Freshwater
· Ecology ·

PRINCIPLES AND APPLICATIONS

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Preface

Ironically, the planet we inhabit is called Earth. What makes planet three of our solar system special is water.

The presence of water on other worlds has a patchy history from the imagined seas of the Moon, canals of Mars and fetid, steamy forests of Venus to more recent, and definite, exploration of the atmospheres of some planets and their satellites. The extraordinary landscapes of Mars are very suggestive of surface water processes long ago.

The Earth alone retains surface water. Most of it makes up the oceans but the whole mass is not fixed. Water evaporates from sea and land, vapour clouds move in the atmosphere and rain falls to refill the seas, icecaps and underground stores and to supply the lakes, rivers, ponds and streams. For all their familiar beauty and importance in our lives, freshwaters are only a tiny proportion of the total water on Earth. They are a unique habitat with distinct flora and fauna, yet intimately linked to the wider world around them and sensitive to changes in this landscape, especially those brought about by humans. This book is written to explore and understand the ecology of freshwaters with three main threads. Firstly, the characteristics of aquatic habitats and, crucially, how these depend on the surrounding land and its use. Secondly, the ecology of the plant and animal communities, their links to the physical and chemical world and interactions with other wildlife. Thirdly, how human activities can perturb and destroy the habitats, their plants and animals and how these effects can be alleviated.

Freshwater ecology is a vast subject. There are many superb, thorough and detailed textbooks covering particular aspects in depth, whole volumes devoted to subjects that can scarcely take up a page or two here. There are also many reports and books that contain practical advice for good environmental management and conservation. Throughout this book references are given to these major texts so that students can follow up the basic principles outlined here and explore areas that interest them in all their complexity. The examples cited in more detail are largely drawn from widely available journals, again so that students can delve deeper. Examples have generally been chosen to point to the characteristic aspects of the topics

under discussion but also links with other patterns and processes, especially to link up ideas across chapters. Some of the practical conservation texts are perhaps less widely available but are worth the extra effort to track down. This is especially important as the links between the pure and applied sides of the science bear fruit and, most important of all, if we are to save our planet's unique freshwaters from the many dangers that threaten.

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1 Water

An enchanted vision of a verdant lake or gurgling stream is a picture that many people conjure up when thinking of freshwaters. These habitats are easy to envisage compared to the grades of terrestrial vegetation or invisible marine currents. Aquatic habitats are discrete, part of the landscape, but clearly delineated. Rivers and streams dissect the land, dividing it up. Lakes and ponds are scattered islands. This apparent separateness is so marked that freshwater ecology exists as a field often removed from wider ecological science.

This image of freshwater as isolated with a peculiar biology all their own is false. All freshwaters, from the longest rivers and broadest lakes to seasonal streams and rain pools, are intimately linked to the world around them. The water arrives from outside and eventually will leave. In between, the water will influence the surrounding land, perhaps directly in floods or erosion or by altering local climates and through the animals and plants using it. The waters will respond to climate. Chemicals will be gleaned from the surrounding area or arrive in the rain. It is very important to appreciate the role of these links between aquatic habitats and the landscape. Natural waters reflect the biogeographical world around them and unnatural waters, those altered, degraded and sometimes completely lost due to our actions, are so because of these same links.

1.1 The hydrological cycle

All water on the planet is linked by one global cycle, the *hydrological cycle*. No aquatic habitats are entirely static. Some water is always being added, some lost and some remains. The overall balance may be markedly in favour of one of these, for example a temporary pool drying out or a stream rising due to meltwater. The cycle can be simplified into a general pattern shown in Fig. 1.1.

A gross global budget of the whole planet's water can be drawn up and Table 1.1 summarizes this huge cycle. Three important points should be
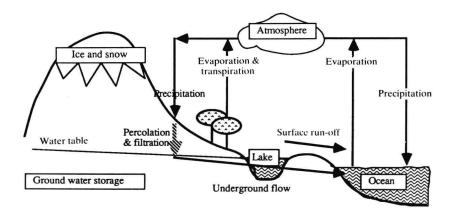
Fig. 1.1   The hydrological cycle. Evaporation of water from non-living sources is supplemented by water loss from plant life called evapotranspiration. This is important in terrestrial systems, and a major source of water loss from freshwaters with abundant emergent plant life.

Table 1.1   Estimated quantities of water in different parts of the hydrological cycle. Despite variations in estimates the same general pattern is evident; freshwater only makes up a tiny proportion of water on Earth, and genuine aquatic habitats such as rivers and lakes an even smaller amount

Component of	Volume ($10^3 km^3$)	% of total water
Oceans	1 320 000–1 370 000	97.3
Freshwater		
Icesheets/glaciers	24 000–29 000	2.1
Atmosphere	13–14	0.001
Ground water (to 4000m)	4000–8000	0.6
Soil moisture	60–80	0.006
Rivers	1.2	0.000 09
Saline lakes	104	0.007
Freshwater lakes	125	0.009

noted. The links between lakes and rivers and the wider world are very evident from even such a simplified scheme. Secondly, the whole process is dynamic. Aquatic habitats are a link in a constantly changing bigger cycle. The water at each stage will react in different ways influencing subsequent links. Atmospheric water vapour, many tiny droplets with a huge surface area, are ideal to dissolve gases, thereby altering the chemistry of the water that then fills the lakes and rivers. Underground water, often heated or pressurized, dissolves minerals. Thirdly, the processes are essentially similar regardless of the size of the water body. Water is entering, remaining and leaving Lake Baikal, the largest freshwater lake on Earth, and is entering,

remaining and leaving a village duck pond. Water enters, flows along and exits the River Amazon and in just the same way forms spatey streams on a mountainside. The scale at which ecological processes are measured and described may dramatically affect some conclusions. Differences in scale, both of time and physical space, should always be kept in mind in ecology. However, the general pattern of the global hydrological cycle is repeated at all scales in freshwater. Just as a gross global budget can be drawn up, estimates for a single aquatic system can be made.

Freshwater habitats may be vitally important parts of the landscape but they never make up much of the total area. An attempt to quantify the distribution of freshwaters in Britain estimated the percentage area occupied by freshwaters at between 0 and 1 per cent of the whole for most of England and Wales, with just a few highland areas with typically 2–5 per cent of their total area as freshwater (Fig. 1.2; Smith and Lyle, 1979).

1.2 Abiotic characteristics of water

As part of a vast geophysical cycle freshwater habitats are provided with water. Water is a very peculiar substance. It is the only liquid commonly found on the surface of the planet apart from occasional tar pits, molten rock, bubbling mud and the metal mercury, none of which is conducive to life. The strange properties of water create physical and chemical conditions to which wildlife must be adapted to exploit freshwaters. These physico-chemical constraints are abiotic (non-living) aspects of ecology and affect all aquatic habitats to some extent. However, the dominant influences vary from habitat to habitat: in rivers, the force of the water's flow may be of prime importance; in lakes, the depth to which light can penetrate may be most important. The same basic principles underlie all habitats and provide the basis for understanding how pollution and mismanagement can destroy systems. How these principles mould and form particular habitats, especially the differences between running and standing waters, will be explored in Chapters 2 and 3.

1.2.1. Physical characteristics of water

DENSITY

Freshwaters are waters in liquid phase, though many regularly solidify and all turn gaseous in part. Most living things also consist largely of water and so have a density very close to that of the medium itself. Living organisms will neither fall through water as they do through air nor, with the exception of tension effects, be able to live on it as they do on land. With little or no effort they can stay within the three-dimensional water column, passively
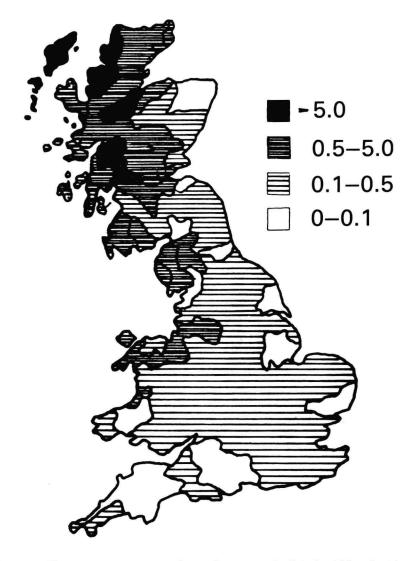
Fig. 1.2   The percentage area of standing water in Britain. (After Smith and Lyle, 1979).

floating and actively swimming but generally benefiting from the buoyancy. This is one unique feature of salt and freshwaters. Terrestrial habitats lack this exploitable matrix. Birds may fly but cannot spend all their lives aloft, unlike fish which can spend all their lives swimming. Many small insects and micro-organisms are blown into the atmosphere but they do not truly live in the air as do plankton in the open water column. Most plankton benefit by

just floating passively in the water column. Many larger animals are able to maintain station by actively swimming, with the buoyancy as an added bonus to support their weight. Plants are also able to exploit an easier lifestyle. Many aquatic plants, relying on buoyancy for support, are flimsy compared to terrestrial forms. Free floating forms occur, some submerged (e.g. water soldier, *Stratiotes aloides* L.) and others on the surface (e.g. duckweed, *Lemna* spp. and water hyacinth, *Eichhornia crassipes* (Mart.) Solms-Laub).

This surface is an additional habitat created by water's peculiar physical structure (Fig 1.3). Water molecules have a marked affinity for each other, due to the electrochemical properties of individual molecules. At the air/water boundary they stick together so thoroughly that a surface tension is set up that will support light weights especially if they are spread out, for example floating leaves or the splayed legs of surface insects, and equipped with water-repellent devices (air-retaining hairs, waxy or oily chemicals). The tension hinders other life. Many aquatic insect juveniles have to emerge as flying adults and require adaptations to break the tension. Flying adults of beetles and bugs have to heave themselves clear. Taking air from above the surface also requires hydrophobic hairs or similar structures to break through the surface tension. The tension traps many terrestrial invertebrates that lack the repellent adaptations, providing a rich source of food (Mason and MacDonald, 1982).
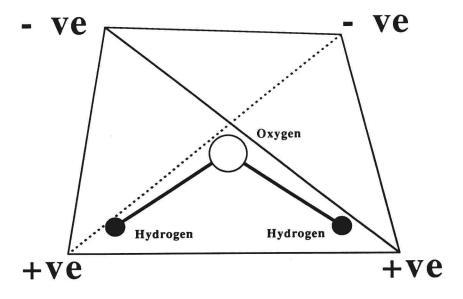

Fig 1.3 Stylized water molecule. The configuration of the oxygen and hydrogen atoms results in a slight positive (+ve) and negative (−ve) polarity in the molecules. The resulting electrochemical bonding gives water its unusual density and viscosity characteristics.

The density of the water column also creates problems. Water masses of different temperature differ in density. Water is densest at 3.95 °C. Water freezes to a solid at 0 °C and the fact that solid ice floats on liquid water would seem very anomalous if we were not so used to it. Solid ice has a regular molecular structure with slight gaps between the molecules. As ice melts, the regular form breaks up and these gaps fill. The density increases. This effect continues until 3.94 °C, so water at this temperature is densest due to the packing. Beyond 4 °C the increased energy of the warmed molecules causes more and more agitation. Above 4 °C the density decreases as the molecules increasingly separate. Their evaporation into a gaseous form is their ultimate fate with increasing heat. Between the extremes of ice and vapour density differences may occur between volumes of water. Currents of different temperature or layers in lakes differentially heated will not readily mix and their boundaries form barriers. To small plankton these may be physical, unable to push their way into denser water. Larger animals may avoid crossing between densities as conditions at one temperature may be poorer, perhaps the temperature itself or some difference in gas or nutrient solution.

The density of water gives the strength to the current in flowing systems. Confluent rivers do not always mix but continue side by side as distinct currents in the same channel. Movement of blocks of water of different density in lakes, as well as currents induced by wind action or rivers entering or leaving will also break up the apparent uniformity of standing waters.

Water even without the additional complexities of chemistry, habitat, plants and animals is a heterogeneous environment in which to live.

RADIATION

The sun's radiation sustains two important aspects of freshwater ecology. One is to heat the medium, resulting in density differences in the water mass, mixing and chemical alterations plus affecting the suitability of habitats depending on the temperature tolerances of the wildlife. The second aspect is providing light to power photosynthesis by plants, whether microscopic algae or macrophytes. Photosynthetically captured energy fuels their growth and eventually the whole community as the living plants or their dead remains are eaten. Visible light (which does not mean only that which is visible to us humans) has an important role as a natural clock governing the behaviours and life histories of many plants and animals. So the quality and quantity of light entering an aquatic habitat and how the water affects its availability are important.

The light penetrating water attenuates with depth. Different wavelengths of light are differentially absorbed. Distilled water, lacking all the dissolved chemicals and suspended particles which add to absorption, attentuates red wavelengths strongly, green and blue less so. However, no natural waters are so pure and organic particles markedly restrict blue light. Green is the

least susceptible but also the least useful to most plants for photosynthesis; they reflect it, so appear green to our eyes (Fig 1.4).

At some depth the energy harnessed by photosynthesis will only just equal the respiratory requirements of the plants. This depth is called the compensation point, generally represented by the lower limit of photosynthetic algae in a lake, though the compensation point for any individual species can also be measured. Above this depth there is enough light to sustain net growth and this is called the euphotic zone. Below is the profundal zone. The precise depth of the compensation point varies with seasons and changes in water colour and cloudiness (generally termed turbidity). As a simple rule of thumb the compensation point occurs at the depth at which 1 per cent of the original incident light penetrates (Fig. 1.5).

Calculations of the precise euphotic zone depth are possible but a simpler and commonly used measure of the turbidity uses the Secchi disc. This is a white disc (sometimes chequered black and white) lowered into the water
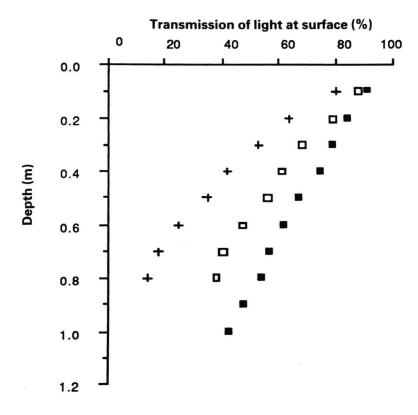
Fig 1.4 Transmission of light through the aquatic habitats: ■, Lake Windermere during an algal bloom; □, River Frome, a southern English river; +, effluent from a sewage treatment plant. (After Westlake, 1966)
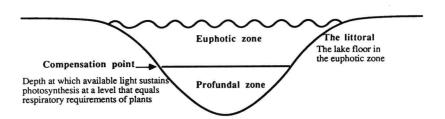
Fig. 1.5 Features of lentic habitats based on light regime. The compensation point, which is the depth at which photosynthesis just compensates for respiration, is taken as the divide between the euphotic and profundal zones. For a particular lake this point is generally marked by algae that can survive in very low light. Compensation points for individual plant species can also be measured.

column until no longer visible. This depth is called the Secchi disc transparency light extinction coefficient. It is named after Professor Secchi, whose efforts to quantify the turbidity were sponsored by Commander Cialdi of the Papal Navy in the nineteenth century. Although prone to differences due to plate size and the operator's skill, plus being only a relative measure of turbidity not absolute light energy, it is none the less a quick and intuitively nice technique.

Light affects the behaviour of organisms. Planktonic algae respond to different light intensity. Some actively swim up or down, for example the dinoflagellate *Ceratium hirudinella* OFM, or perhaps rely on the formation of gas vacuoles, for example many blue–green algae. Algae, especially diatoms, that live on the bottom are mobile and adjust their depth in the substrate as light changes. Algae and macrophytes can even alter the position of the photosynthesizing chloroplasts inside their cells according to light regime. Many animals in the open water column migrate, generally up at night and down during the day, for example zooplankton. Day length affects the life history, development and reproduction of many organisms, relying on light as a seasonal cue, or perhaps to coordinate daily rhythms. Shading and light regimes affect distributions across habitats and on a microscale around individual rocks and plants. Productivity and the growth of plants can be grossly affected, presenting management possibilities by use of appropriate shading. Kirk (1983) provides a very detailed text on light in the aquatic environment and how plants respond.

Much of the absorbed energy becomes heat. Water has unusual heating and cooling properties. Water has the highest specific heat capacity of any natural material, meaning the amount of energy needed to raise a mass of water by 1 °C is greater than that needed to raise an equal mass of any other material by the same amount. Similarly, a mass of water releases more energy as it cools by 1 °C than an equal mass of any other material. From an ecological point of view the basic result is that freshwaters take longer to