Fourth Edition

ECOLOGY OF FRESHWATERS

A VIEW FOR THE TWENTY-FIRST CENTURY

Brian Moss

Emeritus Professor, University of Liverpool, UK

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ECOLOGY OF FRESHWATERS
Dedication

For my wife, Joyce, my daughter Angharad, my friends and colleagues, and all who have not sacrificed their honesty and principles for personal aggrandisement, wealth and power

O quam cito transit gloria mundi
(How quickly the glory of the world passes away)

Thomas à Kempis, 1418

Companion website

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Chapter 1

INTRODUCTION

1.1 WHY?

Textbooks usually sound a bit pompous. It’s in their nature as the factual ‘text’: that which has to be known. Yet some, at least, come from the passions of their authors wanting to pass on their enthusiasms, reflected in the facts. But the relative importance of facts changes as understanding grows and the facts only increase in number as time passes. A huge number appear in articles, books and websites on almost everything, and although there is a lot of repetition, sometimes direct, sometimes just new examples of general principles, and sometimes recycling, by newer methods, of ideas that originated long ago, the amount is nonetheless daunting. Most of the scientific literature is written as if no one wants to communicate anything, anyway. The writing is pompous, self-serving, full of unnecessary jargon and distinctly off-putting. Quite a lot of it is deceptive in that something is written as if it is an entirely new revelation when this is far from the case. I have had to wade through a lot of it, often needing to read things several times for glimmers of understanding to emerge. Not surprisingly the population in general cannot be much bothered with scientific findings. The positive side is that when one teases out the meaning, it is completely fascinating! This is the fourth edition of this textbook. The previous editions have grown bigger and bigger so I decided to write a shorter fourth completely from scratch, mostly because I wanted to break away from the near complete emphasis on Europe or North America that most freshwater textbooks have had. Faced with so much information, however, this proved trickier than I had thought.

My first difficulty was that water is part of everything environmental. You cannot overestimate its importance. Planet Earth is very unusual, in the immediate Universe at least, in having a surface skin dominated by water. Two-thirds of its surface is ocean. Moreover, the evaporation and condensation of water, driven by the Sun’s energy, controls the climate and hence what grows where and how well. The river systems, with their lakes and floodplains, stitch the land surfaces and the coastal seas together (Fig. 1.1) with the threads of water and mineral cycles, yet constitute only a small percentage of the total water. Most of it is in the ocean, polar icecaps or underground in the interstices of soils and rocks. More than 90% of the content of all living things is water; even land animals are totally dependent on a continual supply of it. We ourselves can only maintain our settlements where there is a reliable supply of freshwater, and because surface freshwater is relatively scarce, its division among different people and interests causes major political problems, even wars. If you are to write a book on freshwater, you have, at least, to pretend to be a polymath.
2 Introduction

One relief was that it was to be a book on freshwaters, so the ocean could be nearly ignored – but only nearly! A famous speech by a North American Indian chief, Seathl (Fig. 1.2), contains the sentence ‘All things are connected’. The speech was about the natural linkages between land and, water, plants, animals and people, and there is some doubt that he actually said it. But to a professional ecologist, it rings completely true. All things really are connected. There are people who call themselves lake ecologists (limnologists), river ecologists (potamologists) and wetland, or mire, ecologists, let alone the larger camp of terrestrial ecologists, subdivided into grassland ecologists, forest ecologists, desert ecologists or evolutionary ecologists, community and population ecologists, even theoretical ecologists, who thrive in warm offices rather than wet and windy hill-sides. Yet there is really only one tribe of ecologists and ultimately only one ecological system, the biosphere as a whole. One cannot write a book covering everything, however, so this one tries to single out the catchment (watershed or river basin) as the unit.

All the land surface is divided into one catchment (Fig. 1.3) or another, on which water falls then passes through streams and rivers, lakes and wetlands eventually to the sea or, in very arid regions, which cover nearly half the land surface, as vapour to the atmosphere. All of streams, rivers, lakes and wetlands are basically the same. They are depressions of the land through which freshwater passes, and there are many common features to them. There are also differences based on how quickly the water passes through and it is useful to look at them individually to discern what is happening. But fundamentally they march to the same drumbeat.

The connectedness appears in every aspect of ecology. Every action has consequences radiating in every direction. You cannot dam a small river in the high-lands without having some effect on the river estuary perhaps hundreds of kilometres away. You cannot farm the land and expect a downstream lake to stay the same as it was before. You cannot change the climate and expect everything to go on as usual. The land and the freshwaters together have to be seen and discussed as a whole. Freshwater science is a microcosm of the whole of environmental science. There is something of everything in it.

Fig. 1.1 The Ganges Delta in Bangladesh seen from a satellite. The interconnectedness of the land, the river system and the ocean can be clearly seen from satellite photographs. (Copyright U.S. Nautical and Space Administration.)
There was a difficulty in drawing boundaries with time also. A very well-known ecologist, G. Evelyn Hutchinson (Fig. 1.4), used the metaphor of the environmental (or ecological) theatre and the evolutionary play. As the environment changes (and it does so continually), the players, who can be thought of as the genes, the individuals or the species, must change too if they are to stay on stage. And as each of these players changes, there are consequences for other players, who might be competitors, predators or prey, and who might also have to change. Some reference to evolution is needed, for that is what the process of change in organisms is about. Many of the ecological features of particular organisms reflect the conditions under which they first evolved. Cyanobacteria still retain the preferences for low oxygen waters that hark back to the anaerobic world, two or three billion years ago, in which they originated, but themselves began to modify by evolving oxygen-producing photosynthesis. The adults of many freshwater insects and the flowers of most aquatic plants are essentially aerial for it was from land-based ancestors that they entered the water. Time has many scales. Lakes and rivers have ecological histories, sometimes quite short for many were obliterated by the last glaciation and emerged anew only 10,000–15,000 years ago. Others may have persisted for some millions of years, but because climate changes naturally over that scale, they have been bigger or smaller, freely flowing or isolated from time to time. They also change from year to year and biological changes may be recognizable from minute to minute. The multimillion-year scales of evolution are not a major subject of this book but a study of ecological history is essential to understanding the processes of the present.

The third difficulty was in coping with ourselves. Most freshwater ecologists used to head for the hills in their research. They sought the least disturbed, ideally the pristine environments, where the results of the evolutionary play are still intact and where the design of the environmental theatre has not been wrecked by the incompetent architectural abilities of people. As a result we can draw for you pictures of intensely fascinating ecologies: the floodplain forests of the Amazon, with their seed-eating fish; the connections between wolves and bears in the functioning of river systems of the north-temperate zone; the division of the available food in the African Great lakes among fish so specialized that some scrape the scales or bite the eyes of others. We can take you to lakes and wetlands in seemingly endless landscapes of forest and savannah, steppe and even desert. We can be more escapist than the glossiest of travel brochures.

Yet what we also know is that these gems are just the meagre crumbs of what the world once was like, but no longer really is. People have been around for perhaps
Fig. 1.3 The north-west of England showing the land surface made up from abutting river catchments. The world’s entire land surface is divided up in this way. Many catchments adjoin those of a larger river and eventually discharge to the seas and oceans, but this is not necessary. Many catchments are entirely land-bound and water leaves them, not at an estuary, but by evaporation to the atmosphere.
one or two million years and evolved along with the natural ecosystems that give us great delight. The ways in which people meshed, as hunter–gatherers or even simple cultivators, with other animals and with plants, when people were neither numerous nor too ambitious, are parts of the fascination of natural systems. The reality for recent generations has been very different. The past 200 years have seen the progressive destruction of the detail of the freshwater, indeed of all environments (Fig. 1.5). There is no longer any completely pristine freshwater system in Europe and arguably, since we have contaminated the entire atmosphere with pesticides, emitted gases that fall as acid in the rain, and are now changing the climate, perhaps there are none anywhere (Fig. 1.6). Those who live in cities will see rivers embanked with concrete; the ponds and lakes will often have signs warning of toxic blue-green algae; rivers in the lowlands will have been straightened and the woody debris that was so important for their ecology removed; lakes will have muddy deltas where the products of erosion wash in from cultivated land. The bears and wolves have long gone and even many of the fish that were once common, Atlantic salmon in Europe for example, are now rare. Previous ecological textbooks, including earlier editions of this one, pretended that the world was intact and tagged on human influences as secondary. That is truly no longer the case. The world is heavily damaged and more than half its natural ecosystems are seriously degraded. An honest textbook must reflect this.

So the final difficulty is one of motivation, for both of us, reader and author. Ecologists do not particularly want to write as historians of what once was, but no longer is. They do not want to appear as doomsayers, perpetually depressed and backward-looking. Nor do they want to instil the idea that things are going so steeply downhill that nothing can be done. To undermine optimism and morale is the greatest disservice and is self-fulfilling. Better to see things like this. We are studying perhaps the most interesting scene of the evolutionary play so far. People are immensely successful organisms, arch-competitors that have already out-competed many species and brought many already to extinction, and that milk is spilt.

Yet when one looks at the population fluctuations of an animal or plant, there are times when numbers (and thus impact) rise temporarily above the notional line of carrying capacity. For a very small part, a few decades, of our million-year history we have been above this line. It has had immense effects, but we live on a planet that has its own mechanisms of stabilizing its environment and may make its own adjustments, though these may be something of a shock to our eventual numbers. We can avoid that, however, for we know a lot about how these systems work. We already have the capacity to start readjusting and redesigning so that we maintain ecological systems that will not be the same as those in the past, but which will still be interesting, pleasant and functioning. It is there that freshwater, indeed all, ecological science starts to involve the human social sciences, for all things are also connected with human societies. In the final analysis, our present difficulties, frustrations and depressions can be a significant but reversible blip of human history not the start of an unending nightmare. There is a whole science of restoration ecology (Fig. 1.7):
the putting together again of the bits that have been taken apart.

And against all these difficulties, there is one monumental bastion. Freshwater ecology is immensely interesting. I do not want to sound parochial about this. Anything is very interesting if you go deeply enough into it. But freshwaters are so much a part of our daily lives (go and turn the kitchen tap on) that they have a special place. One of my colleagues illustrated this by asking students to imagine somewhere where they would feel most relaxed. Almost invariably the scene involved water. A few years ago, I was informed by my increasingly bureaucratic University administration that the course (newly called a module) I had taught for several decades in one form or another must have ‘Aims and Objectives’. I replied that these were simple: to interest and enthuse. When they said that was against the rules and not adequate, but forgot to make a rule that I could not write in verse, I produced the following. It’s the theme of this book.

At this module’s end, you’ll know,
That water comes from rain and snow,
Dissolves most things then rests in basins,
And seals the fates of arid nations.

Fig. 1.5 Major damage and losses of major world biomes by 1950 and 1990, and projected on present trends for 2050. Where damage occurs to the biome in general, this is reflected in the freshwater systems contained within it to a considerable extent, for the waters draining the land are greatly affected by what happens on the land. Only the tundra and boreal forests have not suffered very extensive damage. Partly this may be because two groups of aquatic insects, the mosquitoes and the black flies, make them difficult to live in. (Source: Millennium Ecosystem Assessment.)
### Introduction

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<th>Driver’s current trends</th>
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<td>High</td>
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<td>Very high</td>
<td>Very rapid increase of the impact</td>
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**Fig. 1.6** Trends in damage to major world habitats and their reasons. The intensity of shading indicates the degree of damage so far. The arrows indicate whether this damage is decreasing (pointing downwards), staying the same (horizontal), or increasing to a moderate (sloping upwards) or high (vertical) degree. Changes are grouped as habitat change (mostly complete destruction), climate change, invasive species, overexploitation (by fisheries, for example) and eutrophication (pollution by excessive nutrients). Inland waters have suffered perhaps the greatest damage so far and are under the greatest future threats. (Source: Millennium Ecosystem assessment.)
Its stage is shifting, fleet and short;
Life, for its denizens, is fraught.
How well they've coped, you'll clearly see:
The bug, the bloom and the water flea.

Alas what is a wondrous world,
Is by humans often churled.
And so we'll teach of lakes polluted
And bubbling rivers dammed and muted.

And by the end I hope you'll feel
You know the problems, keen and real,
But also see remediation
And share our endless fascination

**FURTHER READING**

I have not peppered the text with numerous references, for the simple reason that there are now so many scientific papers, the text would be overwhelmed if I were comprehensive; and there would inevitably be a great deal of selectivity if I were not. Some worthy people left out might be mortally offended. Information gathering anyway has changed immensely in the past ten years. Use of key words in search systems such as the Web of Science or Google Scholar will turn up the background for any statement with little difficulty. People produce the information however, and they

**Fig. 1.7** The River Brede in southern Denmark was previously greatly modified by straightening and deepening to more efficiently drain surrounding agricultural land. Recently parts have been restored to their former course and the floodplain re-established. Segments of the original straightened channel can be seen along with the restored meanders, side channels and floodplain.
should be given proper credit. I have thus written sections on further reading for each Chapter to do this and guide readers to particularly relevant articles, especially books and reviews.


There is a tendency in education now to be superficial. You do the course, learn the textbook, answer the multiple-choice questions, pass the exam, throw away the notes, and move to the next thing. I think you lose a lot with that approach. I think you learn most from being and doing rather than as a passive spectator, which all that that approach makes you. You get into a subject by project and practical work, seeing what is going on in the field, investigating it. A book cannot give you this, but in Chapter 17, there are several problem exercises, which, if you can produce sensible solutions, will tell you if you have learnt something.
2.1 INTRODUCTION

Water is unremarkable and at the same time, exceptionally odd. The very fact that it is unremarkable (it is the most familiar of substances in everyday life; we handle it almost hourly) is because it is so odd. It is the only substance on Earth that commonly exists in all three of its solid (ice), liquid, and gaseous (water vapour) forms. On a day in spring in the north, when snow is melting, you will be aware of all three together as the water runs out of the melting snow and the vapour from your breath condenses in the cold air. This property is crucial for two reasons.

First, life on Earth depends on there being a liquid available. Biochemical systems cannot function as gases because the dispersion and random movement of the molecules does not allow close control of chemical reactions, nor as solids because chemical reactions are too slow in solids whose molecular movements are restrained. Second, there are no other natural substances that normally occur in quantities as liquids at the Earth’s surface. The nearest are hydrocarbons in oil deposits, but these are already derived from living organisms. Water was necessary for the living organisms that produced them. The very existence of life depends on the properties of water.

The remarkableness rests on the fact that, by rights of predictable chemistry, water should exist only as a gas at Earth temperatures. Water is the hydride of oxygen and should show a graded series of properties with the hydrides of the related elements, sulphur, selenium and tellurium, in the Periodic Table (Fig. 2.1). Hydrogen sulphide, hydrogen selenide and hydrogen telluride are all gases at Earth temperature and pressures. As the lightest of these compounds, hydrogen

<table>
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<tr>
<th></th>
<th>Melting point (°C)</th>
<th>Boiling point (°C)</th>
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<tr>
<td>H₂O</td>
<td>Actual 0</td>
<td>Expected (~100)</td>
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<td>Actual 100</td>
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<tr>
<td>H₂S</td>
<td>~85.5</td>
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<tr>
<td>H₂Se</td>
<td>~60.4</td>
<td>~41.5</td>
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<tr>
<td>H₂Te</td>
<td>~49.0</td>
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Fig. 2.1 The hydrides of the oxygen series in the Periodic Table include water, hydrogen sulphide, hydrogen selenide and hydrogen telluride. Based on the usual progressive change in properties down the columns of the table, water should have much lower freezing and boiling points than it does.
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oxide, H₂O, should also be a gas. Water thus evaporates and freezes at much higher temperatures than expected.

The consequences of these properties are important. The mean air temperature at the Earth’s surface is around 13°C. Earth’s surface extremes of temperature run to well below the freezing point of water (0°C) and to well above it in the molten lavas that emerge when volcanoes erupt. Even elsewhere, the heat of the summer sun can bring the soil temperature to 60 or 70°C, painful to bare feet and perilously close to water’s boiling point of 100°C. Both during a year, and over longer periods such as glacial epochs, changes in temperature can readily shift water from its (to living organisms) usable liquid form, to ice or vapour. Small changes in climate can lock enormous amounts away in polar glaciers or render moist regions arid. Small fluctuations in weather can mean that water supplies dry up or run amok as floods. Freshwater organisms, in the course of their evolutionary history have had to cope with these uncertainties. Human societies, equally dependent on liquid water, face them continuously. Water is abundant on Earth, but mostly in unusable form for land and freshwater organisms and people, as ice, in deep ground-waters or, particularly, as the saline ocean. The usable supply of freshwater is small and vulnerable.

There is more. Water is densest not at its freezing point, but at nearly 4°C above it so that water bodies freeze from the surface (Fig. 2.2), insulating the water underneath from further cooling and generally always leaving liquid water for living organisms beneath the ice. Water also dissolves a huge range of other compounds, making it the near universal solvent that is needed for a biochemical medium; it has a high specific heat, changing temperature relatively slowly and buffering temperature extremes for organisms living in it; it has a high viscosity, making it a ‘sticky’ medium for organisms living in it and its surfaces have a skin, a surface tension. All of these properties have effects on living organisms and rest on the particular molecular structure of water.

Fig. 2.2 Ice, broken off from the melting front of a glacier, floats in the lake formed at the foot of the glacier. The melting ice is at 0°C and the water at a little higher temperature. The ice floats because the water molecules of its crystal structure are more distantly spaced than those in the liquid water.
2.2 THE MOLECULAR PROPERTIES OF WATER AND THEIR PHYSICAL CONSEQUENCES

These are the bare bones of the structure of water: two hydrogen atoms and one oxygen atom, the hydrogens are held at nearly 0.1 nm from the oxygen, jointly making an angle of 104° 27' with it; the six electrons of the outer orbit of the oxygen are shared with the one from each of the hydrogens to give the eight that complete the shell of oxygen and the two that do likewise for the hydrogen. If that were all there was to it, water would be an unremarkable covalent compound and a gas at Earth temperatures. There would be no life on Earth, no ocean, no ice caps, simply a very hot, completely dry, laval waste.

The initial clue to why things are different comes from the angle at which the hydrogens are held. Theory predicts it should be 90° but it is more. The tiny phenomenon that makes all the difference is that the shared electrons are slightly more attracted to the oxygen than the hydrogens. The difference is small, but it makes the hydrogens slightly positive in charge and the oxygen slightly negative. The two slightly positive hydrogens repel one another, widening the angle between them. Much more importantly, since opposites attract, the hydrogen of one water molecule attracts and forms a bond with the oxygen of another. The molecules become joined together in a superstructure (Fig. 2.3) and that is the key.

A solid contains molecules that are very close together, often, as in a crystal, in a fixed geometric pattern. A gas has its molecules bearing no relation to one another but moving randomly at relatively far distances. Liquids have their molecules much closer together than in a gas, but much further apart than in a solid, and without the bonding that occurs to hold many solids together. Water, when a liquid, has its molecules close but also held together by hydrogen bonding, which is what the attraction between hydrogen and oxygen of different molecules is called. To break that structure, to convert liquid water to vapour, requires a lot of energy. Such energy is not available at low temperatures and as much as 100°C is needed for the conversion. Without the hydrogen bonding, water would become a gas at around minus 80°C.

2.2.1 Ice and melting

Ice has a crystal structure based on tetrahedrons of water molecules (Fig. 2.3). This holds the molecules relatively far apart and gives a low density to the ice. Ice floats on liquid water. At its melting point, as more heat energy is applied to the ice, this structure is broken and starts to collapse inwards. The liquid water at the melting point is denser than the ice. The water molecules in the meltwater still retain some structure, held together by the hydrogen bonding, so the total amount of energy needed for melting (the latent heat
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of fusion) is small. Water thus freezes and thaws rather easily. Beyond the freezing point, as the water warms, this structure is retained to a large extent but partly disrupts and freer water molecules start to collapse into the spaces of the structure. The density of the water thus increases a little. By about 4°C, more precisely 3.94°C for pure water under normal pressures, this process of collapse is balanced by the tendency of the molecules to vibrate more vigorously and move away from one another. At 4°C, therefore, the water is at its maximum density and as it warms more, it becomes less dense (Fig. 2.4). In reverse, when a water body cools through 4°C, the 4°C water sinks and colder water starts to float on it, resulting in lower density colder water, at the melting point, layering on the surface, where ice forms. Water bodies thus freeze from the top and because the ice provides some insulation to further heat loss to the atmosphere, it is unusual for them to freeze solid to the bottom.

2.2.2 Buffering and evaporation

Above 4°C, the water steadily gets less dense, so warmer water floats on cooler, but its temperature changes only slowly as heat is applied. This is because water has a high specific heat. It takes a lot of energy to break down the hydrogen bonds that hold water molecules together and because temperature is a measure of the degree to which molecules are vibrating or moving freely, temperature change is resisted. Liquid water thus buffers inputs (or losses) of heat because its structure resists the change. This keeps many freshwater habitats equable with narrow temperature ranges (sometimes only half as much as that of nearby aerial habitats) during the year.

If enough energy is applied, the water approaches its boiling point. This can occur naturally in volcanic areas where water is heated by underlying hot rocks. The heat required to evaporate water at the boiling point is substantial (over six times that needed to melt ice per unit mass) because the hydrogen-bonded structure has to be completely destroyed to convert liquid to vapour. Water is thus slow to evaporate, though with inputs of energy from the Sun and in dry atmospheric conditions where there is a large deficit of moisture in the atmosphere, it readily does so.

2.3 HOW MUCH WATER IS THERE AND WHERE IS IT?

Hydrogen and oxygen are among the commonest elements on Earth. Water is the most common compound in which they occur together. Water is not scarce. There is an enormous amount of it in the oceans, but it is wanting on the land surfaces, in the atmosphere and for the freshwater systems that are linked closely with them. Water is thus the most important limiting factor for plant growth and hence for ecosystem production on land. Freshwater in river and lake systems comprises only 0.02% of the total water on Earth. There is a little more, frozen into the polar ice caps and glaciers (2.1%) and in deep ground-water supplies (0.6%) where water rests in saturated pervious rocks, but the ocean holds 97.2% of the total.

2.3.1 Turnover and the hydrological cycle

On the other hand there is a fast turnover in the water cycle. The water cycle (Fig. 2.5) describes the gross movements of water molecules among the atmosphere, rivers, lakes, estuaries, and the ocean through rain and snow (precipitation), flow and evapotranspiration.
One particular water molecule may spend thousands of years in the ocean but its sister may spend only minutes or seconds in the sea after reaching it from a river before being evaporated back to the atmosphere. On average a water molecule will spend 11 days in the atmosphere before being condensed to rain or frozen as snow, and 2.3 years in the surface water (river/lake/estuary) system. It will spend 12,000 years in the glaciers and 300 years in the ground water. The rapid replacement of water in the surface freshwater system is one reason why restoration of polluted freshwaters is comparatively easy and the long average retention time in the oceans a good reason for avoiding contamination, for the problems can be with us for thousands of years.

### 2.3.2 Changes in geological time

The water balance, the distribution of water among the various components of surface freshwater, atmospheric vapour, ice, ground water and ocean, has varied over geological time, because the Earth’s climate has changed a lot. All surface freshwaters are temporary features in this respect but there has been an ocean continuously for at least 4 billion years, although it has changed shape as continents have moved and with them the pattern of ocean currents and the climate regimes.

There seem to have been three, at least, main states of the Earth’s water balance in geological time. Sometimes almost all of it has been in the ocean, leaving the land surfaces mostly as desert and what remained of the freshwater basins salty through evaporation (see below), as in the Devonian (360–400 Ma; million years ago) and late Permian (250 Ma) Periods. The Carboniferous Period (290–360 Ma) was in contrast clearly a very wet one, judging from the evidence of the extensive swamps that were the origins of coal deposits and there is much evidence of fossil dried-out lake basins from the early Permian Period, which succeeded the Carboniferous. Sometimes, as in the early Tertiary (65 Ma), there has been maximal humidity on land. The wet Tertiary period led to a phase of drying in which large arms of the ocean were cut off and transformed into inland lakes.

The third general state of the Earth’s water has seen much of the water locked into glaciers. The Pleistocene glaciation, from about 1.7 million years ago until 10,000 years ago effectively re-set the landscape of much of the temperate world but there have been several much older glaciations, including one at 600 Ma, which extended from the poles to within 10–15° of the Equator. The lands of the Earth have thus variously been very dry, very wet or frozen. The reasons are complex, but involve the movements of the Earth’s plates, changing the patterns of the continents and oceans, and rhythms in the orbit of the Earth around the Sun, which takes it sometimes slightly nearer, sometimes slightly further away.

We have just emerged from a frozen period that may have begun when continental drift in the late Oligocene (25 Ma) moved Antarctica into its present, polar position creating a circum-polar current around the continent that isolated it from warmer waters moving southwards from the Equator and promoting accumulation of much ice on its mountainous land surface. Ice began to form around the North Pole in quantity somewhat later, only 2.5 to 3 million years ago but the consequences were that high-latitude freshwater systems froze solid whilst those at lower latitudes were wetter through reduced temperatures and lesser evaporation. When eventually the ice started to melt back, temporary lakes formed against the retreating ice front. These could be huge. The Laurentian ice-lake, the precursor of the St Laurence Great Lakes that now straddle the USA and Canada.
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was 300,000 km² in area; a similar large lake preceded the Baltic Sea and there was another in West Siberia which has left no remaining large water body. Expansion, then melting back of the polar and mountain glaciers has caused considerable change to the freshwater systems, including the creation of millions of new lake basins.

The pattern of freshwaters changes also because geological events such as volcanic activity, crustal movements and landslides alter the configuration of the landscape and thus the nature of valleys and basins. Like the effects of natural climate change, such happenings are continual. One lake in Iceland fell in water level by several metres in 2000 because a small earthquake opened up a large crack in the rocks at the edge, down which enormous amounts of water have drained, exposing a large area, now of black lava or beach sands and gravel.

2.4 PATTERNS IN HYDROLOGY

The hydrology of a system is a description of the amounts of water passing through it and their seasonal distribution and variability among different years. This is usually expressed as a hydrograph, a graph of amount of water (the net run-off or discharge, equivalent to the difference between precipitation and evaporation in the catchment) passing down the river system. Hydrographs vary enormously from place to place and between years in the same place.

Polar and high mountain regions (Fig. 2.6) have some of the simplest patterns. Snow accumulates in the catchments in winter, melts in spring and summer to form a vigorous run-off into the basins, passes through the systems with relatively little evaporation and eventually reaches the sea. There are, however, in polar regions, some areas of intense dryness where accumulated snow will usually sublime straight to the atmosphere without an intervening step of liquid water. In some, warmer years, there may be melting and passage of liquid water into basins, but evaporation is intense from these also. The basins may have liquid water in them only in parts of some years. Salts, derived from rock weathering and washed in from the catchment with the water are not washed through but accumulate in salt pans. Systems in which there is a flow through of liquid water are called open or exorheic basins, those in which water leaves the basin only by evaporation are closed or endorheic basins.

In the course of geological time a basin may alternate between endorheic and exorheic dependent on climate change.

2.4.1 Temperate regions

Endorheic and exorheic systems are paired also in cold temperate climates, indeed in all climate regimes. In cold temperate regions (Fig. 2.6), wetter areas will have a pattern in which snow may accumulate on the catchment in winter and the freshwater basins will be flushed with torrents of meltwater in spring. If the region is slightly warmer, rain runs off more or less continuously in the winter and spring. Evaporation will account for some of the water but evaporation rates will be low in the lower temperatures of winter. The net run-off will thus be high and indeed most of the water entering the basins will come in winter and spring. It will not enter evenly, however.

There will be a spate following a period of rainfall or melt, followed by much lower flows in the streams in drier periods. During and just after rain, most of the water will have passed over the land surfaces or perhaps only through the superficial soil layers. In the dry periods, water that has passed into the deeper layers of soil or even underlying rock will supply the streams. This flow is called the base flow. In summer, net run-off is often zero or negative as evapotranspiration accounts for all of the summer rainfall and even some water stored in the soils. There may be brief periods of increased flow following summer storms, but most of the river flow will be maintained from the groundwater store. If there is no store to supply a base flow, the stream will dry up. This is often the case in smaller streams, which have a temporary character to them. In autumn, as temperatures fall, net run-off increases again and the streams rise to their winter levels for several months or for the time before the weather becomes so cold that the snow-beridden landscape freezes and run-off ceases until spring.

Rivers accommodate these seasonal changes in flow by adjusting the size of their beds. Even upland small rivers will have a riparian (bankside) zone that is covered in water during spring at least and sometimes all of winter, but is exposed in summer. Bigger rivers will accommodate the higher flows through the development of features such as meanders and a floodplain (Fig. 2.7). Meanders increase the length of the river and hence the capacity of the channel in summer:
floodplains are the channel that the river needs to accommodate the winter flows. They are parts of the river bed, not dry land that is sometimes flooded. Lakes accommodate these changes in amounts of water entering them from their inflow rivers by changing their levels. This means that parts of their shorelines will be exposed in summer and in shallow basins these may be quite extensive in area. In deeper lakes, the area exposed may be small because the change in inflow is relatively small in relation to the total volume of the basin.

### 2.4.2 Warm-temperate regions

The patterns of cold temperate regions become more exaggerated in the warm temperate region (Fig. 2.6). There will be little or no snow, so water runs off the land...
throughout the winter. The net run-off will be lower, the higher the temperature, because of increased evaporation with increased temperature. Run-off will cease earlier in summer with increased temperatures and resume later in autumn, so river and lake levels will be low for a longer period and the chances of complete drying out in summer will also increase. Shallow lakes will be more likely to dry up completely and the level changes in deep lakes will be more pronounced. On balance, more basins are likely to be endorheic as these conditions become more extreme, and although there is no shortage of endorheic areas in cold temperate regions (in Oregon and the steppes of central Asia for example), there are huge areas in which closed basins are the norm in the warm climates of Australia, the Mediterranean and Middle East, the south-western USA and Africa (Fig. 2.8).

2.4.3 Tropical cycles

Climate in the tropics (Fig. 2.6) gives patterns in which the same interplay of run-off and evaporation is at work but to extremes. The wet tropics, rain forest areas for example, may have continual rain-fed river flow and there may be no periods where rivers are dependent entirely on base flow from ground water, even though there is usually some seasonality in the amount of rainfall. Water levels will change as rainfall changes, often irregularly through the year. In the dry tropics, there may be only short bursts of rainfall: streams may sometimes flow only for a few days at a time before drying up. Lakes may fill with water for a year or two then dry up and become salt pans for long periods, even decades. If they are large enough, they may change level considerably and also respond in area of water, and salinity. In dry periods they will be much smaller and much saltier.

To these general patterns in hydrology set by the climate regime, there will be local complications. A river system in the tropics may paradoxically rise in the dry season. This may be because it is receiving a water supply from the distant reaches of a very large catchment. Water reaches the lower parts of the Amazon floodplain, for example, from snow melt in the Andes, two or three months later. This is the time it takes to travel the distance from one side of South America to the other. All very large rivers will have
similar complications. A second complication is that because water is in such short supply, it is often tapped for irrigation schemes, or flows are regulated for generation of hydroelectricity or irrigation storage. These interventions have often been so considerable that natural patterns have been nearly obliterated. Living organisms, however, have evolved their life histories in response to the natural patterns and such alterations may be terminally disruptive to them.

2.5 BODIES OF WATER AND THEIR TEMPERATURES

Water tumbling down streams and through rivers is generally well mixed and acquires the temperature of its surrounding air after a short period. A polar stream will be frozen in winter and in summer will be cold, perhaps only a few degrees; a tropical one will be well over 20°C for all of the year. The molecular physics of the water molecule will be reflected in how rapidly the water changes temperature, but in little else. Where the water forms a distinctive body, where it is retained en masse for some time – a lake – it is a different matter. Lakes form in dozens of different ways (Fig. 2.9; Chapter 11) but their essence is that the water has a long stay, a residence time generally of weeks to years, compared with rivers and streams where it might only be minutes or days. This residence allows the water mass to display some of the properties of the physical structure of its molecules.

2.5.1 Lakes and latitude

We will take a series of idealized lake basins at sea level from the Poles to the tropics, first a shallow series, then a deeper series. Shallow lakes (say 3 m or so mean depth) can easily be mixed by wind. They will thus be isothermal, the same temperature from top to bottom for much of the year. In summer, shallow lakes will track the changes in air temperature and in the warm temperate and tropical zones they will continue to mix in the winter or cooler season.

Towards the Poles and in the colder temperate regions (Fig. 2.10), however, they will cool more and may eventually cool to 4°C. At this point the dense 4°C water sinks to the bottom and further cooling, if the wind is not too strong, will result in colder water floating on it. Eventually, as the water reaches 0°C at the surface, ice, which is less dense than liquid water, begins to form, with a layering or stratification of warmer waters below it. This is called inverse stratification because the warmest (4°C) water is at the bottom. Under the ice, there is no significant mixing. In some polar and mountain lakes, the ice cover may be permanent, and in warm temperate and lowland tropical lakes, of course, it is absent. In between, the