TERTIARY LEVEL BIOLOGY

Biology of Fresh Waters

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Preface

AS THE MAJOR CONSTITUENT OF THE HUMAN BODY, THE LARGEST SINGLE ITEM of diet, and the most widely used natural medium, there is no denying that fresh water and its quality are of vital significance to mankind everywhere. The once inconceivable idea that this resource could be in critically short supply is now a reality in many areas where rainfall was originally thought to be more than adequate. The main themes of this book — the nature of fresh water as a medium, the plants and animals which inhabit it, and the uses to which it is put by Man — are of importance to everyone concerned with this limited, but fortunately re-cycling, resource.

The publication of another elementary book might rightly be questioned at this time by those active in the field concerned. Several introductory studies of freshwater ecology are already available in the English language, yet gaps do exist, particularly in certain teaching courses which integrate chemistry, botany and zoology. In addition there is a need for a simple account of the major facets of this field that are important to planners, engineers and others concerned with fresh water, who wish to find an opening to the subject, but have neither time nor inclination to study it in depth.

The present volume is intended as a basic introduction to the major aspects of freshwater biology, suitable for many courses in this subject at early undergraduate level. It is hoped that it will also be useful to people in other fields where elementary aspects of fresh water are relevant. It is not in any way intended to be a comprehensive treatise on freshwater ecology, but rather a general survey of the main aspects of the environment and the fundamental topics and methods involved, further details of which can be located by consulting the references listed. All sources of literature used in writing the book are given in the References; to aid readability, many of them are not cited individually in the text. Nevertheless the volume does represent the synthesis of large amounts of data and information published elsewhere (mainly in scientific journals) and I have drawn freely from many hundreds of such sources in writing this book. Where data have been taken direct from specific studies, their sources have been acknowledged individually.

The basis of the manuscript of this book was a series of notes developed by myself during the teaching of theoretical and practical courses in limnology and freshwater fisheries at the University of Glasgow. During re-writing, however, I have been greatly helped by comments and criticisms from many scientists in both teaching and full-time research who have been patient enough to read early drafts of one or more chapters. Most of the improvements in the text are theirs; all errors are mine. My thanks for such help are due to the following: Mr J. I. Waddington and Mr D. W. Mackay (Clyde River Purification Board); Mr A. V. Holden, Mr L. A. Caines and Mr J. E. Thorpe (Freshwater Fisheries Laboratory, Pitlochry); Dr A. E. Bailey-Watts, Mr I. R. Smith and Mr K. East (Institute of Terrestrial Ecology, Edinburgh); Dr F. C. McNaughton (Napier College of Science and Technology); Mr R. N. Campbell (Nature Conservancy Council, Inverness); Mr J. D. Hamilton and Dr B. R. Davies (Paisley College of Technology); Mr A. R. Waterston (Royal Scottish Museum); Mr T. Warwick (University of Edinburgh); Dr H. D. Slack and Dr R. Tippett (University of Glasgow). Several other people were kind enough to comment on specific points raised in some chapters. My wife, Kathleen, has helped with all stages of the book, from criticizing and typing early drafts to its final publication.

Anyone attempting to write a book of this nature risks falling among various stools. Though intended to be international in aspect, parts of it — especially the examples used — are inevitably biased by the fact that I am a zoologist working in the British Isles. Also the text may appear too advanced for some, too elementary for others; to some laymen it may appear too scientific, to many limnologists too general. My excuse is that the area occupied by the contents is where the greatest gap exists. While realizing that the book cannot satisfy everyone, it is hoped that it will be useful and stimulating to many.

PETER S. MAITLAND

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CHAPTER ONE

ENVIRONMENT

THIS INITIAL CHAPTER IS DEVOTED TO THE MAIN PHYSICAL AND CHEMICAL features of fresh water as an environment. Factors related to these properties, but more or less peculiar to either standing water (e.g. stratification), or running water (e.g. unidirectional current), are dealt with in more detail in later chapters. It should be appreciated from the start that all freshwater bodies are dynamic systems, and not only are the organisms in them affected by the physico-chemical conditions there, but also the plants and animals interact and often profoundly influence both the habitat and one another. It is therefore essential to consider the organisms, too, as part of the environment. Initially, only major influences of the organisms on the physical and chemical conditions of the environment are reviewed. Inter- and intra-specific relationships among animals and plants are dealt with in more detail in the chapters pertaining to communities.

The freshwater bodies of the world are relatively unimportant compared on an area basis to most land and sea surfaces. However, some of the largest rivers and lakes are of impressive dimensions and, regardless of size, they and very many others are of major importance in the general ecology and cycling relationships of the regions in which they occur. Fresh water itself and many freshwater bodies are of fundamental importance to Man, and this subject is treated individually in the final chapter of this book.

1.1 Physics

1.1.1 *Radiant energy and optics*

The major source of energy in most freshwater ecosystems enters in the form of solar radiation. The total amount of radiation reaching the surface of a water body depends on the time of year, its geographic position, its altitude, the state of the atmosphere and several other (usually local) factors. In the region of the equator with no cloud cover present, some 515 cal/cm^2 are received per day, with relatively little variation throughout the year (about ±35 cal/cm^2 only). At the North Pole, however, almost 670 cal/cm^2 are received at midsummer, but none at all during a considerable period around midwinter (figure 1.1). The amount of radiation received in any one latitude increases with altitude.

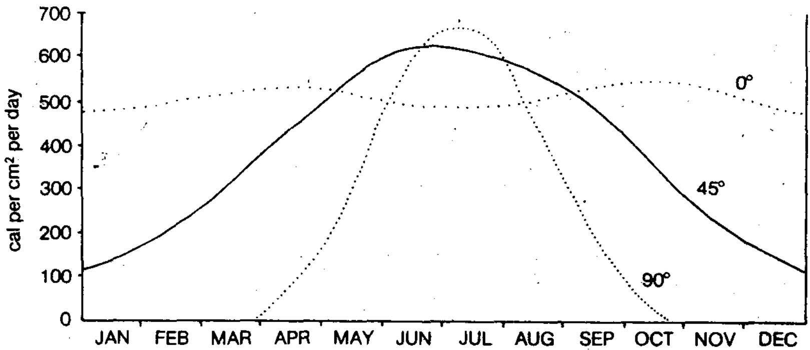

Figure 1.1 The average quantities of energy received from direct solar radiation at different latitudes.

Light falling on water undergoes changes which depend both on the angle at which it meets the water surface and the nature of the water itself. Rays meeting the water surface may be partly reflected and partly transmitted — the latter becoming more vertical in doing so (figure 1.2). The degree of reflection depends on the angle of incidence, and increases enormously as it moves from the perpendicular. Thus, both diurnally and annually, the amount of energy reflected from the surface of rivers and lakes varies greatly according to the height of the sun in the sky. This results in shorter dawns and dusks below water than above; moreover, when the sun is low and the angle of incidence therefore greater, the increasing distance per unit depth through which the rays must pass under water means that they are extinguished even more rapidly. As well as being reflected back from the surface, some radiation is scattered from below the water into the atmosphere. In normal waters the amounts involved in each loss are about the same.

Apart from direct sunlight, the amount of which is dependent on cloud cover, there is also a certain amount of indirect solar radiation received

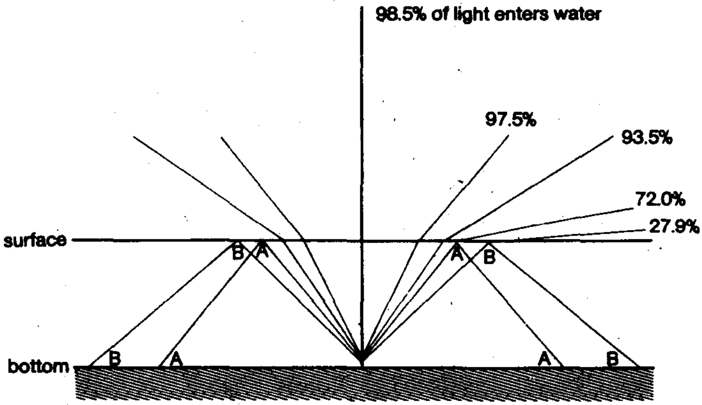

Figure 1.2 The refraction of light through water.

from the sky. This may account for some 20% of the total radiation reaching the water surface, and normally less than 10% of it is reflected.

The portion of radiant energy passing through the water surface is further altered: part is absorbed by the water, by its suspended materials and solutes, and transformed to heat, and part is dispersed. Quite apart from the effects of impurities in the water, such as suspended and dissolved materials which may greatly affect transparency (figure 1.3), there are variations in the transmissions of different wavelengths of light, even through pure water. Short wavelengths travel further than long ones: minimum absorption is at 4700 Å in the blue region, so that in pure water objects at some depth appear blue. Long wavelengths (orange and red rays) are absorbed rapidly: some 90% of wavelengths greater than 7500 Å are absorbed within 1 m in pure water; thus infra-red rays can rarely penetrate far.

Most of the important dissolved solids absorb short wavelengths strongly, and long wavelengths least. When suspended solids are present in small amounts, water is most transmissive to green light; when large amounts of suspended materials occur, transmission is greatest for the longer orange and red wavelengths. As the water transparency decreases, the limit of detectable light (whose wavelength gets progressively longer) approaches the surface of the water. In most situations radiation tends to decrease logarithmically with depth.

The observed colour of natural fresh waters may be due to their actual colour, or an apparent colour made up from this and the influence of other factors. The quality of the incident light, the selective transmission of wavelengths just discussed, the amount and quality of suspended matter, and (in shallow water) the colour of the substrate, are all important. Basically, the colour observed on looking into a river or lake is that of the upward scattered light. Natural systems where the water is

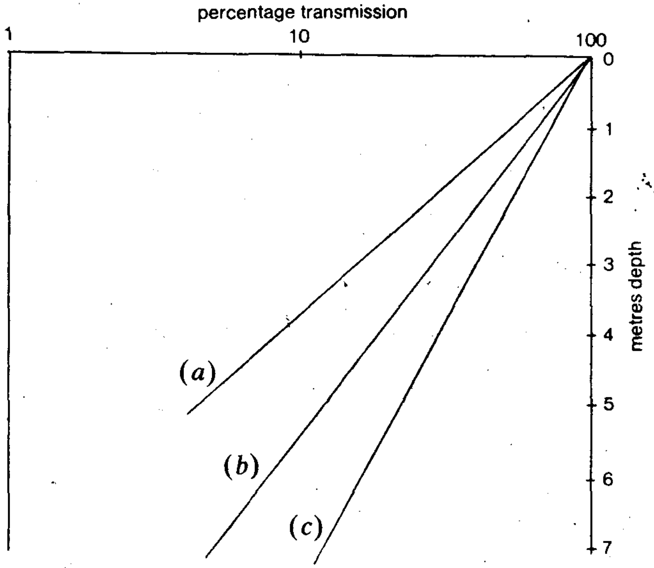

Figure 1.3 The transmission of light in Loch Uanagen in relation to depth. (*a*) blue; (*b*) red; and (*c*) green (after Spence, Campbell and Chrystal, 1971).

relatively pure usually appear very dark, unless they are very shallow (where the colour of the substrate is important) or reflect colour from their surroundings. In waters where there are large quantities of suspended materials, either living (e.g. algae) or inanimate (e.g. clay), coloured light is reflected from these and combines with the transmission effect to give a particular colour. Generally, in natural waters where there are small amounts of suspended matter, the water looks green, but where there are large amounts, the water looks yellow or brown. Of the dissolved substances which influence the selective transparency, humus materials (usually yellow or brown) are important; thus deep waters which are very pure appear dark bluish, but those affected by humic materials may be dark brown or black. In shallow waters of these types the colour of the substrate has a major influence, whereas in waters with large amounts of suspended materials both depth and substrate are relatively unimportant.

In temperate and Arctic areas, ice can also be a major factor in controlling the amount of radiation entering a water body. The transparency of absolutely pure ice is very high and with such "black" ice, a relatively high proportion of the solar radiation penetrates below.

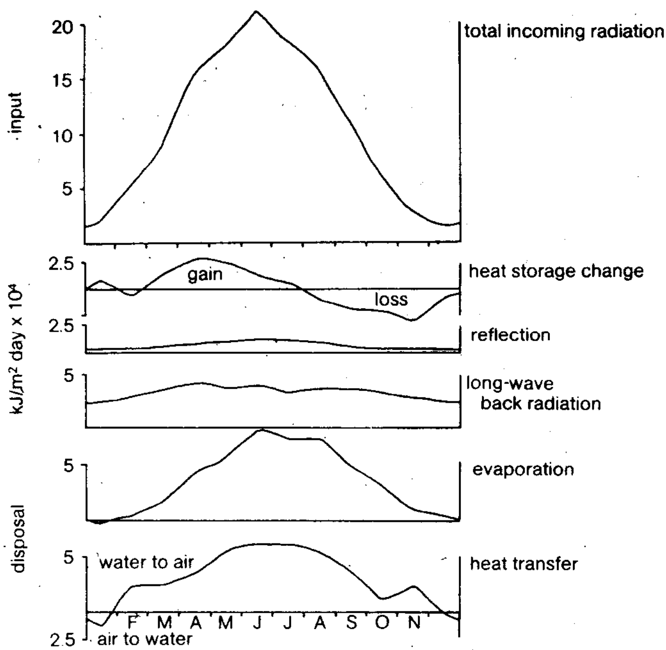

Figure 1.4 Average cycle of radiation balance components in Loch Leven for the period 1968-71 (after Smith, 1974).

Where, however, the ice is less transparent (usually where it has been formed under rough conditions) or covered by snow or dirt, very little energy may reach the water underneath due to loss by reflection or absorption.

Though the specific heat of ice is low (0·5), that of water is high (1·0) and indeed much higher than for many other materials. This property, defined as the number of calories of heat needed to raise the temperature of a unit mass of a material by 1°C, compared with that for water, means that temperature conditions in an aquatic environment are much more stable than those in air: rapid diurnal and seasonal changes of temperature in natural waters are rare — an important factor in relationship to the biology of many aquatic organisms.

In any comprehensive study of a water body it is important to construct some sort of heat budget, and to consider how this varies with season (figure 1.4). Most heat from solar radiation accumulates directly by absorption, though some may be conducted from the air or from the earth beneath. The latter is obviously important for subterranean waters. In some circumstances heat is made available by the condensation of water vapour near the surface. The main source of heat loss is through radiation at the water surface, though losses through evaporation and conduction (at the surface and to the substrate below) are also significant.

1.1.2 *Density and thermal properties*

The earth is unusual among planets in having large amounts of water on its surface. Water itself is remarkable in being almost the only major material existing as a liquid on the earth's surface at ordinary pressures. At 0°C and atmospheric pressure (760 mmHg) the density of pure water is more than 700 times that of air. This means that the tissues of aquatic organisms need far less support than those of terrestrial ones, and there can be a great reduction in skeletal structure — this is especially valuable to large animals. The density of water in different places can vary in time and space, and even small variations are important. They are mainly due to temperature and dissolved solids, especially the former.

Unlike most other materials, whose density increases with decreasing temperature, water reaches a maximum density (1·000) at about 4°C (actually 3·94°C). This critical temperature (figure 1.5) varies according to pressure (an increase of 10 atmospheres decreases it by 0·2°C) and salinity (an increase of 1% decreases it by 0·2°C). Below 4°C, water decreases gradually in density to its freezing point, when the density decreases sharply — ice is more than 8% less dense than water at 0°C. This anomalous temperature/density relationship appears to be due to the differential packing of water molecules at different temperatures.

The results of the anomalous change in density are of considerable significance biologically, as will become clear in succeeding chapters. After cooling, water starts freezing at the surface, but near the bottom of the water body the temperature may be much greater — usually about 4°C. The actual formation of ice cover depends on a variety of factors. The most critical of these are that the water temperature in the whole water body is 4°C or below, and that the weather is clear with little wind.

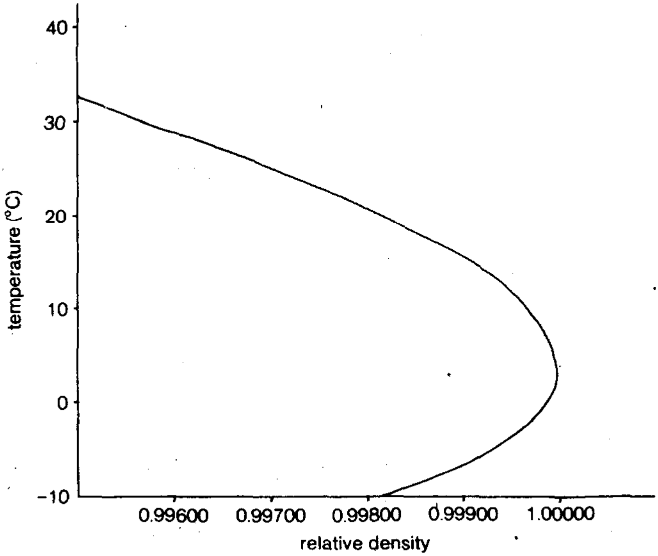

Figure 1.5 The relationship between the relative density and the temperature of pure water.

Conditions for the break-up of ice cover are more or less the opposite of these.

The effects of an increase in temperature on the density of water are also of significance biologically. It is important to note that density changes much more rapidly at higher temperatures than lower; thus a 1° change in temperature at 24°C decreases the density many times more than the same change at 4°C. This is important from the point of view of buoyancy, as planktonic animals, for instance, will tend to sink more rapidly at higher temperatures than at lower ones. This factor is also relevant to the development of stratification in lakes. Because of the great difference in density between water and air, aquatic animals must overcome much greater resistance than terrestrial ones when moving, and must therefore expend more energy for a given return.

The density of water at constant temperature varies with pressure, and increases slowly in a more or less linear fashion with depth. Because of the dual effect of pressure and temperature, the maximum density of water may not occur at 3·94°C but at a lower temperature in very deep lakes; thus it may be less than 3°C at 1000 m. As a result of this, lakes where cold water can be mixed to great depths may have deep-water temperatures lower than 4°C during summer stratification.