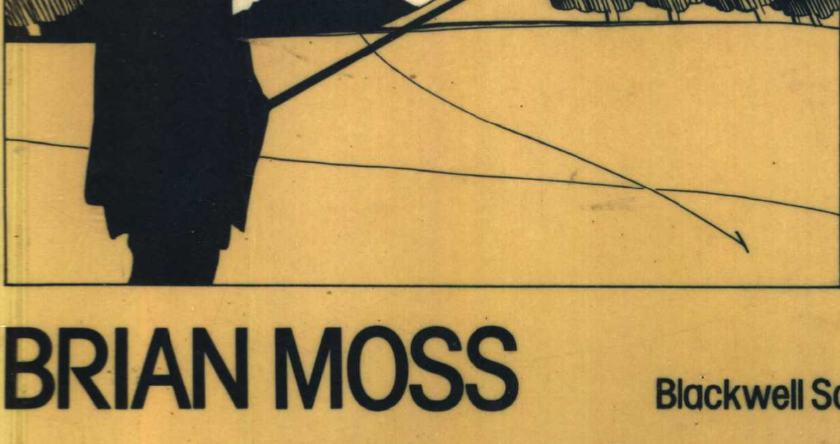
ECOLOGY OF FRESH WATERS



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ECOLOGY OF FRESH WATERS

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TO MY WIFE, JOYCE,
for her love,
TO GABRIEL FAURÉ
for the gift of his Requiem
AND TO H. E. BATES
who knew what it was all about
without the help of this

'Water attracts me as women attract men, as cherries attract blackbirds. I fall for it every time.

And, as I hope these pages will show, I fall for it still. Water has some kind of powerful mystery about it. Still waters, moving waters, dark waters: the words themselves have a mysterious, almost dying fall. Roads, meadows, towns, gardens, woods are man-made; a river is a primeval piece of work. It is ageless but, at the same time, perpetually young. It travels, but remains. It is a paradox of eternal age and eternal youth, of change and changelessness, of permanence and transience. And if there is, perhaps, a dogmatic flavour about these remarks it is comforting to reflect that they will be true, roughly, barring astronomical accidents, in ten thousand years.'

H. E. BATES: *Down the River*, Gollancz, 1937

PREFACE

I have written this book mainly for undergraduates and also for post-graduate students who are perhaps just starting a research project or career in freshwater ecology. Its contents have been subjected to a sort of educational natural selection for it represents the distillation of what several groups of students and I have found mutually interesting. My own predilections naturally are the more prominent—'Thou canst not speak of that thou dost not feel'.

My interest in freshwater ecology, built on what might be a genetic predisposition to the wet and muddy, was fired by two people in particular and this seems the right opportunity to thank them. The earlier was Charles Sinker of the Field Studies Council, whose course on 'Meres and Mosses' at Preston Montford Field Centre in 1960 was my first real contact with aquatic ecology. The other was Dr Frank Round of the University of Bristol who introduced to me in my second undergraduate year, what I recall as the unbelievably interesting, almost romantic notion of lake stratification and the great changes in algal populations throughout the year, based largely on his own work and that of Dr J. W. G. Lund.

Since these first stimuli a very large number of people have helped me and interested me and thus each has made his or her contribution to this book. I hope, at least, that some student reading it might, as a result, start to feel for the subject the same sort of passion that I and many of my fellow freshwater ecologists do.

Norwich, February 1979 BRIAN MOSS

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Dr W. Pennington Tutin very kindly supplied a draft of Fig. 8.2 and a large number of authors, acknowledged in the appropriate places, more than willingly allowed me to use figures from their original work. I am also grateful to the following for granting me permission to use copyrighted material: American Association for the Advancement of Science, Figs. 1.4, 3.15; Akademie-Verlag, Fig. 2.4; Blackwell Scientific Publications, Figs. 2.5, 2.9, 2.6 (part), 3.13, 5.1 (part), 6.3, 6.9, 7.8; Fisheries Research Board of Canada, Figs. 2.7, 2.11, 5.7, 12.2; Elsevier Ltd, Figs. 2.9 (part), 8.6; J. Wiley & Sons, 2.9 (part), 7.1; Duke University Press, Fig. 3.6; The Royal Society, Figs. 3.12 (part), 4.4 (d); Springer-Verlag, Fig. 3.12 (part); American Society for Limnology & Oceanography, Figs. 3.14, 8.1, 12.1; University of Notre Dame, Indiana, Fig. 3.17; The New York Botanical Garden, Fig. 4.2; Liverpool University Press, Fig. 4.4 (b, c); Freshwater Biological Association, Figs. 4.4 (d), 7.4; Academic Press, Figs. 4.6, 5.2; Field Studies Council, Figs. 8.7, 8.8; Sierra Club, Figs. 12.4, 12.5; W. Collins and Dr E. A. Ellis, Fig. 12.6; Dr P. L. Osborne, Fig. 5.1 (part); Oikos, Fig. 5.4; E. Scheweitzerbart'sche Verlagsbuchhandlung, Fig. 5.5; Methuen & Co, Fig. 6.10; Macmillan Ltd, Fig. 6.11; George Allen and Unwin, Fig. 6.12; Oliver and Boyd, Figs. 7.3, 7.5, 9.2, 9.5; Zoological Society of London, Fig. 7.6; *Nature* (Macmillan Journals), Figs. 8.2, 8.3; *Canadian Journal of Botany*, Fig. 8.4; Institute of Biology, Fig. 11.4; Dr W. Junk b.v., Figs. 11.2, 11.3; Cambridge University Press, Fig. 11.5.

CONTENTS

CHAPTER 1

LAKES, RIVERS AND CATCHMENT AREAS

1.1. Introduction

In a classic paper of 1887[140], Stephen Forbes described lakes as microcosms. He laid down some of the ideas of interaction between species and the integration of the ecosystem which are now very familiar to ecologists. He also treated the lake as an ecosystem with a boundary, the water's edge. This was very natural—on one side you got your feet wet, on the other you did not! It is not an idea we hold any longer, however, because quite apart from any pedantic considerations about the transition between open water, marshy fringes and, eventually, dry soil, a lake cannot be understood in isolation, nor even the lake and its inflowing streams. The real unit of study is the catchment area, or drainage basin from which, via its feeder streams, the lake takes its water—water which owes much of its chemical composition to the geology, geography and cultural development of the catchment. Even then the catchment area unit, for which the lake acts as a sink, a rubbish bin for what is washed out of the catchment, does not have firm boundaries. The atmosphere has a role to play and the composition of waters entering lakes may be changed by industrial gases drifting in from kilometres away and dissolving in rainwater falling on the catchment. In lakes which lie in the paths of bird migrations, roosting waterfowl may bring salts in their excreta from feeding areas outside the drainage basin.

1.2 Some basic terms and ideas (Fig. 1.1)

Rain, and any other form of precipitation, is not pure water. It contains significant quantities of dissolved gases (O_2, N_2, CO_2), cations (e.g. H^+, Na^+, K^+, Ca^+, Mg^{2+}), anions (e.g. SO_4^{2-}, Cl^-, NO_3^-, PO_4^{3-}), cation trace elements (e.g. Cu^{2+}, Mn^{3+}, Fe^{3+}, Fe^{3+}), organic compounds, and both organic and inorganic particles. Some of these the rain picks up from tiny droplets of sea spray carried upwards into the atmosphere by wind, some from dust blown from the land, others from the atmosphere itself and products formed from the atmospheric gases in it by lightning. Water dissolves almost everything and limnologists—those who study fresh waters—despite sophisticated techniques, commonly analyse for only a few dozen substances. They could analyse for a few hundred more, and only suspect the existence of many more, particularly organic substances, in rain and natural waters.

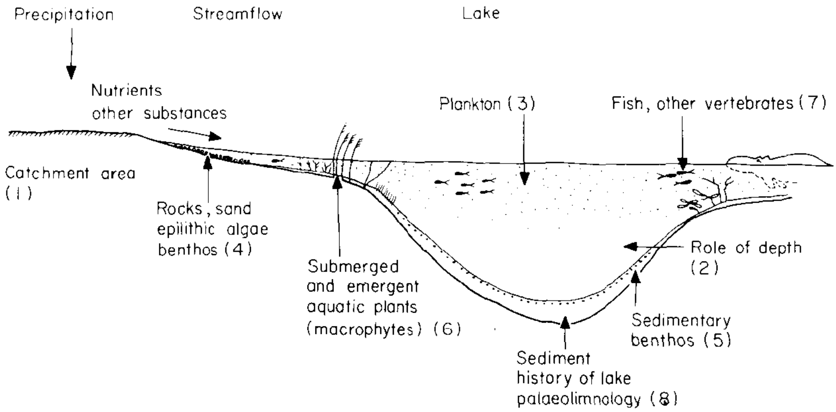

Fig. 1.1. Some limnological terms referred to in Chapter 1. Numbers refer to chapters in which these subjects are discussed in detail.

The concentrations of commonly analysed substances are generally low in rainwater, but as the water percolates through or runs off a catchment it changes chemically through leaching of substances from soil and rocks. The harder the rock, the less the chemical modification, but on softer rocks with deep soils and consequent cultivation there are greater changes (Table 1.1).

Particles are added to the water as it drains through the catchment. These may be inorganic—clay, silt or even sand particles may be carried down, dependent on the violence of the flow—or they may be organic. These will include fine, even colloidal, remains of the decomposition of organic matter in soil which the soil microorganisms are unable further to degrade, and also large and small pieces of barely degraded plant litter washed into the streams. Abscissed leaves are common in forested catchments in autumn, but there is a continual loss of branches, leaves, senescent flowers and pollen to some streams.

In the stream itself there will be changes in the water composition and in the particles carried. Streams high in the catchment will flow turbulently and prevent

Table 1.1. The effect of catchment area on some aspects of drainage water chemistry. All values in mg l^{-1} except pH.

	Undisturbed forest on igneous rock, New Hampshire, U.S.A. (Likens *et al.*[295])		Lowland chalk and glacial drift, agricultural Norfolk, U.K. (Edwards[122])	
	Rainfall	Stream	Rainfall	Stream
Na^+	0.12	0.87	1.2	32.5
K^+	0.07	0.23	0.74	3.1
Mg^{2+}	0.04	0.38	0.21	6.9
Ca^{2+}	0.16	1.65	3.7	100.0
Cl^-	0.47	0.55	< 1.0	47.0
HCO_3^-	0.006	0.92	0	288.0
pH	4.14	4.92	3.5	7.7

much silt deposition, but benthic (i.e. bottom-living) invertebrates including some caddis fly (Trichoptera) and blackfly (*Simulium* spp., Diptera) larvae filter fine organic particles from the water and some of the dissolved substances are used for growth by aquatic mosses and liverworts (Bryophyta), or by layers of photosynthetic algae attached to the rocks. These are termed epilithic algae and they are grazed by other benthic invertebrates, e.g. mayfly (Ephemeroptera) and stonefly (Plecoptera) nymphs, freshwater limpets and snails (Mollusca). Other invertebrates, like the freshwater shrimps (*Gammarus* spp., Crustacea) may feed on the microorganisms, particularly fungi, which colonize pieces of litter lodging in crevices between the rocks on the stream-bed. Carnivorous invertebrates (leeches (Annelida), flatworms (Platyhelminthes)) and some insect larvae prey on the herbivores and detritivores, and fish on any invertebrates or plant material they can use.

As well as taking materials from the water (inorganic nutrients by algae, dissolved inorganic and organic substances by fungi and associated bacteria), this community also adds to it dissolved excretory products, particulate faeces, and the dislodged waste from the break-up of large organic particles during feeding. It also adds members of its own species. Thousands of invertebrates, accidentally dislodged by the current, despite their many adaptations to avoid this, form the 'drift', a downstream flood of floundering benthic animals which form easy prey for the fish.

Organisms adapted to live suspended in water (plankton) do not have time to develop significant populations in fast currents but as the moving water acquires greater volume or discharge and areas of reduced current, there is time for build-up of distinctive plankton populations. Phytoplankton, the microscopic, or sometimes just visible to the unaided eye, photosynthetic plankton comprises an array of algae and photosynthetic bacteria, which is physiologically extremely diverse and encompasses more than a dozen phyla. Phytoplankters are generally adapted to prolonged suspension, not for floating in the precise sense of the word. They may be much denser than water and kept in suspension by convection or wind-induced currents. The zooplankton includes mostly small Crustacea and Rotifera in fresh waters. Traditionally these have been thought to feed on phytoplankton, either by filtration of the smaller ones or by grasping and chewing the larger ones, or, if carnivorous, on each other. The suspended organic detritus brought in continually from upstream is also a component of the plankton community available to the zooplankton, as are the bacteria and fungi which colonize the detritus or live free on dissolved organic substances in the water. Fish may feed on phytoplankton, particularly in the Tropics, and on zooplankton, and in turn fish-eating fish, reptiles, birds and mammals may join the ecosystem.

As lower water flows develop at the edges of a growing river and plankton develops, so also may sediment be deposited on the bottom, providing a rooting medium for larger aquatic plants (macrophytes) and a habitat for mud-living benthic invertebrates. These burrow through the rich deposit or feed on the new supply at the surface of it and include oligochaete worms (Annelida), chironomid larvae (Diptera) and bivalve molluscs. The emergent (from the water surface) reed beds and submerged macrophyte beds also provide a physical habitat for a great diversity of invertebrates and fish and a food supply in the form of epiphytic (attached to plants) algae and bacteria.

A larger and larger river begins to bear fewer and fewer differences from a shallow lake, with its plankton, submerged weedbeds and sediment deposits. It is only when a relatively deep lake basin has been created by natural or human action that a new stage in the river-lake continuum can be distinguished. Such lakes are really rivers in which the flow is so reduced (sometimes becoming zero for lengthy periods) that the water body can acquire a physical structure, either horizontally through the entry of water supplies of different origins, or more usually vertically with a complex layering or stratification. This vertical stratification is created since water rapidly absorbs light and heat radiation, which leads to a layering of illuminated, warmer, less dense water on deeper, darker, colder water. In turn this creates a range of conditions for different chemical processes and living organisms. Because of this, and because of the necessarily longer time that a parcel of water is retained in the water course, the chemical changes imposed on the water in a lake are much greater than in the riverine stretches.

This generalized sequence will not, of course, be found in every river and lake system. In a rocky, mountain catchment, fast flowing streams may discharge directly into a rocky lake basin, carved out by previous glacial action. Such a lake may have few rooted aquatic macrophytes because little silt may have collected from the small upland drainage area, but there may nevertheless be a distinct plankton community. At another extreme, certain lakes in arid regions lose water not by an overflow, but only by evaporation; they may lack vertical stratification because they are shallow and wind can easily disturb any layering temporarily set up; macrophytes may be absent too because such endorheic (internal flow) lakes are usually very saline.

Very deep lakes such as Tanganyika (max. 1470 m) and Malawi (max. 706 m) in East Africa were formed by earth plate separation and are so deep that vertical stratification, established many thousands of years ago, is now disturbed only at the surface and is permanent below 100 m or so. The sea itself can be regarded as a very large endorheic lake, fed by the world's rivers. It is so large relative to the latter that its chemical composition is very constant over much of its volume, thus belying the generalization that chemical changes are greater in lakes than in rivers.

All of these examples emphasize that an understanding of freshwater ecosystems is best obtained in a framework of physico-chemical and biological processes going on in a continuum with as many dimensions as there are components. A traditional classification into streams, rivers and lakes, and into different sorts of lakes defined by certain combinations of features is no longer useful. I am not sure what the 'aim' of limnological research should be; I have always thought that it should be defined by that which interests the individual limnologist, but many of us are interested in what controls organic production in fresh waters and this is a convenient starting point.

1.3 Production in fresh waters

In the 1960's an international effort was made to collect data on productivity from a wide variety of lakes under the auspices of the International Biological Programme. The methods used varied but a synthesis of results made by Brylinsky & Mann[52] seems to include generalizations which most limnologists would accept. Most data were on phytoplankton production from natural lakes, reservoirs and slow-flowing rivers, and Brylinsky & Mann calculated the extent to which productivity, measured as the rate of photosynthesis in the surface waters was correlated with features of the catchment area, water chemistry and geographical location. The sites studied were in North America, Europe, Africa and Asia, with relatively fewer from the tropics than from the temperate zone. This largely reflects the distribution of limnological laboratories.

In the analysis carried out, results were expressed as the degree to which gross (i.e. no correction for respiration has been applied) phytoplankton photosynthesis in a given lake can be predicted from a knowledge of certain factors

Table 1.2. Results of multiple regression analyses comparing the importance of variables for lakes on a global basis compared with those in temperate (39°N–55°N) latitudes (adapted from Brylinsky & Mann[52]).

Variable	Variance explained by each variable (%)	
	All lakes	Temperate lakes
1 Latitude	56	2
Altitude	1	10
Conductivity	8	25
2 Latitude	56	2
Altitude	2	13
Total phosphorus	7	17
3 Latitude	32	6
Altitude	1	4
Chlorophyll *a*	47	27

such as latitude or the total amount of dissolved substances in the water. This degree is expressed as the percentage of the variance in the data explained by each of these environmental factors alone or in combination. The greater the percentage the more closely is phytoplankton photosynthesis correlated with that factor and the more likely is there to be a close causative link.

Table 1.2 gives these data for all of the water bodies (up to 54 of them) studied and for lakes in northern temperate latitudes (39°N–55°N). Conductivity is a measure of the total amount of dissolved electrolytes in the water and phosphorus is an element essential for algal growth but also one of the scarcest. Chlorophyll content is a measure of the biomass of the phytoplankton present.

Globally, latitude is important in determining phytoplankton photosynthesis (and in turn, in a general way, the productivity of higher trophic levels). Latitude is a summary measure of several energy-related variables, being itself a measure of the angle the sun subtends with the vertical at a point on the earth's surface when it is overhead at the equator. Lower latitudes (Equator 0°) have greater solar radiation and higher temperatures than higher latitudes. It is the availability of light energy to power photosynthesis and perhaps the greater rate at which the scarcer nutrients might be recycled at higher water temperatures which might underly the high correlation with latitude. Clearly also the amount of phytoplankton biomass present also helps determine photosynthetic rate and a puzzling feature of the data is that biomass is normally closely related to chemical factors like conductivity and phosphorus availability. Yet these factors seem to be less valuable in predicting photosynthesis on a global basis.

Within a narrow range of latitudes, however, the potential photosynthesis which might be attained with the light energy available may be seriously limited by the supply of nutrients for subsequent growth. In temperate regions (Table 1.2), chemical factors assume a much greater importance, and so does altitude, reflecting perhaps the decrease in mean water temperature in upland lakes.

The data available to Brylinsky & Mann were not perfect, indeed they were probably very varied in quality, but such analysis had not previously been attempted. A subsequent analysis has been carried out by Schindler[451] using part of the original data used by Brylinsky & Mann and many new data, all of which have been screened for their reliability. This analysis seems to have eliminated many of the inconsistencies of the earlier one and points to a much greater role of nutrient availability, particularly of phosphorus. It also finds a possible correlation between nutrient supply and decreasing latitude related perhaps not only to rates of recycling but also to a larger concentration of phosphorus compounds in tropical rainfall. In the new analysis light seems much less likely than nutrient supply to limit production in fresh waters. Nonetheless it has great importance in determining events within lakes and, with nutrients, must be given further consideration.

1.4 Light

The electromagnetic radiation received from the sun at the top of the atmosphere amounts to rather more than is received at the surface of a water body. Some is reflected and scattered and certain frequencies (particularly the very high (ultraviolet) and very low (infra red)) are selectively absorbed by the atmosphere. What remains is rapidly absorbed by water itself and except in the surface few centimetres the light climate underwater is confined approximately to the visible frequencies (13350 cm^{-1} – 28600 cm^{-1}). Expressed as wavelengths these are 750 nm and 350 nm.

Visible light is absorbed by the water itself, dissolved substances and particles suspended in it. In general, the highest and lowest wavelengths (reds and