerned with proton relaxation in water.

MEIBOOM, S. (1961). *J. chem. Phys.* **34**, 375.
MEIBOOM, S., LUZ, Z. & GILL, D. (1957). *J. chem. Phys.* **27**, 1411.
POPLE, J. A., SCHNEIDER, W. G. & BERNSTEIN, H. J. (1959). *High Resolution Nuclear Magnetic Resonance.* New York: McGraw-Hill.
SHCHERBAKOV, V. A. (1961). *Zh. Strukt. Khim.* **2**, 487.

IONIZATION CONSTANT (K_w) FOR WATER (H_2O)

The following data have an error of less than 0·001, and are tabulated as the negative logarithm to the base ten.

T (° C.)	0	5	10	15	20	25
$-\log_{10} K_w$	14·9435	14·7338	14·5346	14·3463	14·1669	13·9965

T (° C.)	30	40	60
$-\log_{10} K_w$	13·8330	13·5348	13·0170

HARNED, H. S. & ROBINSON, R. A. (1940). *Trans. Faraday Soc.* **36**, 973.

IONIZATION CONSTANT FOR D_2O

As well as the tabulated data, the paper by Wynne-Jones from which they are taken also gives values for H_2O which are in agreement to two places of decimals with those of Harned & Robinson above.

T (° C.)	15	25	35
$-\log_{10} K_w$	15·08	14·71	14·37

WYNNE-JONES, W. F. K. (1936). *Trans. Faraday Soc.* **32**, 1397.

ELECTRICAL CONDUCTIVITY OF WATER

Experimentally, the conductivity of any sample of water is partly governed by dissolved ions and the values observed depend on the degree of purity of the water. There is, however, a theoretical minimum which is given by Eigen & de Maeyer (1958) as

$$5{\cdot}45 \times 10^{-8}\ \Omega\ \text{cm.}^{-1} \quad \text{at } 25°\ \text{C.},$$

and this should be compared with the experimental data (e.g. Bjerrum, 1929).

BJER [illegible] (1929). *Int. crit. Tables*, **6**, 152.
F [illegible] DE MAEYER, L. (1958). *Proc. roy. Soc.* A, **247**, 505.

DIELECTRIC CONSTANT FOR WATER (ϵ)

The results of Vidulich & Kay (1962) confirm those of Owen *et al.* (1961) against those of Malmberg & Maryott (1956). The data below are those of Owen *et al.*

T (° C.)	0	5	10	15	20	25
ϵ	87·90	85·90	83·95	82·04	80·18	78·36
T (° C.)	30	35	40	60	80	
ϵ	76·58	74·85	73·15	66·81	61·03	

For a discussion of the dielectric constant of ionic aqueous solutions see Haggis, Hasted & Buchanan (1952).

HAGGIS, G. H., HASTED, J. B. & BUCHANAN, T. S. (1952). *J. chem. Phys.* **20**, 1452.
MALMBERG, C. G. & MARYOTT, A. A. (1956). *J. Res. nat. Bur. Stand.* **56**, 1.
OWEN, B. B. *et al.* (1961). *J. phys. Chem.* **65**, 2065.
VIDULICH, G. A. & KAY, R. L. (1962). *J. phys. Chem.* **66**, 383.

DIELECTRIC CONSTANT FOR D_2O

These values are from Malmberg (1958) (cf. Malmberg & Maryott, 1956, for H_2O) and may be liable to a small error. From the data for water we might expect an error of about 0·2 at 0° C., but less than 0·1 above 20° C.

T (° C.)	5	10	15	20	25	30
ϵ	85·48	83·53	81·62	79·76	77·94	76·16
T (° C.)	35	40	50	60	80	
ϵ	74·43	72·74	69·47	66·36	60·56	

MALMBERG, C. G. (1958). *J. Res. nat. Bur. Stand.* **60**, 609.

DIELECTRIC CONSTANT FOR ICE AND SOLID D_2O

For poly-crystalline Ice-I

$$-0{\cdot}1^\circ\ \text{C.} \quad = 91{\cdot}5.$$

Equivalent solid D_2O

$$1{\cdot}2^\circ\ \text{C.} \quad = 90,$$

$$-2{\cdot}7^\circ\ \text{C.} \quad = 89{\cdot}0.$$

The above data are from Auty & Cole (1952). For data on single crystals see Humbel, Jona & Scherrer (1953).

AUTY, R. P. & COLE, R. H. (1952). *J. chem. Phys.* **20**, 1309.
HUMBEL, F., JONA, F. & SCHERRER, P. (1953). *Helv. phys. acta*, **26**, 17.

DIPOLE MOMENT OF WATER (in benzene solution) = 1·76 Debye units (e.s.u. × 10^{-18})

DIPOLE MOMENT OF D_2O (in benzene solution) = 1·78 Debye units

Müller, F. H. (1934). *Phys. Z.* **35**, 1009.

DIPOLE MOMENT OF H_2O VAPOUR = 1·84 Debye units

DIPOLE MOMENT OF D_2O VAPOUR = 1·84 Debye units

Groves, L. G. & Sugden, S. (1935). *J. chem. Soc.* 1935, 971.

DIELECTRIC RELAXATION TIME (τ) FOR WATER (sec. × 10^{-12})

T (° C.)	0	10	20	30	40	60	80
τ	17·7	12·6	9·5	7·4	5·9	4·0	3·2

Collie, C. H., Hasted, J. B. & Ritson, D. M. (1948). *Proc. phys. Soc.* **60**, 145

VAPOUR PRESSURE FOR H_2O (mmHg)

T (° C.)	0° C.	2° C.	4° C.	6° C.	8° C.
0	4·58	5·29	6·09	7·01	8·04
10	9·20	10·51	11·98	13·63	15·47
20	17·53	19·82	22·37	25·21	28·35
30	31·82	35·67	39·90	44·57	49·70
40°	55·34	50°	92·56	60°	149·5
70°	233·8	80°	353·3	100°	760·0

Keyes, F. G. (1947). *J. chem. Phys.* **15**, 602.

VAPOUR PRESSURE (p) FOR D_2O (mmHg)

T (° C.)	10	15	20	25	30	35	40	45	50	55
p	7·70	10·82	14·97	20·43	27·71	37·11	49·0	64·2	83·2	106·6

Combs, R. L., Googin, J. M. & Smith, H. A. (1954). *J. phys. Chem.* **58**, 1000.

BOILING POINT OF H_2O *v.* PRESSURE

P (mmHg)	720	730	740	750	760	770	780	790	800
T (° C.)	98·49	98·88	99·26	99·63	100·00	100·37	100·73	101·09	101·44

Moser, H. (1932). *Ann. Phys.* **14**, 790.

CRITICAL TEMPERATURE AND PRESSURE

The figures for H_2O are from Osborne, Stimson & Ginnings (1937) and those for D_2O are from Oliver & Grisard (1956).

Critical temperature (H_2O) = 374·15° C.