

Osmotic and Ionic Regulation in Animals

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PERGAMON PRESS

OSMOTIC AND IONIC REGULATION IN ANIMALS

by

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and

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PERGAMON PRESS

OXFORD · LONDON · NEW YORK · PARIS

1964

PERGAMON PRESS LTD.
Headington Hill Hall, Oxford
4 and 5 Fitzroy Square, London W.1

PERGAMON PRESS INC.
122 East 55th Street, New York 22, N.Y.

GAUTHIER-VILLARS ED.
55 Quai des Grands-Augustins, Paris 6^e

PERGAMON PRESS G.m.b.H.
Kaiserstrasse 75, Frankfurt am Main

Distributed in the Western Hemisphere by
THE MACMILLAN COMPANY · NEW YORK
pursuant to a special arrangement with
Pergamon Press Limited

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PERGAMON PRESS LTD.

Library of Congress Catalog Card Number 62-11560

Made in Great Britain

INTERNATIONAL SERIES OF MONOGRAPHS ON
PURE AND APPLIED BIOLOGY

Division: **ZOOLOGY**

GENERAL EDITOR: G. A. KERKUT

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PREFACE

The importance of homoeostatic mechanisms in a living animal cannot be over-estimated. In the field of water and electrolyte metabolism there has been a development of ideas from some sort of chemical and physical equilibrium between the animal and its environment, through a "steady state" concept in which the equilibrium resulted from the interaction of uptake and loss, ingestion and excretion, to the current picture of homoeostasis controlled by feedback mechanisms. It is now recognised that the composition and volume of the body fluids, the production of secretions, and the maintenance of cellular contents are all subject to homoeostatic control, with or without the implication of central nervous control.

The published work in the field tends to follow the same lines of development, firstly with analyses and comparison of the body fluids and tissue contents, later with evaluation of the part played by excretory organs, by swallowing, by secretion and evaporation, and finally with the investigation of the dynamics of control and of the controlling hormones or other mechanisms involved. In 1938, when Krogh published his classic work *Osmoregulation in Aquatic Animals* much of the data concerned analyses of body fluids and the external media, some information was available about excretory organs, and the first experiments dealing with rates of electrolyte exchange were included.

In the succeeding 25 years, there has been a technological revolution in this field as in others. Many new types of apparatus have become available for routine analysis on a relatively micro-scale. Such apparatus allows the accumulation of a sufficient number of data to provide estimates of mean electrolyte levels. One of the greatest advances in this field is, of course, the development of radio-isotope techniques, both in using isotopes as tracers, and in isotope dilution techniques. For the most part, Krogh was able to report on electrolyte exchanges only

in stressed un-equilibrated animals, "washed-out" in distilled water, or "salt-loaded" after sojourn in high salinities. The use of isotopes has allowed the study of electrolyte fluxes through animals in equilibrium with their environments, as well as in stressed conditons, and this has lead on to the study of homeostatic control. Naturally, many difficulties are unsolved: problems inherent in the use of isotopes such as that of "exchange diffusion" or the validity of heavy water experiments, are still matters of controversy.

The literature in the field of osmotic and ionic regulation in animals is immense. We have not intended our book as a comprehensive cover, but have preferred to present a theme of development illustrated by chosen examples from many diverse animal types. Our aim has been to clarify for the student the biophysical basis of regulation and for this reason we have included in Chapter I an elementary account of the principles involved. In the later chapters the specific responses of animals to different environments are discussed in these terms.

Since Krogh's book still stands as an invaluable source of information on the literature up to 1937, we have referred to earlier papers only when specific and detailed information was required. The recent increase in the number of papers published has made it impossible to include more than a selection of them, or even to review them right up to the date of publication. Our original manuscript was completed in mid-1961 and some additional work up to the spring of 1962 has been included. Further significant work continues to appear, but short of delaying publication, it is impossible to include it. We hope that our general approach to the subject and our selection of material will prove of sufficient merit to maintain interest, in spite of this disadvantage.

It remains for us to thank many colleagues who have assisted us by discussion or in more material ways. In particular we wish to thank J. D. Robertson for reading and commenting on the manuscript in the early stages, C. B. Cowey, R. Harden-Jones, R. Holmes, C. R. House, R. Pontin, J. Shaw, D. R. Swift and P. M. Woodhead for allowing the use of some unpublished material; S. Simmonds for Figs. II.6, II.7, and II.11, R. Pontin for Fig. II.10, A. H. Coombes, Birmingham City Analyst, for data in

Table V. 1. Many of the illustrations have been selected or adapted from the published literature (listed below) and we wish to thank the authors and publishers for permission to use these. Finally our thanks are due to the Department of Zoology and Comparative Anatomy, University of Birmingham, and to the Freshwater Fisheries Laboratory, Ministry of Agriculture, Fisheries and Food, for the facilities and opportunities offered to us during the preparation of the manuscript.

G. P.
W.T.W.P.

ACKNOWLEDGEMENTS

A number of illustrations in the text are taken from the literature. A list of the sources of these figures is printed below.

Acta physiol. scand.: Figs. VI. 3, VI. 5, VII. 6—8.

Amer. J. Physiol.: Figs. II. 2, VI. 2, VI. 4, VII. 4.

Aust. J. exp. Biol. Med. Sci. Fig. III. 2.

Biol. Bull. Woods Hole: Figs. IV. 17.

Helv. physiol. acta: Fig. II. 4, II. 5.

J. cell. comp. Physiol.: Figs. V. 11—12, VII. 9.

J. clin. Invest.: Fig. VI. 6.

J. exp. Biol.: Fig. II. 9, II. 12—13, IV. 5—9, IV. 26, V. 1—2, V. 4—8,
VII. 13—15, VIII. 3.

J. gen. Physiol.: Figs. V. 9—10.

J. Mar. Biol. Ass. U. K.: Figs. IV. 19—20, IV. 24—25.

Nature, London. Fig. VII. 12.

Pflüg. Arch. ges. Physiol. Fig. III. 1, IV. 12.

Physiol. comp.: Fig. IV. 21—22.

Physiol. Rev.: Figs. II. 3.

Science: Fig. III. 2.

Sci. Amer.: Figs. VII. 10—11.

Z. vergl. Physiol.: Figs. IV. 11, IV. 14—16, VII. 5, VIII. 1.

Die Binnengewässer, authors A. Remane and C. Schlieper, publ. Schweitzerbartsche, Stuttgart. Figs. IV. 13, VIII. 4.

Comparative Physiology authors C. L. Prosser *et al.*, publ. W. B. Saunders Co. Philadelphia and London. Fig. IV. 18.

Water Relations in Terrestrial Arthropods, author E. B. Edney, publ. Cambridge University Press, Cambridge and London. Fig. VI. 1.

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CHAPTER I

SOME GENERAL ASPECTS OF OSMOREGULATION IN ANIMALS

Introduction

Life began in water, and most probably in sea water. The biochemical processes sustaining life, and fertilization which perpetuates it, can take place only in water, and often in water of a specific salt content. The simplest animals living today are small organisms whose cells are bathed in sea water. From the surrounding sea water they take their food and oxygen, and to it they return their waste products. In more complex animals the tissues are no longer in direct contact with the ambient medium, but are bathed in blood or some other extracellular fluid. These fluids form a private pond supplying oxygen and food to the cells and receiving their waste products. The volume of extracellular fluid is usually much smaller than that of the cells it surrounds, and in these crowded conditions many complex systems have developed to regulate the composition of the fluids. Of these regulatory processes, respiration supplies oxygen and removes carbon dioxide, digestion maintains the level of nutrients, and osmoregulation controls the volume and composition of the body fluids. Not only the excretory organs osmoregulate, but also the body surface and the gut lining, both of which may transport salt and water between the environment and the interior of the body. Excretory systems

can play only a negative part in maintaining body fluid concentrations, conserving or excreting substances already present in the blood, but they are unable to add to the blood substances which are not already present. The activity of the gut and body surface, on the other hand, can play a much more positive role.

The extracellular fluids of most marine animals are in osmotic equilibrium and almost in ionic equilibrium with the surrounding sea water. The development of an internal medium, with its associated control systems, has facilitated the differentiation of freshwater and terrestrial animals which maintain internal media similar in many respects to sea water, despite very different external environments. In freshwater animals, the volume and salt content of the internal medium must be maintained in the face of the degrading effects of osmosis and diffusion, while terrestrial animals must contend with a continual desiccation. The means whereby the water and salt content of the body fluids are regulated in marine, freshwater and terrestrial animals form one of the theses of this book.

In addition to the regulation of the salt and water content of the body fluids, the salt content and sometimes the volume of each cell is actively controlled. Even in simple animals, such as the marine Protozoa, the cytoplasm is richer in potassium than the surrounding sea water. In the same way, the tissues of the Metazoa are richer in potassium and poorer in sodium than their extracellular fluids. The cell surface is thus the site of great ionic activity, excluding sodium from the cell, and usually concentrating potassium. Freshwater protozoans and coelenterates must also regulate osmotically, as well as ionically, at the cell surface, and it is possible that some metazoan cells may also regulate osmotically with respect to the body fluids (Chap. VI, pp.266, 269).

Body Fluids

The following terms are used to distinguish the body fluids.

Whole blood is the liquid collected from the circulatory vessels and includes both the suspended blood cells and the fluid surrounding them.

Plasma is the liquid which remains when blood cells and other solid particles have been removed by centrifugation or filtration.

Serum is the liquid which remains after allowing either whole blood, or plasma, to clot. It is similar to plasma in electrolyte composition, but the clotting process also removes fibrinogen, as well as the cellular elements.

Lymph is present in the vertebrates in body spaces outside the arterial capillary venous network. Like serum, it contains no red cells (erythrocytes) and less protein than the plasma, but it is more than an ultrafiltrate of the blood, although it originates in this way. It may contain a high concentration of white cells (leucocytes) and fat droplets. The protein components of the lymph are different from those of the serum.

The serum and the liquid phase of the lymph are similar to but not identical with the blood plasma in electrolyte composition. The difference in protein content may cause Donnan effects (see below, p.27), and the removal of some of the protein may remove some of the bound ions (see below, p.41). Whole blood usually differs considerably in electrolyte composition from the plasma. In particular, the potassium content of whole blood is much greater than that of the plasma because of the presence of the cells and smaller differences occur in the concentration of other ions.

Extracellular and Intracellular Fluids

In the higher Metazoa, the extracellular fluids are separated into two compartments, a primary body cavity or haemocoel, and a secondary body cavity or coelom. The fluid contents of the primary body cavity are the blood and lymph. The