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THE NEW NATURALIST

A SURVEY OF BRITISH NATURAL HISTORY

LIFE IN LAKES AND RIVERS

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The aim of this series is to interest the general reader in the wild life of Britain by recapturing the inquiring spirit of the old naturalists. The Editors believe that the natural pride of the British public in the native fauna and flora, to which must be added concern for their conservation, is best fostered by maintaining a high standard of accuracy combined with clarity of exposition in presenting the results of modern scientific research. The plants and animals are described in relation to their homes and habitats and are portrayed in the full beauty of their natural colours, by the latest methods of colour photography and reproduction.

THE NEW NATURALIST

LIFE IN LAKES AND RIVERS

by

T. T. MACAN

M.A., PH. D.

and

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M.A., PH.D.

WITH 45 COLOUR PHOTOGRAPHS
BY JOHN MARKHAM AND OTHERS
68 PHOTOGRAPHS IN BLACK AND WHITE
20 MAPS AND DIAGRAMS



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EDITORS' PREFACE

DR. MACAN and Dr. Worthington, the collaborators in this scholarly and interesting book, have been colleagues for many years. Both are connected with the Fresh-water Biological Association's laboratory on Windermere in the English lakes.

The subject of life in British lakes and rivers occurred to the Editorial Board early in the planning of the NEW NATURALIST series. No sooner had the idea come to us than we invited Dr. E. B. Worthington to be the author of the book. Shortly after he had accepted the invitation, however, he left Windermere to take up an important appointment in East Africa. He suggested, when this happened, that the major task of the book should be taken over by his younger colleague, Dr. Macan, and that the final work should be a collaboration of the two of them. The happy result of this suggestion is now before the reader, who will agree that Dr. Macan and Dr. Worthington have written an admirably lucid and vital book on a somewhat neglected subject.

One of the points made by teachers of ecology in the last twenty years to their students is that the animal and plant community can be readily studied in a pond or a lake. That this is so the authors of this book, which is entirely ecological in its outlook, make quite clear. Moreover, in so far as it can be made simple they make it so. Nevertheless the reader, when he has finished the book, will realise that the solutions of many problems of life in lakes and rivers (solutions which have been often arrived at by workers at Windermere) have only served to create more problems—problems wider and more fundamental than perhaps anybody ever suspected, problems that reach far into the very structure of biology.

First appointed in 1935, Dr. Macan returned to Windermere in 1946 after five years as specialist entomologist in the Army. Dr. Worthington, well known on account of his explorations of the African lakes, came to Wray Castle as Director in 1937, when that post was

first created. Since 1946 he has been Scientific Secretary to the East Africa High Commission, in which position he has been surveying all East Africa in order to ascertain how and where the resources of science might be used to promote prosperity and well-being.

THE EDITORS

AUTHORS' PREFACE

IT IS becoming increasingly difficult to write a book which is not out of date in a number of minor, and perhaps a few major, particulars, because advances in every field are continually appearing in print and no-one can hope to keep abreast of all of them. The present authors do not venture to hope that they have not erred, but they have been in what are undoubtedly the most favourable circumstances for writing a book of this kind. Members of the staff of a fresh-water biological station, they have been surrounded by colleagues each an expert in one of the fields touched in the following pages. Moreover, these colleagues have been willing to read through chapters on their subjects and draw attention to errors and defects. Mr. H. C. Gilson has read chapters 1, 2, and 4; Dr. C. H. Mortimer chapters 2, 4, and 9; Dr. J. W. G. Lund and Dr. Hilda Canter have assisted with the botanical parts of several chapters; Dr. W. E. Frost has read chapters 11 and 12; Mr. E. D. Le Cren chapters 12 and 13; and Dr. C. B. Taylor chapters 14 and 15. Captain C. Diver, C.B.E., Director of the Biological Service, and Mr. F. T. K. Pentelow of the Ministry of Agriculture and Fisheries have criticized chapters 8 and 14 respectively. It is appropriate to acknowledge at this point that the editorial board has made many helpful suggestions.

No less important is a lay impression, since it is not for specialists and professional biologists that this book is primarily written. For this we are indebted to Mrs. Zaida Macan, who has read through the whole typescript; and to Mr. Maurice Illingworth, owner of the tarn shown in Plate XI facing p. 80, who has read chapter 12.

We record all this kindness with gratitude and take the opportunity to thank those who have helped us.

INTRODUCTION

It is interesting to speculate on the contents of an Atlantic Charter drawn up by any species of animal other than man. We may start by comparing the lot of man with that of the rest of the animal kingdom, which is separated by a lower grade of intelligence. People are not often drowned as a result of catastrophic floods, few are blown to destruction by strong winds, and death in a forest or heath fire is a rare calamity; nor do abnormal spells of hot or cold weather claim many victims. The same is true for all large animals. But for innumerable small ones such dangers are great, and the populations of many are seriously depleted at intervals by one or other of these causes. A final calamity, which does not often befall man, though it befalls other animals of all sizes is death at the hands of some beast of prey.

Medical science has rendered the more advanced sections of the community secure against many of the disease-causing parasites which formerly destroyed them in large numbers; plague (the black death), typhus (gaol-fever), and cholera may be mentioned as diseases that once took a heavy toll of life in the British Isles, but do so no longer. In less advanced parts of the world, disease still brings death to enormous numbers of human beings, and in this respect there is not so much difference between man and the other animals.

Death from starvation may have two causes: the food of a particular species may fail on account of some climatic irregularity, or may be eaten up by some other animal. We avoid the first of these eventualities by means of a highly organized system of transport; when the harvest fails in one part of the world, food is brought from somewhere else. But the recollection of the Bengal famine will serve as a reminder that this danger is not wholly eliminated. Against animals which eat the same food as himself, man brings to bear all the resources of science, and wages a never-ending war on rabbits, rats, grain-weevils, slugs, caterpillars, and a host of smaller pests. Lower animals cannot attack their competitors on anything like the

same scale; until recently it might have been stated that they could not do it at all, but now it is known that certain organisms can produce chemical substances that kill competitors—penicillin produced by the mould *Penicillium* is the obvious example—and this process is comparable with the steps that man takes to safeguard his food supplies.

Were we writing about philosophy and not natural history, we should of course have to insert a passage about the perils peculiar to civilization—death on the roads from motor vehicles, and other accidents with machines, destruction by high explosives and other weapons of war, and mass annihilation by atomic bombs. However, we are not. The purpose of what has been written is to stress that the life of a small animal—and it is with such that this book is mainly concerned—is a continual struggle of extreme severity. The physical environment, predators, parasites, and competitors all have to be contended with. The response has been steady change and continual modification. Some animals have won and held a place where physical conditions are easiest—but dangers from predators, parasites, and competitors consequently greatest. Others have become adapted to conditions where life is difficult—but where accordingly there will be fewer other organisms to harass them. Fresh water provides some of the most striking examples of the latter.

It might appear at first sight that the gulf between land animals and water animals is great, and that the easiest way into fresh water is from the sea. But, although an animal or plant may pass from marine to freshwater conditions with no alteration of structure, the change confronts it with considerable functional or physiological problems. The concentration of salts is generally much lower in fresh water than in the sea and moreover liable to considerable variation according to rainfall and other factors; from the biological point of view the constancy of the marine environment is one of its most notable features. Further, conditions vary widely from one freshwater locality to another. An animal proceeding up the Hampshire Avon, for example, would find, if it turned aside into one of the tributaries coming from the New Forest, an acid water, poor in dissolved salts, very different from that which would surround it if it followed the main river to its source at the foot of the chalk downs. These chemical conditions have proved a barrier which only a few marine animals have surmounted. Some of the snails, the bivalve

molluscs, the fresh-water shrimps, and the fishes are the most familiar.

(Actually it appears from an examination of the groups to which present-day fresh-water plants and animals belong, that it has been easier to invade fresh water from land than from the sea.)

The animals of marine origin occupy in fresh water the same sorts of situation that they occupied in the sea, and they have not changed greatly. As a result of isolation they are now quite distinct from their nearest marine relatives, but they present no peculiar fresh-water facies. Some of the land-animals, too, have effected the change to fresh water with little alteration; others with no more than some general adaptation such as the conversion of appendages from legs to paddles. But some of the animals from the land, having once established themselves in fresh water, have become considerably modified to live in one particular and difficult part of the underwater world such as a torrent; others have achieved remarkable physiological adaptations, such as the ability to live without oxygen. It is among these specialists that we find the peculiar and characteristic fresh-water types.

The main problem confronting an animal taking to the water is how to obtain its oxygen. Often the difficulty is not great, because many land animals live in damp places and have a moist surface. If they are quite small, this surface is all they require for respiratory purposes, and accordingly it does not matter greatly whether air or water is the medium beyond the layer of surface moisture. The problem is not quite as simple as this, but we need go no further for the present.

(Other animals, whose land ancestors were probably less dependent on humid conditions, spend their lives in the water, but have developed a variety of methods whereby they can utilize atmospheric oxygen. The familiar water-beetles swim to the surface with the aid of their hind legs (which, with the transfer to water, have been modified into efficient paddles), and take in a bubble of air between their backs and their wing-cases. Some snails come to the surface to fill a lung. Mosquito larvae—the well-known wrigglers of the domestic water-butt—feed at the surface with breathing-tubes penetrating through to the air. The rat-tailed maggot has a remarkable telescopic appendage, so that it can walk on the bottom and keep in contact with the air at the same time. Other animals take in oxygen as a gas but nevertheless

live perpetually submerged. Several groups—none of them very familiar to the layman—have a close-set pile of unwettable hairs. Withdrawal of oxygen for use by the body from the gas entrapped in this pile causes a partial vacuum, which is filled by oxygen dissolved in the water. Others tap the gas-filled tubes inside plants by means of some part of the body modified for the purpose.

Fresh water has presented invaders with a variety of problems, and no animal has solved all of them ; none is found in all the habitats and most are confined within a rather restricted range.

The surface offers a rich hunting-ground, for many land animals fall into the water and are held there helpless by the force of surface-tension. Two groups of insects have mastered the art of living on the surface film, and are able to prey on these unfortunates. They are, however, confined to small pieces of water or sheltered bays, presumably because the effort of keeping station against the wind in the middle of a big sheet of water is too great. The pond-skaters have developed long legs and proceed somewhat after the manner of long-oared skiffs. The other group, the whirligig beetles, have shortened and flattened their legs till they resemble more the paddles of a canoe ; by means of them they move over the surface with great rapidity. The way of life of these surface-dwellers calls to mind that of the wreckers who once gained a livelihood round our coasts, though they are not able to take measures to lure their victims to destruction.

Quiet shallow conditions, where mud settles and rooted plants—all incidentally of terrestial origin—provide shelter, oxygen, and food, are probably the most easy to colonize ; that is, they present the would-be inhabitant with least in the way of physical and chemical difficulties. But life is not easy in this habitat because there are so many different types of organism and competition between them is severe. (The water-beetles and water-boatmen pursue their prey through the underwater jungle with the speed and grace of terrestrial felines ; dragon-fly nymphs lurk concealed like a crocodile in a water-hole ; the tiny *Hydra* trails its tentacles in the water like a fisherman setting out his net.) Against these marauders the caddis-larvae seek protection within a cumbersome house of stick or stone, and snails can withdraw into their more neatly-made shell. But the snail's shell, the caddis-larva's house, the dragon-fly nymph's protective coloration, and the beetle's speed may alike prove unavailing when fish come nosing through the undergrowth in search of food. They are not the

only enemies, and some birds and the water-shrew also hunt in this territory.

In deeper water, if it is too dark for plants to grow, the mud offers a substratum which is often rich, because the remains of animals and plants rain upon it from above. Here the chief inhabitants are mussels, worms and midge-larvae, most of which are modified for burrowing and for feeding on minute particles. The diversity of form is not great, though the number of individuals may be colossal.

In yet deeper water conditions may be extremely difficult, because there is no oxygen for part of the year, but some animals, notably midge-larvae, have solved this physiological problem, though exactly how they have done it has not been discovered.

In the open water also the variety of form is not great, though numbers may be. Some small animals, such as the water-flea, resemble their counterparts in the sea, but the marine zoologist inspecting a fresh-water catch is immediately struck by the lack of diversity. This is partly because many marine animals which lead a fixed or relatively sedentary life have a free-swimming young stage. This presumably serves the end of dispersing the species. In the circumscribed conditions of fresh water such a stage is of less advantage for this purpose, and might indeed prove a danger by being carried away to the sea before it was ready to settle. Fresh-water animals which have come in direct from the sea have almost all lost the free-swimming stage, which their nearest marine relatives possess.

One representative of that enterprising group the insects inhabits open water, and provides one of the most remarkable examples of adaptation that the animal kingdom has to show. It is the larva of a mosquito-like fly, and is known as the phantom larva. Its body is transparent, a feature found in nearly all animals with this way of life, presumably because it renders them inconspicuous to their enemies. The breathing-tubes, in other insects continuous from back to front, are vestigial except for paired air-sacs fore and aft. These are hydrostatic organs by means of which the animal can maintain itself at any desired depth. The earliest workers supposed that it functioned like a submarine, pumping fluid in or out of ballast tanks as required. Later observers, noting that the bladders never contained fluid, postulated that they worked like the swim-bladders of fishes, and secreted or absorbed oxygen. Finally, when a technique for analysing the minute quantities of gas in the bladders was evolved, it was dis-

covered that the walls of the bladders expand or contract as the result of nervous stimulation, and the gases dissolved in the body-fluid diffuse in or out accordingly.

Rocky shores of lakes are startlingly barren places compared with those of the sea; there is no canopy of weeds nor incrustation of barnacles and other sessile animals. The two are not strictly comparable, because in fresh water there is no tide and the water may sink slowly to a low level and stay there during a long spell of fine calm weather. But even below this level there are not many living organisms. Probably this is due to a poor food-supply, for hard rocks and waters that are not rich in nutrient substances commonly go together. Perhaps this is an environmental niche that has not been completely filled; the fact that neither rocks nor wood are attacked by boring organisms in fresh water, as they are in the sea, suggests that this idea is not as revolutionary as it may seem at first. Further, the zebra mussel, the only fresh-water bivalve that can attach itself to a hard substratum as the marine mussels do, has only recently entered fresh water.

On a rock-face in a lake the only plants are green algae, and the only animal the fresh-water limpet.) This is actually descended from terrestrial stock, though superficially it resembles the marine limpet closely except in size. Smooth rock in a stream may have some covering of moss, which harbours many animals. If it is bare, it may be covered by great numbers of buffalo-gnat larvae, which spin a web across its surface and attach themselves by means of a circle of hooks on a basal pad. They obtain food by straining the current with hairy mouth-appendages.

Smooth rock is not found very frequently, and, where wave action or running water prevents the settling of finer particles, the bottom usually consists of stones and boulders. Several animals have adapted themselves to these particular conditions. Some mayfly nymphs, such for example as those of the March Brown, have flat bodies and strong claws, and can crawl over the surface of a stone, where they graze on the attached algae, in such a way that the current cannot get beneath them and pluck them off. Certain caddis-larvae spin nets between the stones in a stream and subsist on the debris which these nets strain from the current.

These animals are specialists. They have solved the main problem of life in swiftly flowing water—anchorage; and two, having sur-

mounted this difficulty, have turned the peculiarity of the medium to their own advantage—the constant flow brings them their food. The modifications of the specialists render them unable to compete with other animals except in the habitat to which they are adapted. Except in extreme conditions, specialists and non-specialists are found side by side. In streams, for example, many animals without any particular modifications for life in running water occur beneath the stones. One of them, the larva of the daddy-long-legs, is not greatly different in structure from its relative the leather-jacket, which lives in the soil and damages lawns and pastures by eating the grass-roots. Another, one of the commonest, is the fresh-water shrimp (*Gammarus pulex*), a rather incompetent swimmer which is washed away at once if caught by the current. It is one of the most successful of all fresh-water animals. It may be abundant in quiet weed-beds, and sometimes, apparently when fish are very few or absent, it may live in the open water of lakes. But it is not ubiquitous and some of the chemical problems posed by fresh water have proved too much for it ; it is not found where the calcium concentration is very low, and it also requires a relatively large amount of oxygen in the water.

There is another difficulty with which fresh water confronts animals and plants that seek to live in it—it may dry up. Many fresh-water organisms have, accordingly, developed a resting stage, which is resistant to desiccation and probably plays an important part in dispersal as well as survival. Some animals have specialized in the temporary habitat, thereby gaining certain advantages, for they make a quick start when water reappears, and can exploit the resources of the pond before it fills up with competitors coming from permanent pieces of water. Many mosquitos lay drought-resisting eggs in damp hollows, and no development takes place till the hollows fill with water. That beautiful animal, the fairy shrimp, is found only in temporary pools, and survives the dry periods in the egg-stage. In England it is rare, but in Iraq, for example, where there are innumerable pools that fill when the high river-level causes the water-table to rise in spring, but are dry throughout the rainless summer, it is one of the commonest pond animals.

Nobody in these islands has far to go to find a piece of fresh water, and his search will usually take him into pleasant surroundings. He will not find the gaily coloured, almost gaudy, creatures that the seaside naturalist encounters ; most fresh-water animals are rather drab. On

the other hand neither land nor sea animals can so easily be kept and watched at home. Moreover a day's pond-hunting is not rendered fruitless by rain, as is an excursion after butterflies and many other land creatures. The fauna is, as we have just seen, the product of a difficult environment, a severe struggle for existence, and the adaptability and plasticity of living organisms. In consequence it shows a fascinating diversity of form and function, which cannot fail to appeal to all who are interested in wild creatures and how they live.

CHAPTER I

FIRST PRINCIPLES

LIFE IN LAKES AND RIVERS is studied by three different sorts of naturalist, whose spheres of interest all too rarely overlap. First there is the naturalist with a pond-net who collects the smaller animals and plants of the water; secondly there is the naturalist with a fishing-rod, who classes organisms according to their relationship to fish; finally there is the naturalist with field-glasses for whom rivers, lakes and reservoirs are places where interesting birds and mammals may be observed. This book attempts to link these three fields together, to relate them to the geographical background, and to discuss the conflict which is bound to centre round them in a thickly populated and heavily industrialized country.

The fisherman is often less interested in the question of what kinds of animals and plants occur in a given set of conditions than in the question of how many, or rather how much, and this question is also fundamental for naturalists of the other two classes. The answer, as given by the study of productivity, has provided a central connecting theme in the pages that follow. Productivity must ultimately depend on the amount of non-living material brought into a body of water in solution and in suspension, and so the story starts with the geology of the surrounding land. Closely bound up with this is the way in which the body of water was formed. When the primary nutrient materials reach the water they are utilized by plants, and plants always form the first link of the biological food-chain. Succeeding links are provided by various invertebrate animals and finally fish. At all stages living organisms die and decompose, resolving eventually into the simple substances from which they are built up. The mechanism of this process is studied by the bacteriologist. The result presents the chemist with many of his problems, and takes him particularly to the mud over

which the water lies. This may be at a considerable depth and far below the point to which light penetrates sufficiently to make plants grow. The return of these substances to the upper layers, obviously of great importance to the biological cycle, involves an incursion into the field of physics.

Fish with predaceous habits are generally the final link of the food-chain within the water itself. But the chain continues on to the land and into the air, for there are piscivorous birds and mammals which the fresh-water biologist must study.

Man himself exerts a profound effect on life in fresh water. First, since earliest times he has striven to keep water within defined limits by means of drains and flood banks. More recently he has taken to using rivers as convenient agents for the removal of his waste products. Sewage, in moderate amounts, enriches water as it enriches land, but in excess it uses up all the oxygen in solution, with disastrous effects on most living organisms. In conflict with those who have wastes to dispose of are those who wish to see their waters well stocked with fish. These people, too, have played a big part in altering the conditions of water-life. Finally, man is to-day faced with an ever-increasing problem of obtaining for domestic use water containing the minimum possible amount of life.

Many insects start life in the water but end it as terrestrial creatures with the power of flight. Their life-histories have fascinated naturalists for a very long time and they attracted the attention of some of the first workers in the field of fresh-water biology. But studies involving all the animals, all the plants, the chemical and physical background, and the inter-relationships between them were not made until later. To work of this kind the terms limnology, hydrobiology, or fresh-water biology are applied indifferently. The pioneer was Professor F.-A. Forel who, in 1872, settled down to a lifetime's investigation of Lake Geneva or Le Léman. His main publication runs to three volumes, the first of which appeared in 1892, and considers the lake from thirteen different aspects.

In 1884 scientific investigation of fishery problems with a view to legislation started in Hungary, and in the two succeeding decades research stations with the same object sprang up all over Europe. In 1890 Professor Otto Zacharias started a station for fundamental research at Plön in Schleswig-Holstein. It was a private venture but it was supported by the State. With its foundation Germany took the lead in

both applied and theoretical research and she retained this position until the recent war. Professor August Thienemann was director at Plön during the period between the wars, and his name is associated with many limnological studies, particularly those relating to the classification of lakes according to oxygen concentration, and according to the species of midge (Chironomidae) found in the bottom mud. Stations for fundamental research were started in other countries in the years which followed, usually in connection with universities. The best known to-day are : Hillerød in Denmark, opened in 1900 by the University of Copenhagen and made famous by Professor C. Wesenberg-Lund, who devoted the first ten years to plankton problems and has since studied the biology of many invertebrate groups ; Lunz, opened in 1905 on an Alpine lake in Austria ; Aneboda, started in 1908 by the University of Lund in Sweden and associated particularly with the name of Einar Naumann, who elaborated theories of lake classification ; and Tihany on Lake Balaton in Hungary. Most other countries in Europe have some limnologists among the staffs of their universities, and usually at least a small research station used in summer-time. There are also a number of institutions devoted to the study of purely practical problems. The farming of fresh-water fish is widely practised in Europe and it has been the subject of a large amount of research.

Development in America was similar ; the first station was founded in 1894 by the University of Illinois. To-day the United States have a great many stations, some run in conjunction with universities and others independent. The latter are almost all concerned with problems of wild life conservation, and in the application of science to sporting fisheries America easily leads the world. The most notable American advances in theoretical limnology are associated with the names of E. A. Birge, C. Juday and Wisconsin University. To-day many American universities pursue a policy of applied research, at least in part; there is a vigorous school of fundamental hydrobiology centring round Professor G. Evelyn Hutchinson of Yale University.

Great Britain has lagged far behind and it is interesting to quote the words of Professor Charles A. Kofoid (1910) who, in 1908 and 1909, toured the research stations of Europe. He writes : " The direct support of biological stations by educational funds of local or state origin, often in connection with universities, so generally prevalent in other European countries, is almost wholly lacking in Great Britain."

" The stations have been forced, therefore, to turn to memberships of supporting societies composed to a considerable extent of scientific men themselves, to private benefactors and to the commercial interests of the fisheries for aid. The result has been a relatively meager and fluctuating financial support . . . and a relatively very large absorption of the funds and activities of the British stations in scientific fisheries work."

However, in spite of this, or should it be because of this, the " meager and fluctuating financial support " having deterred all but the most determined and enthusiastic from seeking employment of this sort, Kofoid's opinion is : " The scientific fisheries work done by the British stations is unsurpassed in its excellence and effectiveness."

Marine problems have always taken pride of place in Britain. As befitted the leading maritime power of the day, she was the first to send out a major expedition to explore the depths of the ocean, when it was first realized that life existed there. H.M.S. *Challenger* set out early in 1873 and was at sea until late in 1876. Soundings, collections of animals and plants, chemical analyses, meteorological records, and other scientific data were obtained in all parts of the world, and the total achievement was considerable. It was the culmination of a collaboration between science and the Royal Navy which had been yielding fruit for a century or more. One of the junior scientists was a certain John Murray, who later, as Sir John Murray, became head of the Challenger Office, and was responsible for seeing the final volumes of the reports through the press, many years after H.M.S. *Challenger* had been relegated to the scrapyard.

He found time to organize Britain's first important contribution to limnology—the Survey of the Scottish Fresh-water Lochs, carried out between 1897 and 1909. This was a private venture undertaken after he had ascertained that the Lords Commissioners of the Admiralty were not concerned with fresh water, and that the Survey Department of the Office of Works (late Ordnance Survey) was not interested in anything except the surface of bodies of fresh water. Five hundred and sixty-two lochs were surveyed and, though sounding was the principle activity, sufficient observations on temperature were taken to provide the data for a theory about the circulation of water in the deeper parts of lakes—a theory which is still accepted to-day. Plankton collections were made but other biological observations were few.

In 1901 Mr. Eustace Gurney started a station on Sutton Broad in

Norfolk, and during the succeeding years a vigorous programme was carried out here under the direction of his brother, Dr. Robert Gurney. It was, however, a private venture and it lapsed when the Gurney brothers moved away from the neighbourhood.

The next event of importance in the history of British fresh-water biology was the issue in 1915 of the final report of the Royal Commission on Sewage Disposal, appointed in 1898. This Commission had carried out a careful examination of almost all aspects of the problem, even to the extent of inaugurating research to obtain certain information which it deemed essential. That our rivers are still polluted by sewage must be laid at the door of the legislators and not blamed on the Royal Commission.

Between the two wars several rivers were surveyed by staff of the Ministry of Agriculture and Fisheries. The primary object was to discover the effect of pollution on animals and plants, but obviously in order to do this it was necessary to survey unpolluted stretches for comparison, and the result was an important contribution to knowledge about the fauna and flora of uncontaminated rivers. During the same time Dr. Kathleen Carpenter of the University College of Wales investigated stream faunas and the effect on them of pollution from lead mines. This work established a tradition of fresh-water biology in Wales which has persisted ever since.

In the twenties the foundation of a station for fresh-water biological research in Britain was discussed. A number of distinguished men of science came together and worked hard exploring ways and means. The interest of universities, academic societies, fishermen, and water-works undertakings was aroused and, when, in 1930, subscriptions totalled £575 and promise of a grant of about the same amount had been obtained from the Government, the time to start was deemed to have arrived. Ideas about a new building properly equipped had to be abandoned, and search was made for an existing building which could be adapted. It had been decided that Windermere was the most suitable location, and on the banks of this lake the committee found that a place called Wray Castle was only partly occupied. It appeared to be suitable and in October, 1931, work started in a Victorian country house built externally in the style of a medieval castle.

At the beginning there were two naturalists, Mr. P. Ullyott and Mr. R. S. A. Beauchamp, and one laboratory assistant, George Thompson. The apparatus and general facilities were meagre, as may be

appreciated from the amount of money available. Further subscriptions were raised, and by the end of 1935 there were five research workers and three assistants. In the following year a committee from the Development Commission inspected the laboratories and the work in progress, and, as a result of their visit, a bigger annual grant from the Treasury became available. One of their recommendations was the appointment of a full-time director, this office having previously been honorary and filled by Dr. W. H. Pearsall (now Prof. W. H. Pearsall, F.R.S.), at that time Reader in Botany at Leeds University.

Expansion continued and in 1947 there were ten research workers, twelve laboratory assistants, and an instrument-maker. Wray Castle was now too small to provide, as it had done hitherto, laboratories, and living accommodation for unmarried members of the staff and visiting research workers, and in 1948 what had been the Ferry Hotel was purchased to take its place.

As a final introductory topic, physical and chemical properties which affect living organisms demand brief notice. Warm water is lighter than cold water and so floats on it, a phenomenon which leads to temperature-layering of lakes in summer, and thereby exerts a profound effect on the animals and plants. This subject is explored further in later chapters.

In the present chapter we shall notice only some of the properties of water at low temperatures. Water is densest at four degrees above freezing point on the centigrade scale. This is 4° C., since freezing point is at 0° on this sensible scale, but 39·2° on the Fahrenheit scale, which is still in common use in Britain, and on which 32° is the freezing point of pure water.

As the surface of a lake cools down in the autumn, the upper layers sink and displace warmer water from below. This process goes on till the temperature is uniform at 4° C. from top to bottom. Water colder than 4° C. is less dense and therefore floats at the surface, and, if there is no wind to stir it up and mix it with the water below, this surface layer will be quite thin. Further cooling leads to the formation of ice. There can then be no physical mixing due to wind and, if cold conditions at the surface persist, the effect can only pass through the water by the slow process of conduction. In Britain, therefore, ice never gets very thick.

If water were to become steadily denser until freezing point was

reached, a body of water would attain a condition where the temperature was uniformly just above freezing point from top to bottom. Further cooling would presumably cause the whole mass to freeze solid. It has been stated in print that such a state of affairs would mean that nothing could live in fresh waters in temperate latitudes. This is hardly likely to be true because a number of animals can withstand being frozen solid, but it is certainly more convenient, particularly for man, that water is heaviest at 4° C.

For every thirty feet that an object sinks below the surface of the water the pressure upon it increases by one atmosphere. The pressure in deep water has been brought vividly to the notice of many a biologist who has inadvertently lowered a water sampler unopened into deep water, and hauled it up to find quite flat what had been a cylinder (Plate IIa, p. 37). Water itself is almost incompressible, and, if it were quite incompressible, Windermere, which is 219 feet or 67 metres deep at the deepest point, would be only a millimetre or about 1/25th of an inch deeper than it is at present. There is not, therefore, a big increase in density with increasing depth and no grounds whatever for the popular idea that objects thrown overboard in deep water do not go right down to the bottom, but float at a certain depth, light objects reaching a point of equilibrium before heavier objects; anything of higher specific gravity than water will go on sinking till it reaches the bottom. The pressure inside an aquatic organism is approximately the same as the pressure outside, and creatures which live in deep water do not, therefore, possess adaptations to withstand pressure as is sometimes supposed. Rapid progress from deep to shallow water may prove disastrous for any animal, because bubbles of gas appear in the blood on account of the reduced pressure; swim-bladders of fish may burst.

Water is twice as viscous near freezing point as at ordinary summer temperature, and this has an important bearing on the rate at which small bodies sink.

The surface tension of water is a physical factor which looms very large in the lives of animals and plants below a certain size. Some animals such as the water-crickets (Plate XIXc, p. 112) can support themselves on the surface of the water by it, and snails and flatworms can sometimes be seen crawling along the underside of the surface film. Occasionally aquatic creatures get trapped in the surface film and are unable to get back into the water. Terrestrial animals that alight on

the water surface frequently find themselves entrapped, and at certain times of year these unfortunates make quite an important contribution to the food supply of certain predators which dwell in or on the water.

Any natural body of water will contain a certain amount of dissolved matter, the quality and quantity of which will depend on the geology of the land over which or through which the water has flowed. It is possible to recognize certain types, though generalizations are not very profitable because modifying factors are numerous. The main substances in solution in some of the chief types of water are shown in Table 1.

TABLE I

The metallic and acidic radicles of the commoner dissolved substances in certain natural waters: figures in parts per million.

	Ennerdale, Cumberland	*Cambridge tap-water*	*Braintree, Essex*	*Burton Well*	*Sea Water*	*The Dead Sea*
Sodium	5·8	1·8	343	51	10,720	142,945
Potassium		7·5		57	380	44,186
Magnesium	0·72	26·5	15	39	1,320	413,241
Calcium	0·8	51	17·5	159	420	171,534
Chloride	5·7	18	407	90	19,320	1,819,600
Sulphate	4·6	16	96	378	2,700	6,237
Carbonate	1·2	123	218	121	70	trace
Silicon dioxide	1·6	—	2	9	1·4	trace

Ennerdale is an extreme example of a soft water. Cambridge tap-water is a fairly typical hard water derived from a drainage area in which there are chalk downs. The radicles present in much greater amount in the Cambridge water than in the Ennerdale water are calcium, magnesium, and carbonate. The Burton well-water is included as a curiosity which may be of interest to beer drinkers; it has an unusually large number of radicles present in high or relatively high concentration. The permanent hardness of Burton water is due to gypsum—calcium sulphate. A chloride content higher than usual is commonly due to spray from the sea, to wind-blown sea-sand, or to pollution. In inland areas well away from any maritime influence the chloride content is often examined as a routine part of the test for pollution.

If a water containing calcium carbonate flows through a soil containing sodium, sodium displaces calcium and the calcium goes out of solution. An example of such a water is that from Braintree in Essex shown in column three of table 1 ; water draining from a calcareous region passes through the Thanet Sands, which are marine in origin, and emerges with quite a small amount of calcium in solution. This displacement of calcium by sodium is the essence of the " Permutit " process for water-softening. Incidentally hard waters are frequently softened before being supplied to consumers. This is now a practice of the Cambridge Water Supply Company ; Cambridge tap-water to-day contains less calcium than is shown in table 1, in which the figures are from an analysis made before the softener was installed. Very soft waters, on the other hand, are sometimes treated with lime in the belief that defective teeth in the local children are due to the low calcium content of the water ; but no convincing proof that this is so has ever been given. Very soft waters sometimes corrode pipes, owing to the presence of humic acids, and this can be cured by adding lime.

Further figures may be found in Suckling (1944), where there are seventy pages of them, not only from all parts of the British Isles but from other parts of the world as well.

The sea contains the accumulation of salts brought down by fresh waters over a period of aeons. Calcium has been lost from sea-water generally not by precipitation but by incorporation into the skeletons of animals, which have later died and fallen to the bottom of the sea. Small, single-celled animals play a greater part in this process than larger ones ; for example, *Globigerina* ooze, which covers vast areas of the bottom of the ocean, is made up chiefly of the calcareous shells of a small single-celled animal bearing that name. Present-day chalk downs were formed under the sea by the accumulation in this way of the skeletons of myriads of tiny animals.

A similar concentration of salts takes place in lakes occupying areas of inland drainage, where there is no outlet and the water lost by evaporation is equal to the amount flowing in. In some such lakes the process has gone further than in the sea. Common salt or sodium chloride is the most abundant chemical substance in the sea ; but the Dead Sea has reached a stage where there is some precipitation of sodium chloride, and this substance is present in smaller amount than the more soluble magnesium chloride. The proportions of these two

salts in the River Jordan are the reverse of those in the Dead Sea. But there are no drainage areas in Britain without egress to the sea, and therefore discussion of such places is outside our present scope.

There are many substances present in water in very small quantity. It is known that on land and in the sea some of these so-called trace elements are important biologically and the same is probably true in fresh water.

No mention has been made so far of nitrates and phosphates, which are usually present in fresh water. As will be seen in a later chapter (see Fig. 2, p. 22) they are essential for plant growth, and during the course of plant growth their concentration in the water is reduced. The fluctuation throughout the year is large and a single value for any one piece of water is, therefore, of no great significance.

Finally, of extreme importance to living organisms is the amount of dissolved gases in the water. Under average conditions at 0° C. (32° F.) there will be about 10 cubic centimetres of oxygen and half a cubic centimetre of carbon dioxide dissolved in one litre of water, that is 100 parts and 5 parts per million respectively. The concentration falls with rising temperature and at 20° C. (68° F.) there will be only about 65 parts of oxygen and rather less than 3 parts of carbon dioxide. A figure showing so many parts per million of oxygen is, therefore, not very valuable, and the usual practice is to express the concentration as the percentage of the saturation concentration at the temperature prevailing when the sample was taken. Fifty parts per million of oxygen would be 50% of the saturation value at 0° C. but 77% at 20° C.

Animals use up oxygen and produce carbon dioxide and plants do the same in the dark. While illuminated, the latter do the reverse, absorbing carbon dioxide and producing oxygen. Still water with much vegetation in bright sunlight may for a period have more oxygen in solution than the normal maximum at the temperature prevailing. This condition, which is unstable, is technically known as super-saturation.

Decomposition also uses up oxygen, and serious pollution, by sewage for example, exerts its effect on the fauna by depleting the water of oxygen.

One rather important point is that, if water is quite still, oxygen or any other substance in solution can only pass from a region of higher to a region of lower concentration by diffusion, and this process is extremely slow.

CHAPTER 2

A TYPICAL LAKE

WHAT is happening in a lake on a still sunny day early in the year when there is beginning to be some warmth in the sun? With increased temperature the tempo of life will quicken, but the answer to the question is more far-reaching than that, and must be examined in some detail.

There will be a period after the coldest part of the winter when, from top to bottom, the lake will have a uniform temperature of 4° C., or a degree or two above it if the winter has been a mild one. The left-hand side of Fig. 1 shows the actual state of affairs in Windermere in February, 1948. As the sun gathers strength and the days lengthen, the upper layers of the lake will be warmed—only the upper layers because the heating part of the sun's rays is soon absorbed in water. Many people bathing on a hot still day have had the experience of diving through a pleasantly warm layer of water at the surface into startlingly cold water below. Warm water floats on cold water. Perhaps the first fine spell is followed by a stormy period, and the warm upper and cold lower water is mixed, but sooner or later the two layers are established with such a big temperature difference between them that they remain separate for the rest of the summer.

Once it is firmly demarcated, the warm upper layer of water increases in temperature relatively rapidly, and it also increases in depth because, when disturbed by the wind, it mixes with eddies of cold water from below. The cold lower layer has no source of heat, except perhaps from a small amount of mixing with warm surface water. The right-hand side of Fig. 1 shows that by mid-summer the upper layer is many times warmer than in winter, but the lower layer has increased in temperature by no more than a few degrees. Between

the two there is a short depth of water in which the temperature drops rapidly. The warm upper layer is known as the epilimnion, the cold lower layer as the hypolimnion, and the region of rapidly dropping temperature between them is the thermocline. Greek scholars will have no difficulty with these terms, others may be puzzled to remember which of the first two is which, but there is a simple mnemonic, for *epi-* and *upper* begin with vowels and *hypo-* and *lower* with consonants.

Wind is the next factor. Blowing over the surface of a body of water it will set up a current which carries water to the leeward side. Obviously there must be a compensatory return current. This will flow along the bottom of the epilimnion where it floats on the hypo-

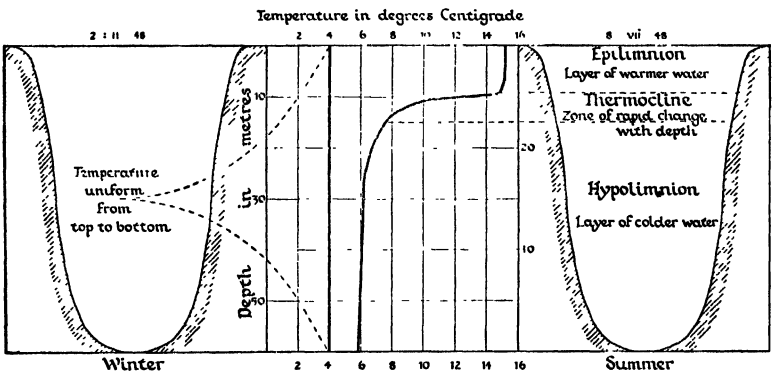


FIG. 1
Temperature of Windermere at different depths on February 2nd, 1948, and July 8th, 1948 (from data supplied by Dr. C. H. Mortimer)

limnion, and therefore the wind keeps the epilimnion in constant circulation. There will be some eddying and turbulence and this will keep the water of the epilimnion thoroughly mixed. In Britain totally windless periods seldom last long.

Wind will also blow the epilimnion bodily to one side, for the difference in density between epilimnion and hypolimnion is slight, and will push it into a wedge deep at the leeward and shallow at the windward end of the lake. The process may go so far that there is no epilimnion at all at the windward end and hypolimnion water comes to the surface.

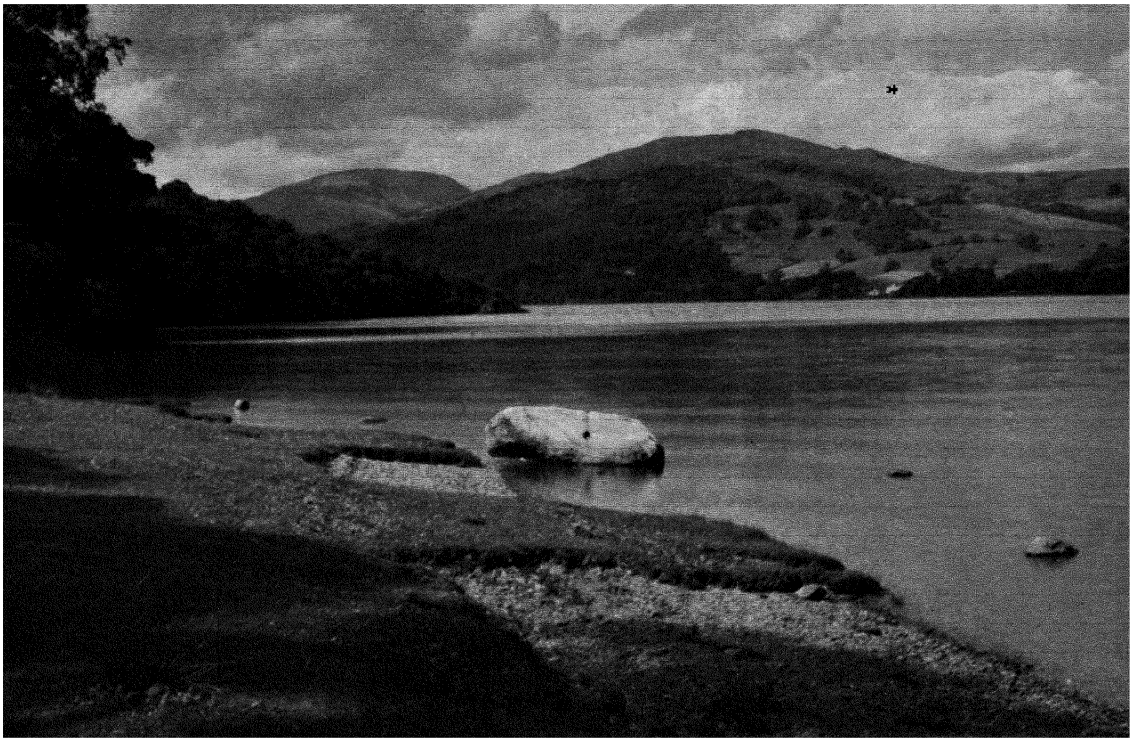


PLATE I

Glacial drift shore with Bannisdale Slate promontory in the background. Windermere, Lake District June

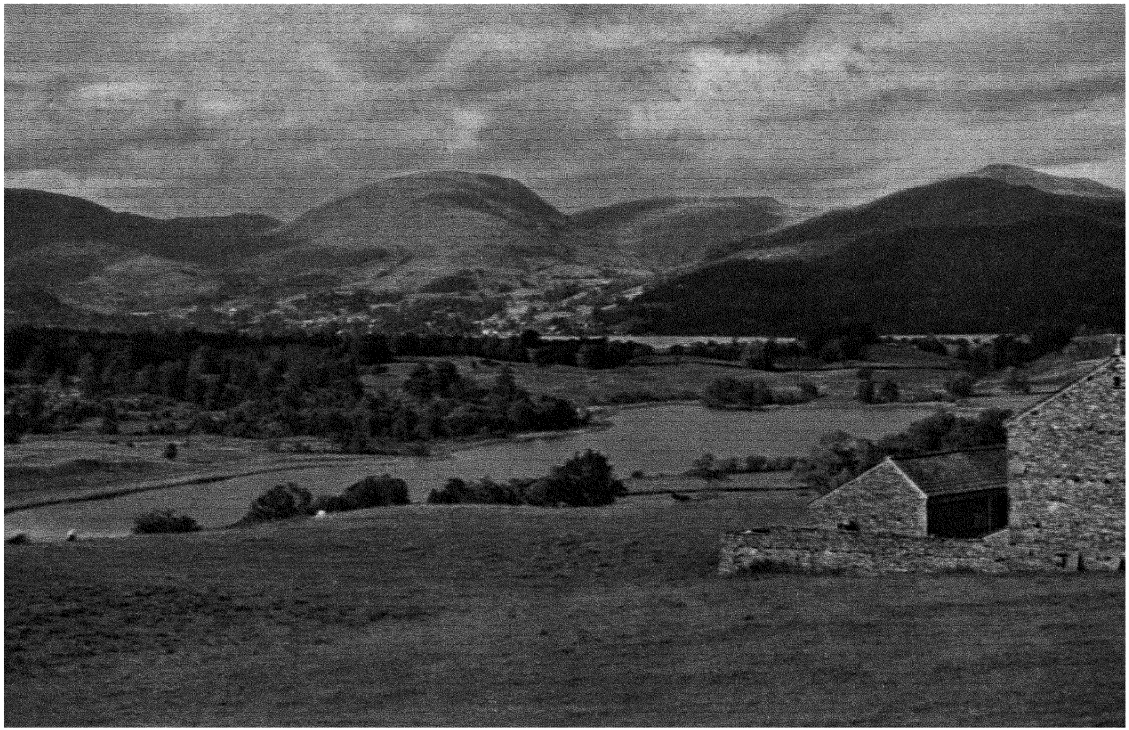


PLATE 2

John Markham

Reed-fringed glacial lake. Blelham Lake, Lancashire. June

Chemical analysis shows that the water of the hypolimnion is well mixed, for the concentration of dissolved substances is the same at all depths, but how this comes to pass is a point of controversy. One idea, now generally held to be erroneous, was that the circulating epilimnion set the hypolimnion revolving too by friction, as it might be two wheels pressed one against the other. A more widely accepted view—actually one of the oldest, since it was a product of the Bathymetric Survey of the Scottish Lochs—is that the mixing is due to seiches. When a strong wind drops, the epilimnion, piled up on one side, will roll back until it is level, and then it will overshoot and pile up on the other side. It will continue to oscillate like this for some time before settling to complete rest, and the phenomenon is known as a seiche. The tilting of the thermocline is considerable, but the rise and fall at the surface is very small and detectable only with the aid of sensitive recording instruments. Oscillation of the hypolimnion to and fro over irregularities on the bottom and sides of the lake sets up eddies which mix the water.

The rivers and streams flowing into a lake are usually at a temperature well above that of the hypolimnion and accordingly will mix only with the epilimnion.

With the shortening of the days in autumn, particularly if there is a fine spell with cold clear nights, temperature is lost by radiation during the hours of darkness. The epilimnion begins to cool down and eventually a gale will obliterate it, mixing it completely with the hypolimnion. This completely mixed state persists throughout the winter.

There remains one other factor to consider before anything living comes into the picture. The sun's rays have been considered so far only from the point of view of their heating properties ; for the activities of plants light is more important. Light rays do not penetrate far into even the purest water, and in most waters there is something extraneous to reduce their penetration still more. Any sedimentary matter in suspension, any colouring such as that derived from peat, and living organisms themselves all absorb rays of light. Fig. 7 (p.55) shows that in three Lake District lakes light goes farthest into the pure and barren waters of Ennerdale Lake, less far into the richer waters of Windermere, and least far into the peat-stained and rich waters of Bassenthwaite. Since light does not penetrate far into water, plant growth is only possible in the upper layers, and is nearly always confined to the epilimnion.

May we recapitulate here, since so much of what follows depends

on the physical conditions which have just been discussed. During the summer months the lake is divided into an upper warm epilimnion and a lower cold hypolimnion, which are to all intents and purposes completely separate (Fig. 1), and all plant growth takes place in the epilimnion.

Algae (minute floating plants) are present in the water all through the winter. Some time in the early months of the year, for reasons which are at present unknown and which pose one of the main problems of the day, these algae begin to multiply. The important species in Windermere is *Asterionella formosa*, which belongs to the diatoms, a

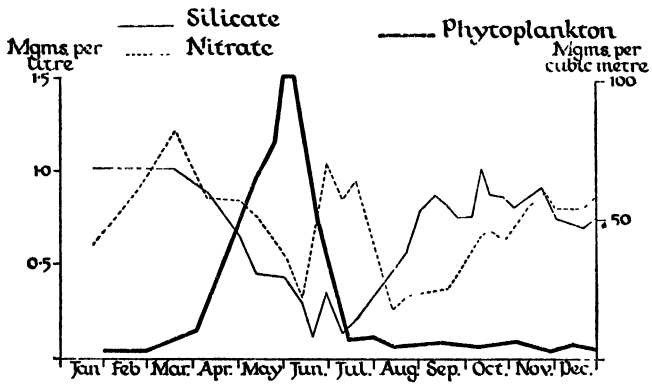


FIG. 2
Increase in phytoplankton and decrease in the concentration of certain salts in Windermere in 1936

group characterized by a skeleton made of silica. *Asterionella* removes silicates from solution in the water to build this skeleton, and it also removes phosphates and nitrates to make proteins. When it has become very abundant, continued multiplication uses up these solutes more rapidly than the streams and rivers bring them into the lake. The concentration falls until there is so little of one of them that *Asterionella* can no longer take it up. The limiting substance is silicate. Fig. 2 shows how the increase in the number of plant cells corresponds with a decrease in the concentration of silicate, and also how, when this reaches a certain low point, the numbers of *Asterionella* begin to fall,

and to fall rapidly. Other algae flourish in water of the composition now obtaining, and take its place as the commonest species. There is a succession of different kinds all through the summer, but none attains an abundance comparable with that of *Asterionella*. We have chosen to illustrate these chemical changes with figures for an actual year, rather than with an average based on several years, and there are therefore in Fig. 2 certain events peculiar to 1936 which require explanation. Nitrate concentration falls parallel with the fall in silicate and the rise in phytoplankton, but the close parallel is partly coincidence, and a fall in the nitrate concentration in the lake in spring is due mainly to events in the drainage area. After reaching their lowest value both nitrate and silicate show a sudden increase : this was caused by a flood after a long dry period.

Light penetrates into Windermere sufficiently far to permit plant growth down to a depth of about 30 feet (10 metres or so).

Rather later than the main abundance of algae comes the period when the minute floating animals or zooplankton are present in great numbers.

These various plants and animals are continually dying and decomposing, broken down by various agencies about which we do not know very much at the present time. Fungi and bacteria set upon their dead bodies and reduce them to fine particles and simple compounds, which serve as food for other organisms, so that there is a constant process of breaking down and building up in the epilimnion. But some of the decaying fragments, with the organisms breaking them down, fall through to the hypolimnion, and we must leave them for the moment to describe what has been happening in the hypolimnion. More important perhaps is what has not been happening ; there has been no plant growth, because it has been too dark, and therefore no utilization of the dissolved substances for want of which algae have been dying in the layers above. Evidently division into epilimnion and hypolimnion reduces the productivity of a lake.

The decaying matter which falls down to the hypolimnion continues to decay, though at a slower rate on account of the low temperature, and it uses up oxygen. There is no source from which the oxygen in the hypolimnion may be replenished, and consequently the concentration falls steadily all through the summer ; it may reach nil if the lake is a rich one and the hypolimnion small—an important point, as will be seen in the next chapter.

The decaying matter may eventually reach the bottom, and here some of it is locked up for ever, as may be deduced from the finding of organic matter deep down in mud cores where it has lain for several thousand years. Some of it is eaten by the animal inhabitants of the bottom mud, and some of it is broken down into simple substances by bacteria and other agents. But these simple substances cannot reach the surface layers, where they could be used for building up more living matter, until hypolimnion and epilimnion mix in the autumn. By then biological activity is reduced, and by the time there is a big demand again for dissolved nutrients in the following spring, much of the supply will have been washed out of the lake. On the average, water takes nine months to pass through Windermere, and therefore during the winter there will be considerable depletion of the dissolved substances released from the hypolimnion by the autumn mixing. Again it becomes apparent that the formation of a hypolimnion prevents the development of the full potentialities of a lake.

Large fragments hardly decay at all in the cold mud at the bottom of deep lakes, as was demonstrated in a gruesome way a few years ago when a small lake in Norway was drained. During the previous centuries there had been a number of drowning accidents in this lake, and, when the accumulated mud at the bottom was being removed, several of the bodies, some of which could be identified and dated by reference to local records, were unearthed. They were in a remarkably complete state of preservation and looked rather like Egyptian mummies.

Dr. C. H. Mortimer (194-142) has recently shown that, when there is oxygen at the surface of the mud, iron is present in the oxidized ferric state and forms a colloidal complex with various other substances. This colloidal complex tends to hold the simple products of decay, and therefore augments the locking-up process caused by the slow decomposition in the mud. But, if all the oxygen is used up, the ferric iron is reduced to the bivalent ferrous state, which goes into solution with consequent breakdown of the colloid complex. This liberates the other substances, and Mortimer was able to show, both in an artificial experiment in an aquarium and in a lake, that the disappearance of oxygen from the hypolimnion is followed by an increase in the concentration of silicate, phosphate, ammonia, and iron in the water. It will be seen in the next chapter that this phenomenon is of fundamental importance.

The above are factors which affect the plants and animals living out in the open water of a lake and in the mud below it.

A different assemblage of living things inhabits the shallow regions near the shore, and this population too is affected by physical and chemical processes. The most important is wave-action. The effect of this factor depends on the nature of the land on which it acts. Waves beating upon rock will disintegrate the weaker patches and leave the harder ones projecting as ridges of the type shown in Plate 3 (p. 28), but the total effect is small ; waves beating upon sand or peat, on the other hand, will erode the shoreline rapidly. Many lakes are surrounded, partly or entirely, by moraine deposits known by various names such as glacial drift, boulder clay, till, or sammel. Waves eroding a shore of this type leave in situ only the larger stones and boulders and carry away the finer particles, which eventually come to rest in deeper water away from the shore, or in some sheltered bay. The coarsest particles

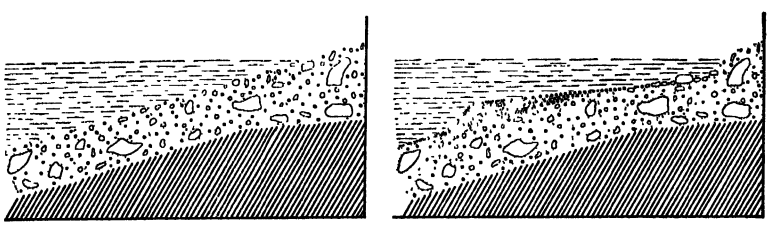


FIG. 3
Diagram of the erosion of a boulder clay shore to give a wave-cut platform

will be moved the least, the finest the greatest distance, and there will therefore be a graded series passing into deeper water farther away from the shore. The processes of erosion and deposition result in what is known as a wave-cut platform and are illustrated diagrammatically in Fig. 3.

Sometimes the material removed is not carried out at right angles to the shore but at an acute angle so that, when it settles, it forms a spit. Such formations are of importance to animals and plants because they create areas of quiet water which are the resort of certain species unable to tolerate the conditions on a wave-beaten shore.

Deltas are even more important features of the lake shore. They

may be no more than bulges in the shoreline, or, at the other extreme, they may cut a lake in two. Good examples of deltas at all stages are to be seen in the Lake District lakes. Plate VIII (p. 59), shows a small delta on the near side of the river flowing into the head of Windermere. The delta of the Measand Beck stretched two-thirds of the way across Haweswater, before this lake was dammed in 1941 to provide more water for Manchester. A stage further can be seen in the valley of Buttermere and Crummock Water, which were left by receding glaciers as one large lake. Since then Sail Beck, flowing in from the east, has cut the original lake into two and its delta now provides the half-mile of flat land in the valley floor between the two lakes. Another pair of lakes, Derwent Water and Bassenthwaite, show a still more advanced stage. Here again the two were formerly one, but the River Greta has poured so much silt and gravel into the original lake that there is now a full two and a half miles of plain separating the north shore of Derwent Water from the south of Bassenthwaite.

Some of these deltas are much too large to have been brought down by the little streams existing to-day, and much of the material was probably swept down during the last stages of the Ice Age by the bursting of ice dams and other minor cataclysms.

We may pass from generalities to describe a portion of the shoreline of Windermere, for it illustrates several of the points already made, and is referred to later when the fauna is discussed. The shoreline in question is bounded to the north by a ridge of rock jutting into the lake. The sides of this promontory, which is known as Watbarrow point (Fig. 4) are smooth, and run down at a steep angle to a depth of nearly 100 feet. To the south the same kind of rock, Bannisdale slate, is exposed at the edge of the lake, but weathering and wave-action have broken it up considerably, and the products of its disintegration litter the lake floor. They are large flat angular slate-like stones. Moon (1934), who has studied this region of the lake, refers to it as the "Bannisdale" shore and contrasts it with the "drift" shore which lies to the south (Plate I, p. 36). The drift shore consists of stones and boulders but these are round, not flat and angular, and there are finer particles between them. This shore has been formed by the erosion of a mound of boulder clay or glacial drift, somewhat after the manner shown in Fig. 3. The hinterland of the Bannisdale shore is covered by woodland, but that of the drift shore has been cleared of woodland at some time and is now pasture. This is not coincidence; where the

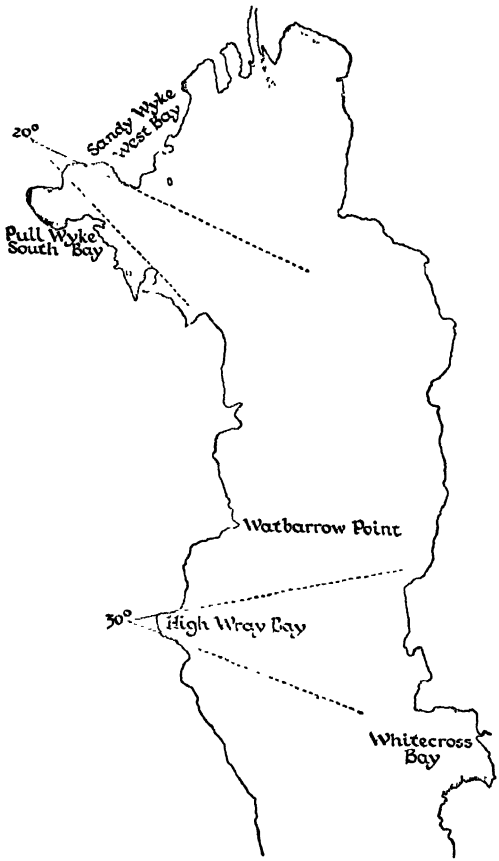


FIG. 4
Windermere, north end showing reed-beds. Reed-beds are stippled
Scale, 2 inches = 1 mile

underlying slate is not covered with glacial drift, the topsoil is often so thin, and rocky outcrops are so frequent, that cultivation of the land is not feasible; but where the rock is covered by boulder clay, it has been worthwhile to remove the forest and bring the land into agricultural use.

Fig. 4 shows that at the south end of the drift shore there is a bay—High Wray Bay—which is somewhat protected. Only the comparatively rare easterly gales will blow right into it, and the range of direction of wind from which it gains no protection at all is but 30°. High Wray Bay is floored with sand.

Sandy Wyke Bay farther north is more sheltered. The range of direction of wind which will blow straight into it is only 20°. But a glance will show that the amount of exposure is not to be measured entirely by the angles drawn in Fig. 4. If a wind blowing in the direction of the more southerly of the two pecked lines bounding the High Wray Bay angle veer slightly, it will still drive waves into part of the bay, and it must shift through nearly another 30° before complete protection is obtained. But if a south-easterly wind that just blows full into Sandy Wyke veer but a few degrees, the projecting coastline will shelter the bay almost completely. Sandy Wyke Bay is also sandy, but there is a big reed-bed growing in it.

Only a north wind will blow right into Pull Wyke S. Bay, but it will traverse so short a stretch of water that the waves raised will not be of significant size. This bay is floored with fine mud. The vegetation shows the zonation typical of quiet conditions. In the shallowest water there are various emergent plants such as reeds, rushes, sedges, and horsetail; in deeper water there are plants with leaves floating at the surface, such as water lilies; and beyond them are plants, such as pondweeds, stoneworts and quillwort, which live totally submerged throughout life.

A problem which cannot be passed by is the difference between a lake and a pond. One definition maintains that any piece of water which is so shallow that attached plants can grow all over it is a pond. The pedant has no difficulty in picking holes in this definition and pointing out that the depth to which attached plants extend varies very much with the transparency of the water; a cattle pond only a foot deep may be without vegetation in the middle because the light is cut off by innumerable small organisms which live in the open water and batten on the nutrients supplied by the dung. Or the nature of the substratum may be unsuitable for attached vegetation. Another school holds that, if a body of water becomes divided into epilimnion and hypolimnion and remains so divided throughout the summer, it is a lake and not a pond. One weakness of this view is that the number of different bodies of water which have been kept under

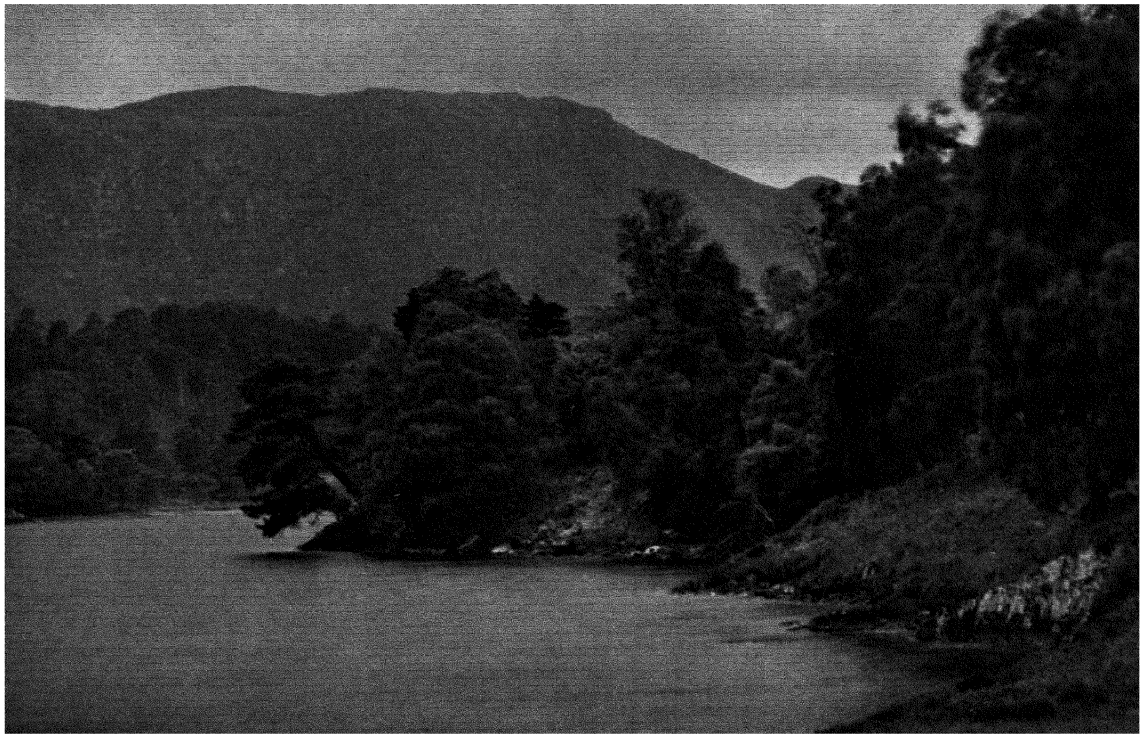


PLATE 3

John Markham

Rocky shore Loch Affric, Inverness-shire. June

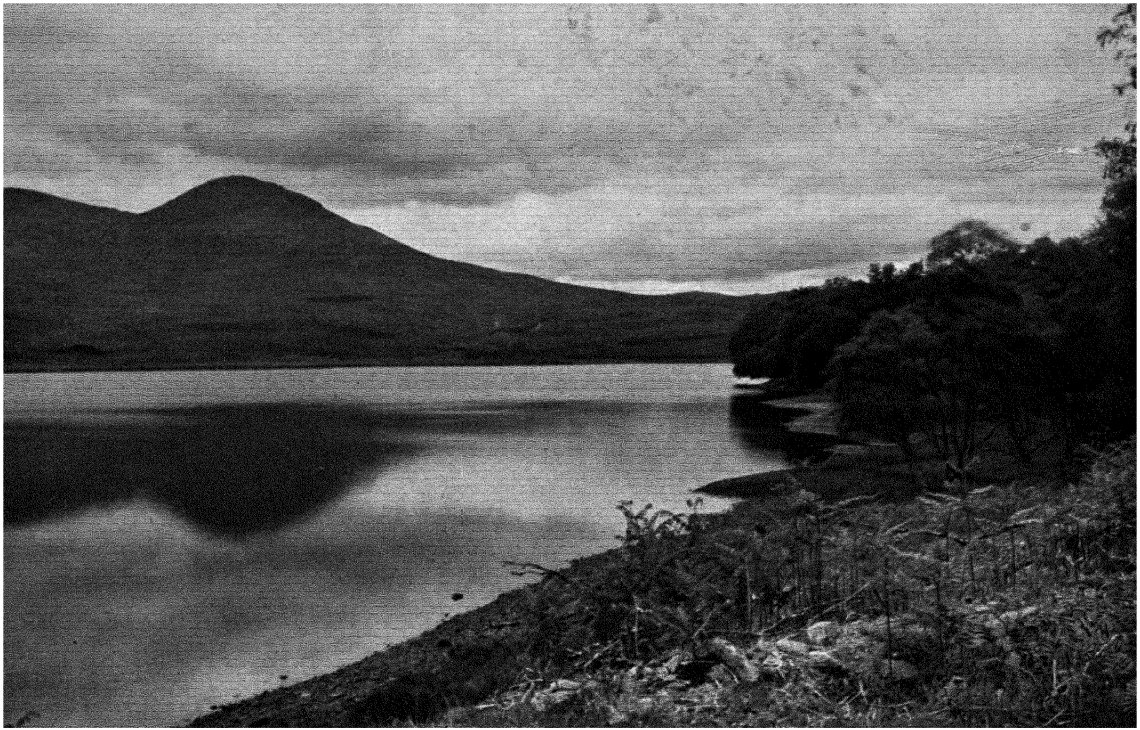


PLATE 4

John Markham

Glacial lake showing drift shore Loch Culen, Easter Ross June

regular observation is very small, and the data are insufficient to establish or disprove the distinction.

It can be objected to both these definitions that they involve the idea of depth whereas the general feeling is that a lake is large and a pond is small, irrespective of depth. Some Norfolk Broads have vegetation in the deepest parts but few people would be prepared to refer to them as ponds. There is, on these grounds, something to be said for the definition that a pond is so small that its edges are not appreciably eroded by wave action. Clearly the available data are insufficient to distinguish between lakes and ponds and we use the two words in this book with their usual rather vague meaning, implying no scientific distinction.

CHAPTER 3

APPARATUS FOR STUDYING LAKES

SCIENCE strides forward rapidly. Half a century ago the student of water biology was content perhaps with a pond-net and some bottles ; but now there is a big assemblage of apparatus used for his purposes, and every year some new gadget is invented. This chapter is devoted to these things because their use has in large measure provided the knowledge on which the rest of the book is based, and a handy account of them is much needed in the limnological literature.

The study of lakes and rivers developed rather later than the study of the ocean, and therefore it had the advantage of a lot of previous trial and error in devising instruments for special uses under water. Moreover, iron and steel do not rust and corrode so quickly in fresh water as in the sea, and waves are usually smaller, so that small and light instruments will usually serve their purpose adequately if manipulated by careful hands. The problems in fresh water are, however, in some ways more difficult because large boats provided with power are not often available, and it is frequently necessary to use the instruments from small row-boats or even from the bank.

For work in open water the first essential is a winch with a sufficient length of cable, preferably thin wire, to reach to the bottom. A very useful type of light winch which can be put on to any row-boat is made by the firm of Friedinger of Lucerne (Plate II, p. 37). It has the advantage that the wire is paid out over a pulley block of special circumference to which is attached a cyclometer, so that the depth at which the instrument hangs below the surface is shown accurately to the operator in the boat. With such a winch the different instruments for measuring temperature or light intensity, and for collecting water samples or plankton, can be lowered easily to any depth. It is often

necessary to operate an instrument at a considerable depth in the water before hauling it back to the surface, and this may be achieved by despatching a so-called messenger down the wire. The messenger is usually a lump of metal with a hole drilled through it; on reaching the instrument at the bottom of the wire, it strikes some projection which is arranged to release a catch in order to perform the necessary operation.

An example is provided by the reversing thermometer shown in Plate IIb, facing p. 37. The thermometer is mounted on a pivot about its middle, and the pivot has a spring which turns the thermometer upside down when the catch at the top of the frame is released by the messenger. This reversal breaks the mercury column, and so, when the thermometer comes to the top, it shows the temperature at the depth at which the messenger struck it; warmer water through which it may pass leaves it unaffected. The ordinary clinical thermometer works on somewhat the same principle.

The thermometer has to be specially built to resist the high pressure which obtains under water and so it is a comparatively large instrument, which will not immediately take up the temperature of the surrounding water. Accordingly it has to be left for a few minutes at each depth from which a reading is desired, and since, further, it must be hauled to the surface to be read, the taking of a series of observations is a long process. Work can be carried out much more rapidly with an entirely different kind of instrument which was devised a few years ago (Plate III, p. 44). It depends on the principle that, if two wires made of different metals are joined together at the ends, and these two ends are at different temperatures, a small electric current passes through the wires. If there are many such pairs of wires, or thermocouples as they are called, the current set up is measurable on an ordinary galvanometer. The reading is directly proportional to the temperature difference and may be converted to degrees centigrade by means of a simple calibration table. The instrument which is lowered in the water consists of many pieces of wire, one end of each pair being immersed in a thermos flask containing melting ice, and therefore keeping a temperature constant at freezing point, and the other end projecting freely into the water. The thermos flask of ice, together with the wires, is enclosed in a stout metal casing to protect it from the high pressure, and connected to the wires is an insulated electric cable coming up to the surface, where it is connected to a sensitive galvanometer in the

boat. The exposed ends of the wires immediately take up the temperature of the water with which they are in contact, so that the temperature at any depth can be determined with speed and ease by an operator in the boat lowering the instrument to different depths and recording the reading of the galvanometer at each. Ice is not always obtainable, and frequently the thermos flask is filled with surface water, of which the temperature is measured with an accurate thermometer. The conversion of the galvanometer reading to temperature is then more complicated, but the advantages gained in the field are often reckoned to outweigh this. In a few years the thermocouple technique will probably be obsolete, for the very latest idea is to pass a current through a wire made of a substance of which the electrical resistance changes much with small changes of temperature. As with the previous technique there is virtually no delay while the temperature of the surrounding water is being taken up, and readings are obtained without the apparatus being brought to the surface. It requires a battery, which the other method does not, but no thermos or heavy casing to protect it and, on balance, the advantages appear to lie with the new method.

Apparatus of a somewhat similar kind is used for measuring the amount of light penetrating below the surface, which, we have seen, is so important in determining the depth of plant activity. A photo-electric cell, contained in a pressure casing, is connected to the surface by wires, and a window facing upwards is inserted into the pressure casing so that rays of light penetrating from the surface can strike the cell. They cause a small electric current, varying in amount according to the intensity of the light, and this can be measured in much the same way as with the temperature apparatus by a galvanometer in the boat.

When measuring sub-aqueous light, it is necessary to lower the instrument from a long support projecting sideways from the boat, because otherwise the boat would shade the instrument hanging beneath it. Not only the general intensity of light below the surface, but also the kind of light, is of great importance. This can be determined with the same instrument by covering the window with filters of various colours.

There is a much simpler but useful instrument for giving a rough idea of the clarity of water, known as Secchi's disc after the scientist who first used it. This consists of a white plate of 20 cm. (8 in.) diameter,

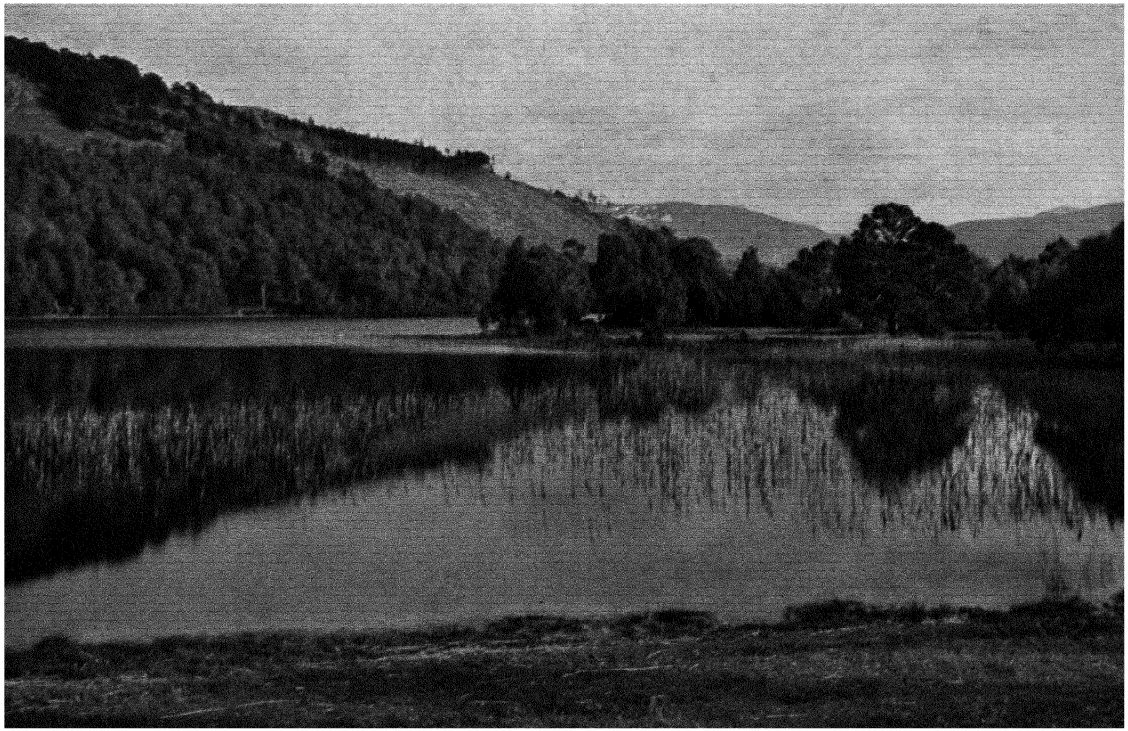
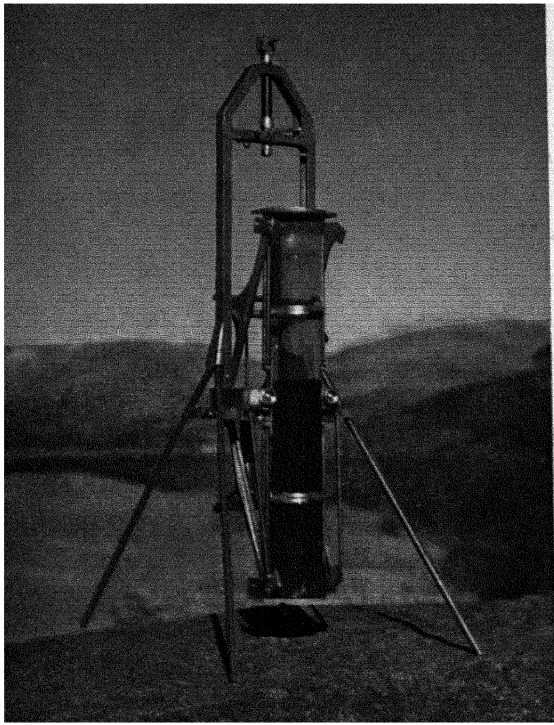


PLATE 5

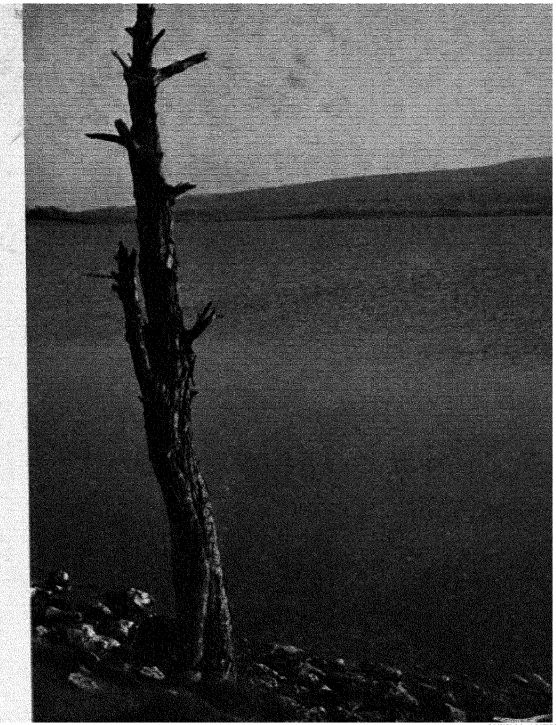
John Markham

Reeds developing in a bay. Loch Phitulais, Inverness-shire. June



E. D. Le Cren

a. Jenkin Surface Mud Sampler, with sample showing darker oxidised layer at surface. March



b. Stony shore. Malham Tarn, Yorkshire. May

PLATE 6

which is lowered below the surface to the point at which it becomes invisible to the naked eye. This is, of course, a crude way of measuring how far light can penetrate, but Secchi's disc is very easy to carry about and use, and is accurate enough to provide comparisons between different types of water.

For most kinds of chemical work on water, and also for studying microscopic life, it is necessary to obtain samples of water from different depths. Here again the simple expedient is adopted of despatching a messenger down the wire to close a water-bottle at the desired depth. A variety of different kinds of water-samplers are used for this purpose; a simple one is illustrated in Plate IIa, facing p. 37. The instrument is a metal cylinder open at both ends so that when it is lowered it will pass through a column of water without disturbing it much. It is halted at the required depth and a messenger is sent down the wire. This releases lids which close over the top and bottom of the cylinder and are kept tightly in place by strong springs. The apparatus is now quite watertight, and can be hauled to the surface with a sample of water from the depth at which it was closed.

This self-closing metal water-bottle is an excellent instrument for many purposes, but for the study of bacteria, of which very many kinds inhabit fresh water, it is no use. The spores of bacteria are everywhere —in the air, in the water, on one's fingers—and accordingly a water-sampler for bacteriological investigations has to be arranged so that every part of the instrument which comes in contact with the actual sample of water collected can be sterilized by heat and kept in a sterile condition until the sample enters it. The principle was therefore adopted of using glass sampling vessels of a simple and standard pattern, held in a metal framework fitted with the necessary gadgets to operate an opening and closing device. The bottle is sealed with a bung pierced by two tubes. One is long and runs down to the bottom of the flask, and the other ends flush with the inside of the bung and is bent into an S-shape outside. A U-shaped piece of glass rod fits into a length of rubber tubing attached to each tube. When the bottle is at the required depth, a messenger is sent down to release a strong spring which pulls the glass rod out of the two tubes. Water runs down into the flask through the long tube, driving air out of the other tube until the flask is completely filled. A bubble of air remains in the bent tube so that no mixture can take place between the sample in the flask and the surrounding water during haulage of the whole apparatus to the

surface. In practice, a number of flasks, each with its stopper and tubes, are sterilized in the laboratory and then a series of samples for bacteriological examination can be taken at different depths or at different places during the same outing.

For collecting the innumerable other kinds of microscopic plants and animals, all of them larger than bacteria, but some of them much too small to be seen with the naked eye, there are many kinds of apparatus. Only the more important ones are described below. First there is the ordinary pond-net, generally one of the most useful pieces of apparatus. A convenient pattern consists of a circular metal ring about nine inches in diameter, detachable from the pole by a socket and thumb-screw. The net bag can be made of stout canvas or silk gauze of any desired mesh according to the kind of animal or plant which it is intended to capture. For the plankton which lives floating in the water, the net is best made in the form of a cone at the end of which a glass or celluloid bucket about one inch in diameter is inserted. It is convenient to have one such conical net of coarse-mesh silk (60 meshes to the inch), and another identical in shape but in fine-mesh silk (180 to the inch). Each of these can be mounted on a metal ring with the same fitting for the pole, so that the three nets together with one pole make a useful all-round collecting outfit.

The fauna and flora of the shallow water is very abundant and varied. A qualitative survey of the animals inhabiting weeds may be made with an ordinary pond-net, but it is frequently desired to know how many there are in a given area. The device shown on Plate V, p. 54, is designed for such quantitative surveying though it can only be used in quite shallow water. It is a metal box of known area open at the bottom. It is carried out to the desired position, lowered over a suitable patch of weed, and pressed a little way into the bottom material in which the vegetation is growing. The two handles are then pulled apart; these bring two jaws together, and the bottom of the box is closed. The apparatus is then lifted, the water runs out through holes provided for that purpose, and a sample of weed and the animals living in it remain. Another apparatus designed for quantitative collecting near the shore, especially on a stony bottom, consists of a large and modified version of the pond-net. The frame is square instead of round and the side of the square farthest from the handle is flattened and sharpened into a blade which can be pushed through the stones and gravel. The operation is easier if the pull of the net is set at an angle

to the square frame. At the narrow end of the canvas bag is fitted a metal bucket which has a detachable funnel inside it, so that the larger stones are prevented from mixing with the animals, as the latter fall into the bucket. The funnel also prevents the escape of these animals, many of which are active. This instrument has been used satisfactorily for the quantitative sampling of the bottom-living animals by first marking out a precise area of the bottom, say a square yard, and then working the net thoroughly throughout this area.

The number of animals on a given area of stony bottom can be ascertained more accurately by means of a simple device, the invention of which is usually attributed to the late Mr. A. C. Gardiner. It consists of a frame of known area—a square of one-half or one-third square metre is convenient. The frame is covered with fine metal gauze to prevent animals slipping through, and the gauze is strengthened underneath by a layer of stout wire-netting. The tray thus formed, or more usually a number of such trays, is laid on the bottom in shallow water and is covered over with a layer of stones or gravel reproducing the surrounding substratum. If left in position for a few weeks, the material on the tray is completely colonized by the organisms typical of the surrounding area ; and thus a known area of the substratum can be lifted up intact and every organism inhabiting that area can be examined. Trays of this type have been used very successfully not only for sampling the bottom fauna but also for ascertaining the rate at which the animals colonize new ground, for example when the water level of a lake or river is raised during time of flood.

The muddy deposits at the bottom of most lakes are very uniform, and a small quantity of the mud requires a great deal of sieving and sorting to find out what animals are contained in it. Therefore in modern practice samples of soft bottom deposit are nearly always collected with a grab, which picks up the deposit from a known area of lake floor. The Petersen grab (Plate IV, p. 45) is practically a miniature version of the big grab or excavator used by contractors. The instrument consists of two halves hinged at the top, so that, when lowered in the open position, it comes to rest on the bottom with jaws open and covering an exact area, usually about one square foot, though smaller models are preferred by some workers. As soon as the grab touches the bottom, tension on a bridle holding the jaws apart slackens, and the catch between the bridle and the hauling rope drops off. When the hauling rope is tightened again it now takes up the slack

of a second bridle which brings the jaws of the grab together, and the whole apparatus is then hauled to the surface.

A more elaborate but more efficient instrument is the Ekman grab, which consists of a box and jaws not unlike the hand-grab described above and depicted on Plate IV, facing p. 45. But the jaws have no handles and they can be closed when the grab has penetrated into the mud after passing through a considerable depth of water.

When a sample of mud has been obtained, it is placed in a sieve, or better a series of sieves having different mesh, and then swilled with water or hosed so that the mud is washed through, and the animals are left behind clean.

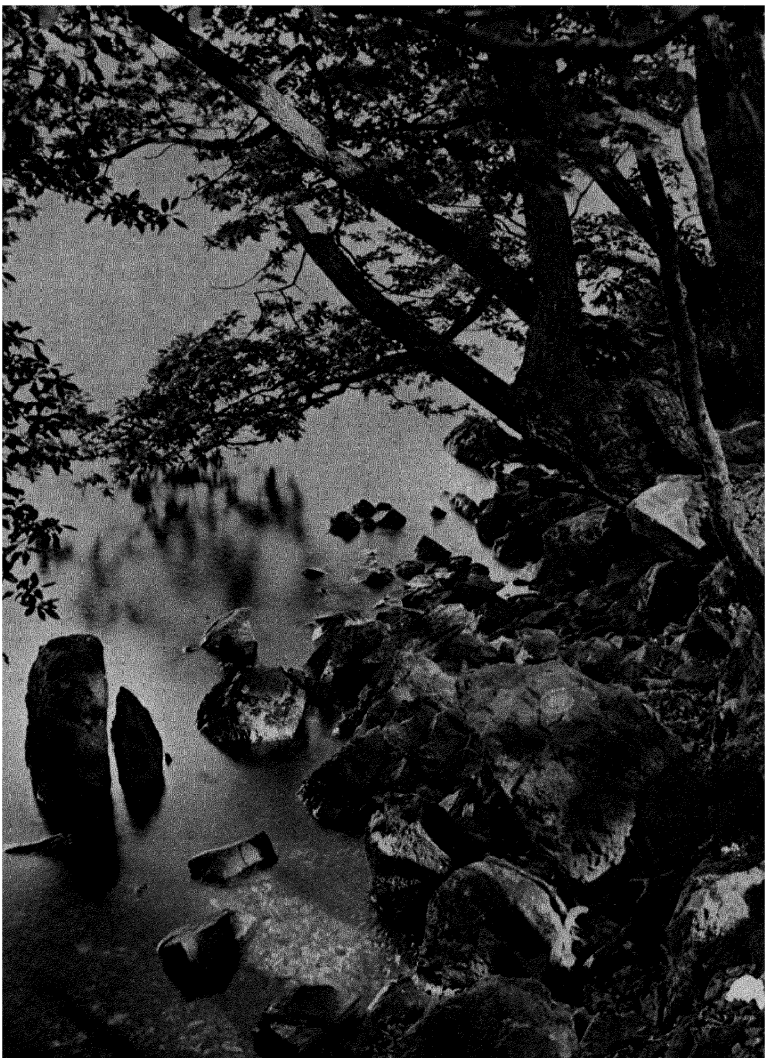
A great part of the fauna of the bottom mud, the stones, and the weeds, is made up by insect larvae and nymphs, many of which cannot be identified at the present time. Plate IIIb, opposite p. 44, shows a floating cage which captures the adult insects as they emerge, and so, since adult insects can be named, this apparatus is a valuable adjunct when it is desired to discover exactly what species are present. The cage is of wood with celluloid top and sides, and fits into a floating frame from which it can be lifted when the catch is to be taken out.

Methods of collecting plankton—the small floating animals and plants—depend on the purpose for which the collection is required. If the collector merely wishes to know what species are present, the net attached to the pond-net stick, already described, will serve his purpose, provided that he is collecting in a shallow piece of water. In a deep lake the usual method is to lower a net on a wire from a winch and haul it up from near the bottom to the surface ; horizontal tows are open to the objection that both the total density and the species composition of the plankton varies with depth.

If the object is to discover how much plankton is present, vertical hauls with a net can also be employed, but it is essential that the net be provided with a propeller in the mouth and a recorder—Dr. Mortimer at Wray Castle used an old clock-face and its hands—or some other device which will measure the amount of water which actually passes through the net. No net filters a column of water having a diameter that of the net mouth and a length the distance which the net is towed ; some water is pushed ahead and out to the sides, and the amount will increase as the catch accumulates and blocks up the holes of the net.

Much work has been done to discover at what depth animal plankton

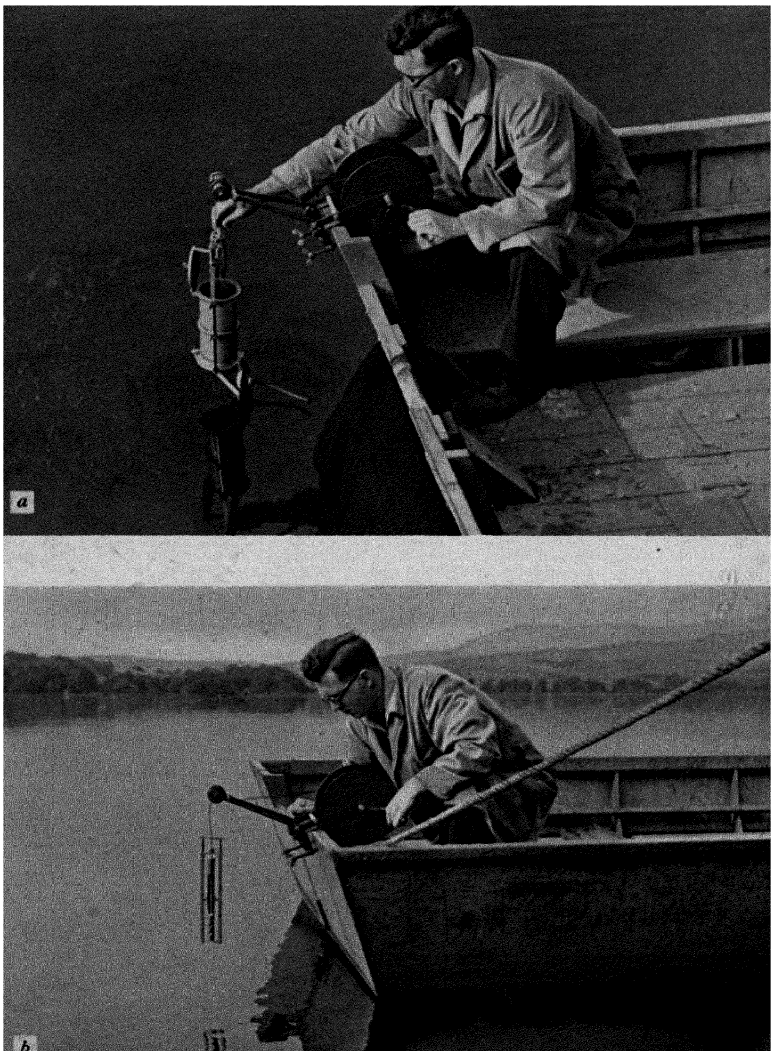
PLATE I



John Markham

Bannisdale shore, Windermere, Lake District

PLATE II



Photographs by John Clegg

a. Water-bottle and Friedinger Winch
b. Reversing Thermometer and Friedinger Winch

organisms are at different times of day, and it has usually been carried out with a net which can be hauled for a known distance and then closed, so that it does not fish any more. One such net has two attachments to the rope or wire by which it is lowered, one direct to the circular frame at the wide end, and the other looped round the middle of the net in such a way that when it is pulled it throttles the net. In operation the net is first lowered to the required depth, in the open position but with the narrow end first so that nothing enters it. Then it is hauled vertically at constant speed, say from 100 metres up to a depth of 90 or perhaps 80 metres, when a messenger is sent down the wire. It releases a catch which sets free the bridle to the mouth of the net, and the only attachment is now the noose round the middle of the net. Hauling continues but now the net is hauled by the cord throttling its middle so that it arrives at the surface containing only the plankton caught during its period of fishing from 100 to 80 metres. The narrow end of the net is fitted with a little metal bucket and tap, so that the plankton can be run out with the water in the bucket into a suitable receptacle. The process is then repeated, perhaps for each 10 or 20 metres, right up to the surface, and subsequent examination of each of the samples gives a picture of the vertical distribution of each organism in the plankton from near the bottom up to the surface. The throttling mechanism is not wholly satisfactory as, when the net is set free from the first attachment and before it has been closed by the throttle, it may drop, and lose part of the catch. At Wray Castle a net with two lids, which can be released from the vertical open position by a messenger, has been used.

As noted already, the filtering powers of a net decrease as the catch accumulates so that an error is introduced, even though great care is always taken to haul the net at the same rate. For this reason, and also because a net is a conspicuous moving object which animals can see and may avoid, some workers have dispensed with the net for investigations of this kind and adopted other devices. One of these is the plankton pump. A long tube of rubber hose is lowered to any required depth, and then a pump sucks a known quantity of water through it for filtration in the boat. Another device, developed especially by American biologists, is the plankton trap, which is made of cloth or gauze on a framework. It operates on the same sort of principle as the water-bottle illustrated in Plate IIa (p. 37) : a cylinder open at both ends is lowered rapidly to the required depth, where the ends are suddenly closed. The

capacity of the trap is usually several cubic metres, and it is obviously bound to be rather a cumbersome piece of apparatus.

All the methods for collecting plankton so far described depend on the principle of filtering in order to concentrate the organisms before their examination. Unfortunately the organisms vary so much in size that no form of filtering is entirely satisfactory: either the mesh of the filter is so large that the smaller organisms escape, or so small that it is scarcely permeable to water. In order to obtain a really accurate picture of the smallest forms, it is necessary to take a complete sample of the water in which they are living and to concentrate them by allowing them to sink to the bottom of vessels in which the water sample is placed. This method, the Utermohl method of estimating phytoplankton, is particularly useful for quantitative work on the smaller forms of plant life. Samples of water are collected at different depths by means of the closing water-bottle or the bacteriological sampler described above, and are placed in glass tubes of which the bottoms are made of extremely thin glass like the cover slips used in microscopy. A special microscope, arranged in such a way that the view is from below upwards through the very thin glass, is used for examining and counting the minute organisms sedimented to the bottom of these tubes.

It has already been mentioned that the bottom deposits of lakes are important not only in providing a substratum for plants and animals, but also as a source from which nutrient substances diffuse into the water. Therefore many recent developments in research have been concerned with these deposits, and the first problem was how to obtain samples for detailed examination. It is easy enough to collect material with a grab or dredge, but samples obtained by this means are so stirred up that they are useless when the object is, for example, to compare the chemistry of the top few millimetres of the deposit with that of the water immediately above it. For this purpose a rather complicated apparatus has been devised, and it is illustrated in Plate 6, facing p. 33. It consists of a large glass tube, three inches or so in diameter, held by a band about its middle on to a metal frame, standing on four spreading legs. The sampler sinks into the soft mud when lowered to the bottom, but without disturbing it, and then, a messenger sent down the wire having released a catch, two pairs of arms travel forward to place a cap on either end of the glass tube. The speed at which these caps move into position has to be very slow in order not

to disturb the mud and water in the tube, and this is effected by means of a pressure chamber of the same kind as that used for preventing doors from slamming. When closed, the glass tube contains a sample of the top few inches of deposit together with the water above, and the caps at either end are held tightly in place by springs. At this point the whole apparatus is hauled to the surface gently to avoid disturbance. The glass tube is detached from the frame, and the sample of bottom deposit, complete with the water immediately above it, just as it was at the bottom of the lake, can be carried into a laboratory for chemical and other tests. The person who devised this most useful apparatus was a retired engineer, Mr. B. M. Jenkin, and it is worthy of note that the first experimental model, which he made largely out of meccano, operated so well that it was still in frequent use at the laboratories of the Fresh-water Biological Association at Windermere ten years later.

Mr. Jenkin was set another and much more complicated problem, namely to devise an instrument capable of extracting cores from the bottom deposits in lakes, if possible to a depth of 20 or 30 feet below the mud surface. A good deal of trial showed that an ordinary open tube or pipe was useless for this purpose because it compresses and disturbs the layers of deposit too much. After some thought, Mr. Jenkin hit upon the idea of a sampler which could be thrust into the deposit first and then made to carve out a core by means of a curved cutting blade working on a long pivot. The business end of the instrument, which cuts out the core, is about four feet long, and consists of a tube cut in half lengthways and covered with a metal plate except for a slit down one side. A second half-tube lies within the first, attached on an axis in such a way that it can be rotated out through the slit. When the apparatus has been driven to the required depth, the inner half-tube is rotated, its sharp leading edge passes out of the slit, and, travelling through 180°, comes up against the far side of the plate. Between the inner half-tube and the plate there is now a sample of mud isolated from its surroundings with the minimum of disturbance. The rotation of the inner half-tube is effected by a system of cogs and a driving-wheel worked by a wire from the surface. The cutter can be attached to a series of tubes so that it can be driven to the desired depth in the mud before it is operated. The force required to press the whole instrument into the bottom is provided by a series of heavy lead weights, of which the number is adjusted according to the depth at which the

particular sample is required. Thus a complete core, say 20 feet in length, is obtained in a series of overlapping cores each four feet in length.

The method of using this instrument is briefly as follows. First a pontoon with a derrick is firmly anchored over the spot from which the core is to be taken. Next a flat weight on a thin wire is lowered to the bottom to serve as a guide and as an exact measure of the depth to which the main instrument is subsequently lowered. Then the coring machine itself is lowered from the derrick on a stout wire with a pair of arms clutching the aforementioned guiding wire. The machine is allowed to sink into the deposit to the required depth, when a sample is required from near the surface; for a deep core the machine is allowed to sink as far as it will go and driven the rest of the way. Then a messenger is despatched down the guiding wire in order to release the arms, and the guiding wire is hauled up, an action which also operates the machinery for cutting out the core. It remains for the whole machine to be hauled to the surface and laid flat before the half revolution of the cutting blade is reversed and the core is exposed ready for transfer to the laboratory. It will be appreciated that the successful handling of this apparatus is no mean task; in fact it requires a team of three or four operators well trained in the particular functions which each has to perform at the right moment. With its aid, however, a large number of cores, some of them covering 21 vertical feet of deposit, have been collected from many parts of Windermere, and these have provided valuable information about the history of lakes since the Ice Age (Chap. 4, p. 42).

One other piece of apparatus of an entirely different character has been found useful in the study of bottom deposits. This is the echo-sounding machine, of the kind which uses super-sonic sound waves, that is waves so short that they cannot be heard by the human ear. The apparatus consists of an oscillator which transmits super-sonic sound waves at regular intervals, and a receiver which picks up these waves after they have been echoed from the bottom. By various electrical devices the time taken for each transmitted sound to come back, which gives a measure of the depth, is recorded by a revolving pen working over a piece of paper which is sensitized with an iodine solution, and is arranged to move at a constant speed past the revolving pen. The whole outfit, known as the Huson Echo Sounding Recorder, is sufficiently compact to be used in an ordinary row-boat, and as the boat proceeds

the depth of water is recorded on the sensitized paper. In 1937 one of these instruments was used to make a very detailed bathymetric survey of Windermere, the whole lake being covered in a series of cross-sections about 50 yards apart. When the records made during the survey were examined closely, it was apparent that not only could the depth of water be readily ascertained, but some very interesting information was also provided about the bottom deposits. There were apparently two bottoms, as will be seen from a glance at Plate VI, facing p. 55. It was suggested that this was caused by one echo coming back from the surface of the mud, and another going farther and coming back from the underlying rock. This suggestion was not as easy to prove as was thought, when details came to be worked out. Eventually during a survey of Esthwaite Lake the record shown on Plate VI was obtained ; there, according to the theory, the underlying rock was breaking through the mud and projecting as a bare ridge. That such a ridge did exist was easy to show, and the original idea that the two bottoms represented the mud surface and the rock surface respectively was confirmed. And so an echo-sounder survey of a rock basin lake shows the depth of bottom mud as well as the depth of water, and this, as will be seen later, is a piece of information which limnologists are glad to have.

CHAPTER 4

DIFFERENT KINDS OF LAKES

LAKES, geologically speaking, are transitory features of the landscape. The biologist who studies a lake is likely sooner or later to find that the answer to some problem he is seeking to solve is to be sought in past history, and particularly in the way the lake was formed. Lakes and ponds have originated in many different ways and much ingenuity has been devoted to fitting them into schemes of classification. We shall not dwell on the groupings and subgroupings which have been suggested, but, in the first part of this chapter, prefer to take the lakes as they come, starting in the north of Scotland and travelling southwards.

The Great Glen is a tear in the earth's surface, and Loch Ness, which lies in it, provides an example of a lake associated with faulting. Loch Ness is 21¾ miles long and a little under one mile in average breadth, so it is a long and narrow lake; its greatest depth is 754 feet (230 metres) and its mean depth 433 feet (130 metres), so it is deep and steep-sided. Its mean depth is greater than that of any other British lake by quite a big margin, though there is one, Loch Morar, which is deeper at the deepest part (1017 feet = 310 metres). All these features are characteristic of tectonic lakes, that is lakes formed originally by movements of the earth's crust. Also in this class are some of the most striking lakes of the world, such as the Dead Sea and the lakes in the Great Rift Valley of Eastern Africa. These were caused partly by lateral tearing, as is the Great Glen, but there followed a lowering of a strip of the earth's crust so that what is now the floor of the rift valley was once level with the high land on either side.

Most of the other lochs in the Scottish Highlands owe their present form to the work of ice when the country was covered with it during the Ice Age (Plates 3, 4, 7, 8, 9), and so were the llyns of the Welsh

mountains and the lakes of the English Lake District. Indeed, nearly all the larger stretches of water in Britain were formed by glaciers, at least in part. In some cases their basins were gouged out by glaciers flowing down mountainsides, usually in valleys cut by a stream in an earlier, more clement period. When the mass of snow and ice and rubble reached the bottom of the slope it dug into the ground and excavated a great trench. This trench became the basin of the lake when the glacier retreated with the onset of warmer conditions. The mass of material which the glacier plucked from the land it passed over was deposited in mounds or moraines at the snout of the glacier, and some glacial lakes are dammed up by a moraine which makes them deeper than if they were contained in the actual excavation alone. Glacial lakes, like rift valley lakes, are usually long and narrow and relatively deep ; Windermere, for example, is 10½ miles long but only half a mile wide on the average, and 219 feet deep at the deepest point. Their sides tend to be straight (Plates VIII and IX, pp. 59 and 64) and any major irregularity in the shore line is often of more recent age. Lakes of this type were formed only in hard rocks where the relief was rugged, and steep valleys concentrated the glacier and directed its excavating effort to a circumscribed area.

Also of glacial origin are the smaller lochans, tarns, and the small lakes in cirques, corries, or cwms (Plate X, p. 65) which are often to be found near the tops of mountains. They are frequently circular in outline and they mark the place where the snow or ice piled up and a glacier took its origin.

An ice sheet covering a plain did not excavate because its effort was dispersed and not concentrated, but it did give rise to lakes none the less. As might be expected these are of a different type ; Loch Leven is an example and no fisherman requires a biologist or geologist to tell him that there is something fundamentally different between Loch Leven and the Highland lochs. As the ice sheet which covered Scotland began to recede, a large lobe of the glacier flowing down the Forth Valley became isolated in the centre of the Kinross plain. It was surrounded by clay, stones, boulders, and suchlike products of ice erosion washed along in the water from the melting glaciers, much of it coming through a pass in the Ochils from the Tay Valley. A considerable depth of this material was deposited on the plain, but in the middle there was this big block of ice melting slowly because of its large size, like an iceberg in the North Atlantic. When it finally disappeared it

left a hollow where it had been sitting and this filled up with water to become Loch Leven. The shape of Loch Leven is quite different from that of either glacier-cut or rift valley lakes : it is not much longer than broad, one axis being $3\frac{2}{3}$ miles and the other $2\frac{2}{3}$; its mean depth is only 15 feet and its greatest depth only 83 feet.

The Cheshire Meres were formed in a similar way to Loch Leven, although subsidence of the land surface also played a part. Outside Britain there are many lakes of the same type : two groups, which are referred to in later chapters because they have been studied in much detail, are the numerous lakes in the Wisconsin area of North America and the Baltic lakes of Denmark and the North German coast.

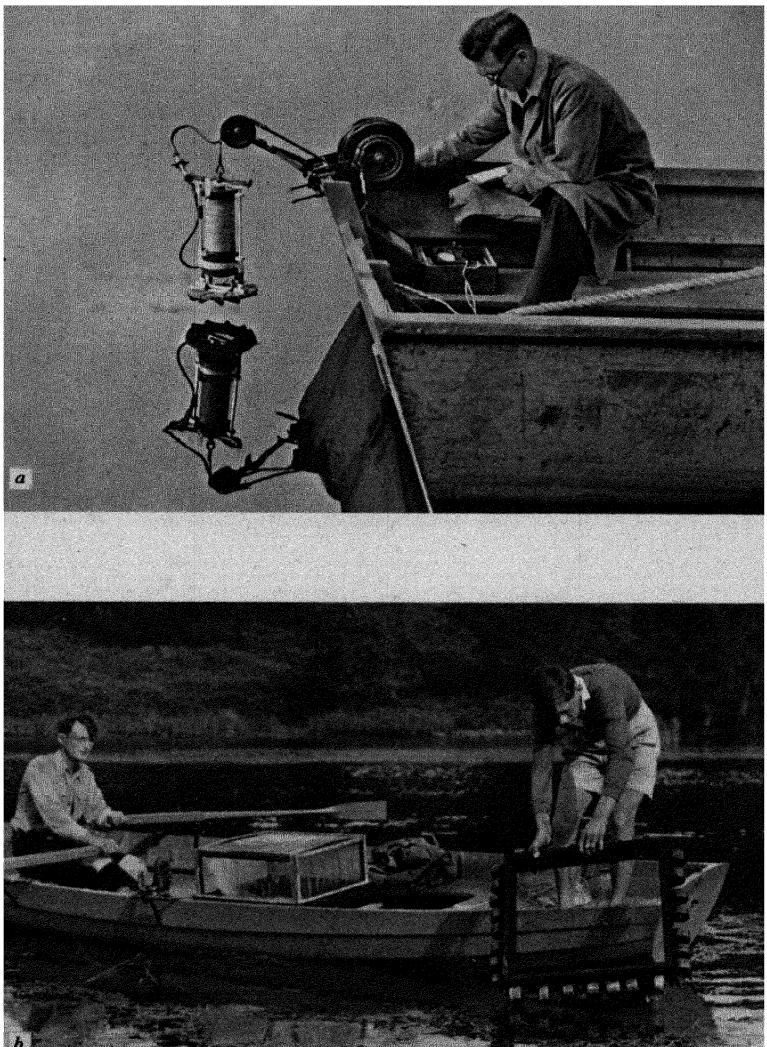
Also characteristic of mountainous areas are the much smaller peat pools (Plate 10, p. 51). These may occupy holes where stone for a wall or a house has been quarried or sometimes a rock basin of natural origin, but most of them are formed by the growth and then the erosion of peat. Some of the largest are to be seen on the Pennines, for the Pennines have flatter tops than the mountains in Scotland, Wales, or elsewhere in Britain, and it is on flat places that these pools develop. Vegetation, of which bog-moss (*Sphagnum*) is usually an important constituent, dies and accumulates over a long period of years, building up a bed of peat. At a certain stage, for reasons which are not at present understood, the peat becomes unstable, and hollows are eroded by the action of wind and rain. The surface becomes dotted with small pools and, as further erosion takes place, these coalesce. Finally a channel becomes eroded through the rim of the peat bed and all the water runs away. The building-up process then starts again.

Larger bodies of water on the Pennines are few, apart from man-made reservoirs which are now characteristic features of the landscape.

Lough Neagh in Northern Ireland is the largest sheet of fresh water in the British Isles, with a surface area of 153 square miles. It was formed in a way different from that of any of the other lakes so far encountered, and is volcanic in origin. There was no volcanic mountain like Etna or Fujiyama, but basaltic lava welled up from fissures in the ground. It flowed freely over the countryside and eventually solidified as a flat plate-like capping. Later it sagged in the middle and the depression so formed is Lough Neagh. The greatest depth is only 56 feet, so it is even shallower than Loch Leven.

There remain to be explored the more recent geological formations of south-east England, and on them there are few large bodies of fresh

PLATE III

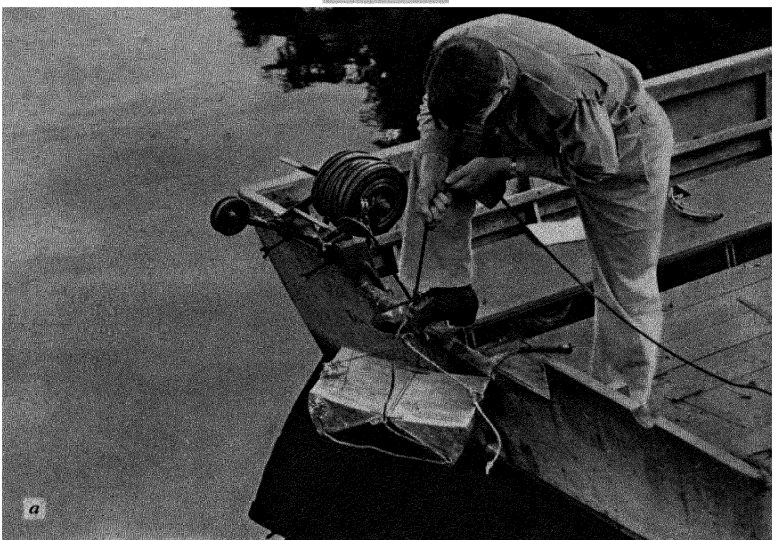


Photographs by John Clegg

a. Temperature Recorder and its galvanometer

b. Floating Cage. The cage itself may be seen in the boat; the float which supports it is being lifted out of the water

PLATE IV





Photographs by John Clegg

a. Petersen Grab open
b. Petersen Grab closed

water, though they are not on that account of any less interest to the fresh-water naturalist. The best-known sheets of water are the Broads of East Anglia (Plates 11 and 12, pp. 62 and 63). Geologists are not yet agreed how they came into being. They lie in the courses of rivers traversing a flat plain immediately before discharging into the sea, but whether the rivers have impeded their own courses by dropping silt, whether the outflow has been raised by sandbanks thrown up by the sea, or whether there has been a slight tilt in the land, is not settled.

A river tends to build up a deltaic plain at the end of its course and it inundates this plain every time it rises a little above its normal level. Parts of the plain will be under water only at the height of a flood, parts will be permanently marshy, and parts will be under water all the year round. This is the normal and accepted state of affairs in regions of the world where man has done little towards controlling and taming nature : the Rivers Tigris and Euphrates may be taken as an illustration (Fig. 5, p. 46). In Britain, however, man has long since decreed that there is a place for everything and the place for water is within well defined banks ; any breaking out and overflowing is an irregularity and often a catastrophe, and the victim of a flood is not consoled by the assurance that it is " natural."

The East Anglian fens are somewhat similar in their origin to the Broads. A flat clay-floored valley opening into the Wash was flooded by the sea after the Ice Age, owing to a slight lowering of the land level. Silt banks deposited by the sea gradually cut it off and it became a great inland lagoon. It was quite shallow and rich in nutrient salts. Conditions were, therefore, good for plant growth and the resulting vegetation was luxurious. The dead remains accumulated and formed peat which filled up the lagoon rather rapidly, speaking in geological terms, till open water was left only in a few meres, which must have been very like the Broads to-day. Man coveted the rich soil and in the seventeenth century he successfully started drainage and reclamation. Now the meres have gone, the natural vegetation is to be found only in a few carefully tended preserves, and the fenland presents to the pond-hunter no more than an endless series of ditches, great and small.

Travelling a little farther south, we come to the chalk region ; and a more waterless expanse than a chalk down cannot be found anywhere in the country. But even here there is something to interest the fresh-water naturalist. Man has been wont to run stock over the downs for centuries and, in order to provide them with water, he has

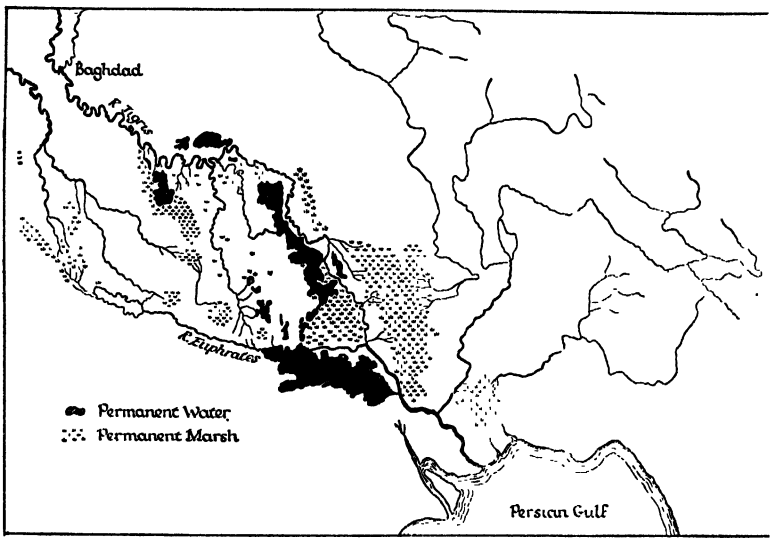


FIG. 5
Lower courses of the Rivers Tigris and Euphrates
Scale, 1 inch=90 miles

built ponds which have received the name of dewponds. There are few subjects about which more nonsense has been written than that of dewponds. One explanation offered, even by people who should know better, is that dewponds are made by a secret process which insulates them from the surrounding land. When heat is lost at night by radiation from the surface, warmth from the lower layers is conducted upwards, and so the temperature at the surface does not reach a very low point; but this upward conduction cannot affect the dewpond because it is insulated. Accordingly, it is alleged, the dewpond area gets very cold, the atmosphere above it is chilled and moisture is deposited. The difficulty about this theory is that, if the dewpond were so effectively insulated from the land below, it would get very hot when the sun shone on it by day and much water would be lost by evaporation. Furthermore, considerations of the respective latent heats of water and chalk (that is the amount which a given volume of each would lose in a given time) have been ignored. Several people have examined the problem both experimentally and theoretically and the whole fallacy has been

exposed more than once. Mr. A. J. Pugsley (1939) has recently returned to the attack in a small book published by *Country Life*, but it would be optimistic to expect that the myth has been exploded. There is certainly a secret process in the making of dewponds and it has been handed down from father to son in certain families, but its aim is the construction of a waterproof bottom which will last for many years without cracking.

The dewpond, in effect, is a shallow pan of concrete or clay, and, though sometimes it is situated on top of a hill (Plate 13, p. 68) where it must rely entirely on rain, often it is located to take advantage of storm water, particularly where a road presents an impermeable surface. The belief that dewponds date back to the Neolithic Age is erroneous.

We have now worked our way down to the south of England and come to the coast to study a fresh-water lake which owes its origin to sand-banks thrown up by the sea. To the west of Bournemouth lies Poole Harbour, a big enclosed area connected with the open sea by a small entrance, which cuts through a narrow strip of land and so makes two peninsulas. The one which lies to the west is known as South Haven Peninsula, and a conspicuous feature of it is the Little Sea, a shallow lake over 70 acres in extent. Particular interest lies in the fact that the origin and development of Little Sea can be traced in detail from the information given on old charts. The first of these, dating from the reign of Henry VIII, is not very accurate, but from it and one or two later charts a fair deduction is that the peninsula then comprised only land of the Bagshot Sand formation, with a small more recent sandspit at the tip. This is shown in Fig. 6a on p. 48, but the sea and the area between tidemarks is omitted from this figure, as any attempt to include them would be based largely on conjecture. A chart of 1721 is remarkably accurate. It shows that a sandbank, thrown up parallel with the land existing in the previous century, has enclosed a lagoon which is apparently a sheet of water at high tide but at low tide an expanse of bare sand, except for water standing in drainage channels. There is a wide beach, shown stippled in Fig. 6b, and a detached sandbank lying to the north of the channel draining the lagoon. Rather more than a century later, in 1849, a survey shows considerable development; a second ridge has been thrown up parallel to the first in the northern half and a marshy area indicates the depression between the two; a third is foreshadowed by a long sandbank which now bounds the outflow on the seaward side; it is shown white in Fig. 6c, the convention used to denote land above

high water, though strictly it should be stippled as, according to the chart, it was covered by the highest tides. The sea runs in and out of the channel between this bank and the second ridge, and water apparently stands in the north and south portions of the lagoon at all stages of the tide. To-day (Fig. 6d) there are three dunes, and the

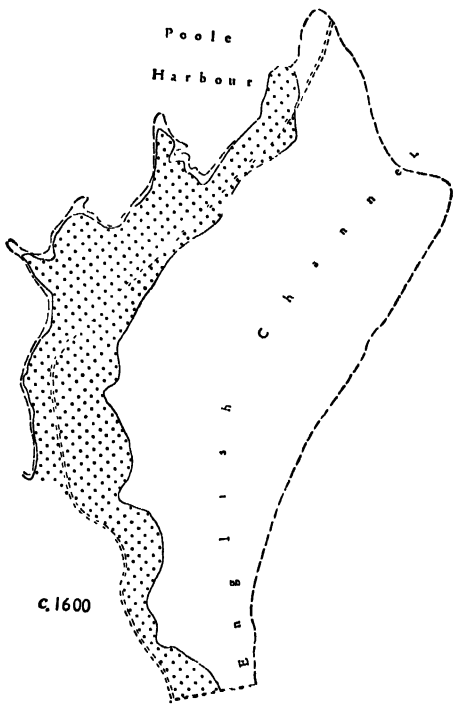


FIG. 6A
Formation of the Little Sea, *c.* 1600
Scale, 2 inches = 1 mile

Little Sea is an inland lake with water which is actually soft and rather poor in dissolved salts. Other, smaller, bodies of water have come into being and the slacks between the dunes are extensively marshy; man-made cuts traversing them testify to an attempt at some earlier date to drain them, presumably to obtain pasturage.

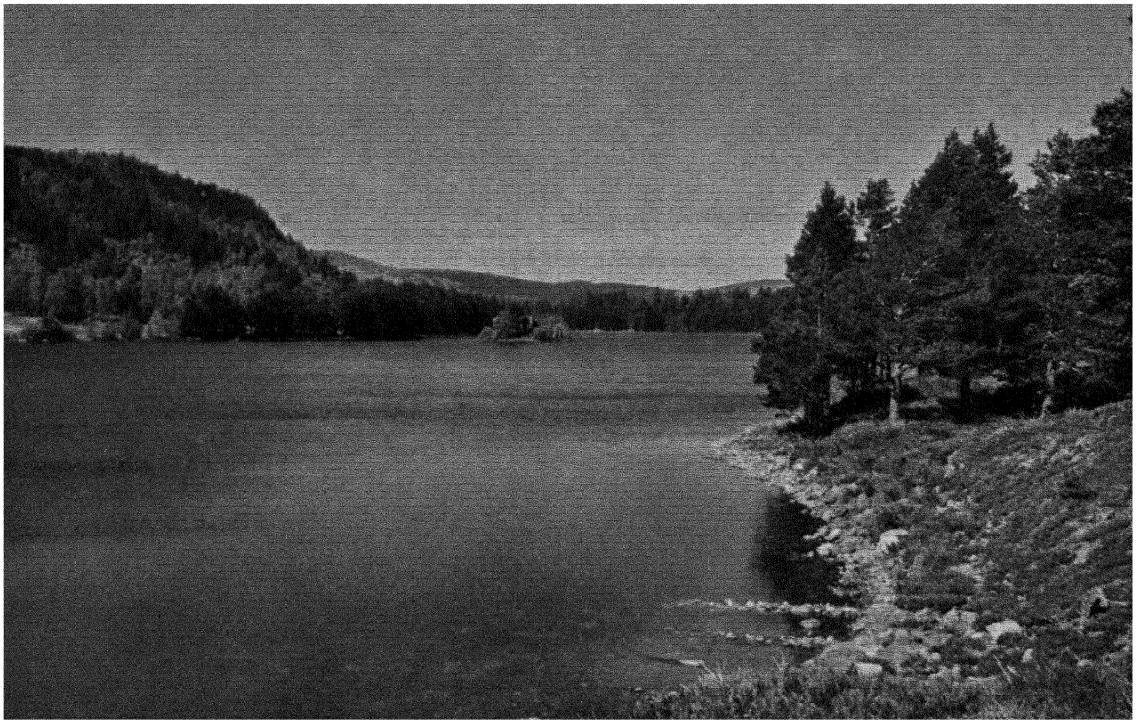


PLATE 7

John Markham

Glacial lake. Loch an Eilean, Inverness-shire. May

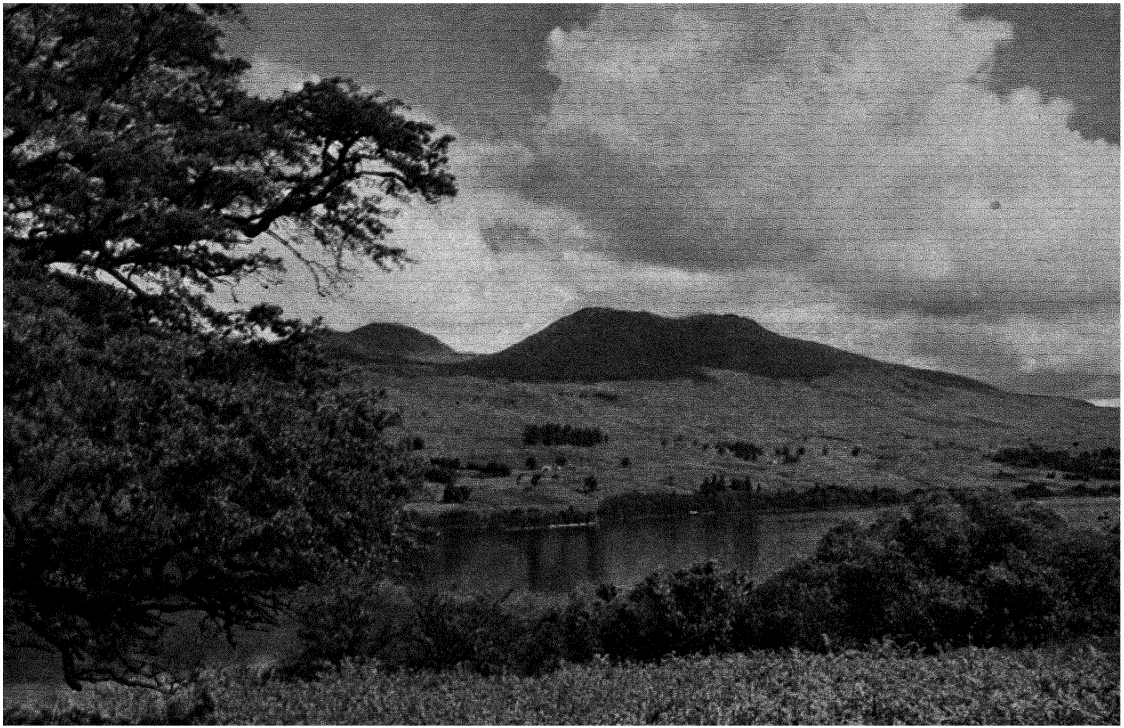


PLATE 8

John Markham

Glacial lake. Loch Tay with Ben Lawers behind, Perthshire. June

And so, thanks to the painstaking research of Captain C. Diver (1933), it is possible to reconstruct in detail the changes which brought Little Sea into existence. There are other sheets of fresh water of similar origin, but no one has pursued inquiries into their early history.

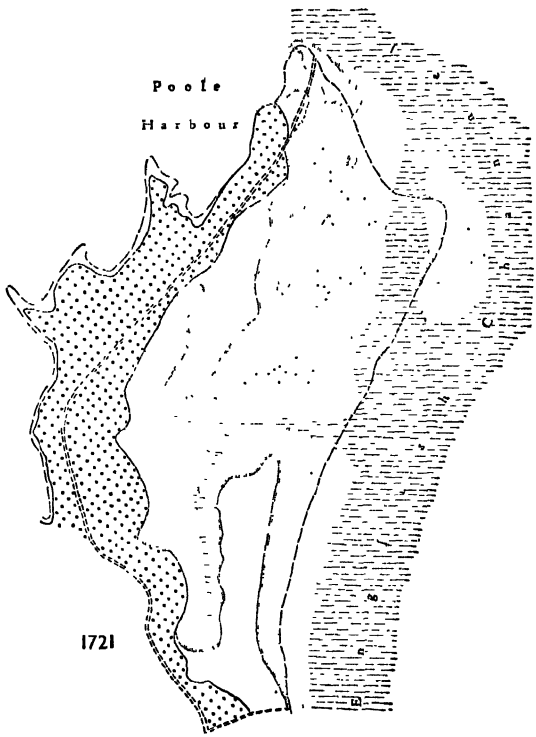


FIG. 6B
Formation of the Little Sea, *c.* 1721
Scale, 2 inches = 1 mile

Some have obviously been formed more simply, and Llyn Maclog and Llyn Coron in Anglesey, for example, lie in long transverse depressions which the sea has blocked at the ends with sand.

Wherever man has had available an impervious soil he has tended to make ponds and lakes, to provide him or his animals with a water

supply, for ornament (Plate 14, p. 69), or for sport. A favourite site is a narrow valley which can be flooded by the erection of a dam (Plate XI, p. 80), for building a dam is comparatively simple, while sufficient excavation to make a pond of reasonable size is a big and costly undertaking. Where there is hard impervious rock, fish-ponds are sometimes

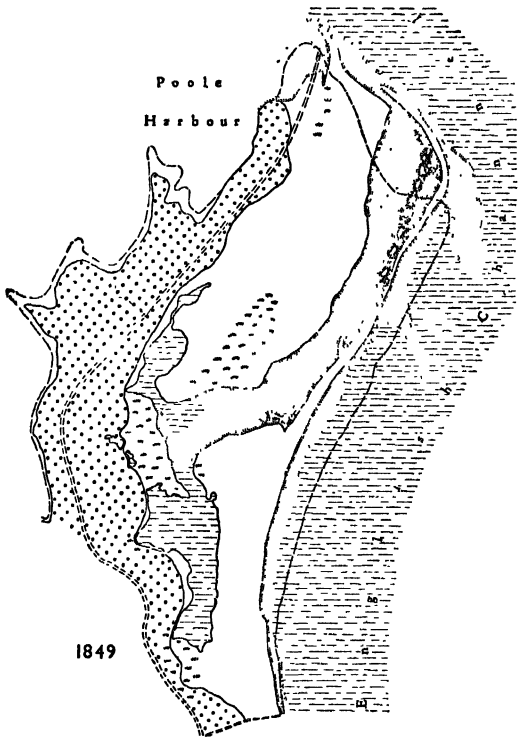
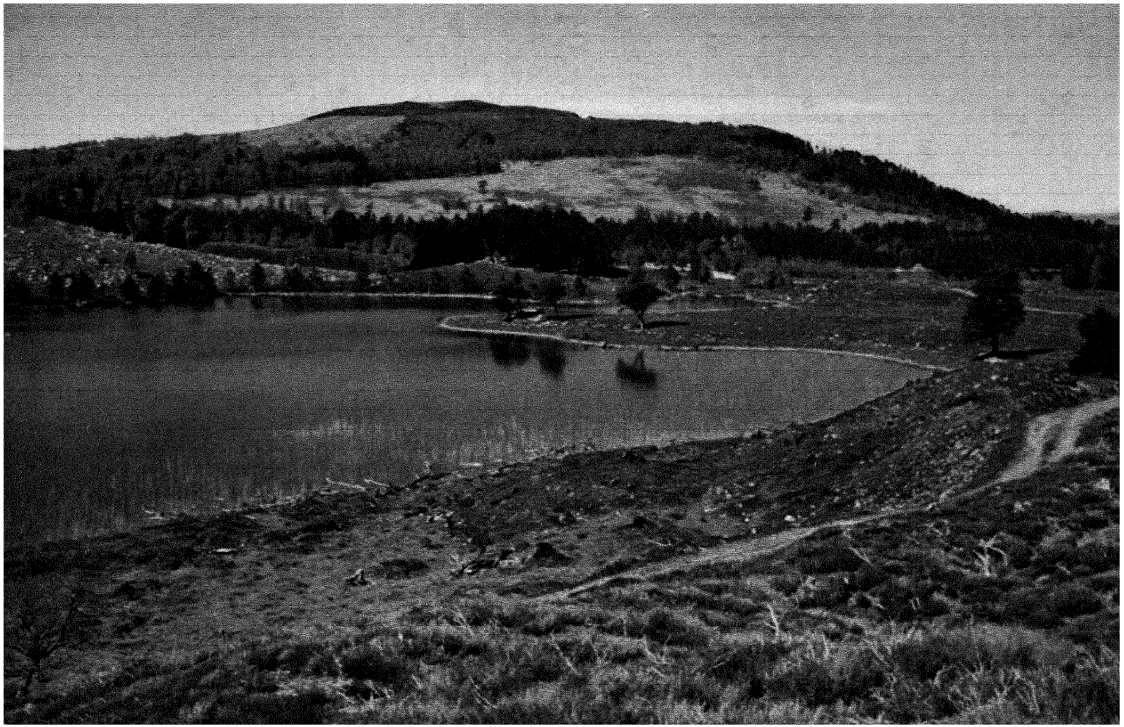


FIG. 6c
Formation of the Little Sea, *c.* 1849
Scale, 2 inches = 1 mile

very numerous ; for example, in the southern part of the Lake District the staff of the Fresh-water Biological Association have nearly fifty under observation within easy reach of their laboratory.

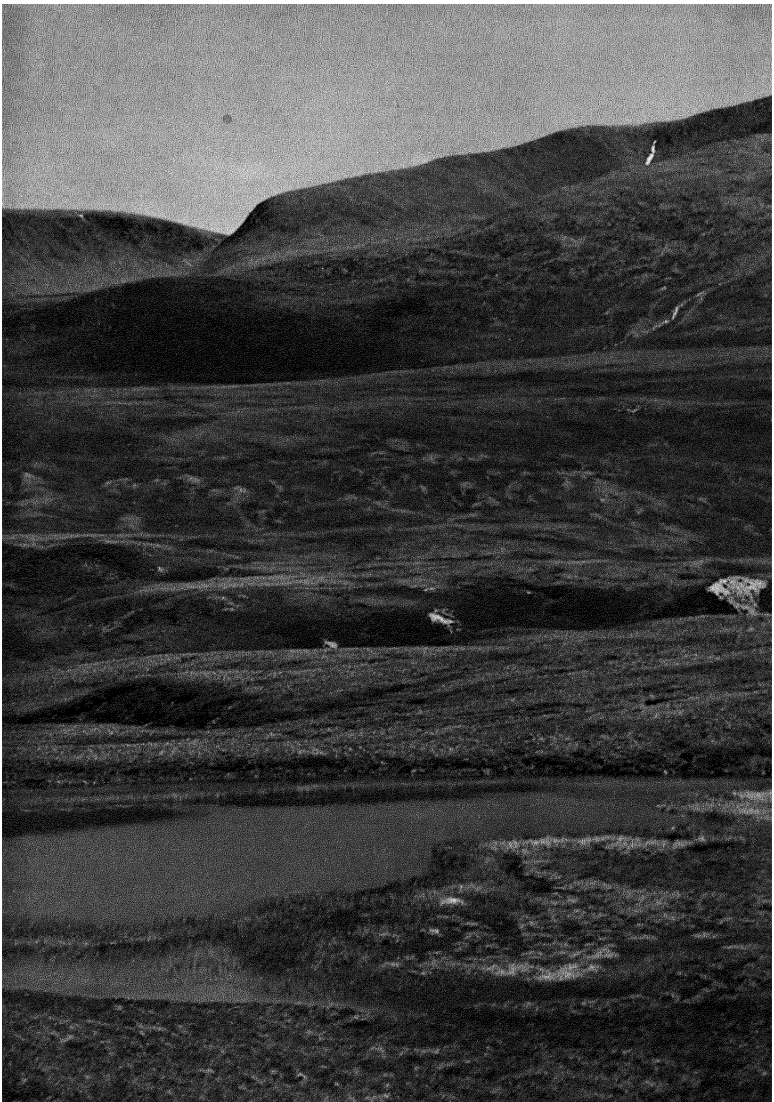
On heavy clay soil the farmer frequently digs a hole in every field in order to form a pond from which his animals may drink. Many



John Markham

Glacial lake Loch Gamhna, Inverness-shire May

PLATE 10



Peat pool, Cairngorms May

other pieces of water are the by-products of man's activities. Quarrying for stone, or digging out clay for bricks, produces an impermeable basin which the rain will ultimately fill. Excavating sand and gravel for railway ballast and other purposes may extend down below the water-table so that a pond results (Plates 15 and 16, pp. 76 and 77). Under-

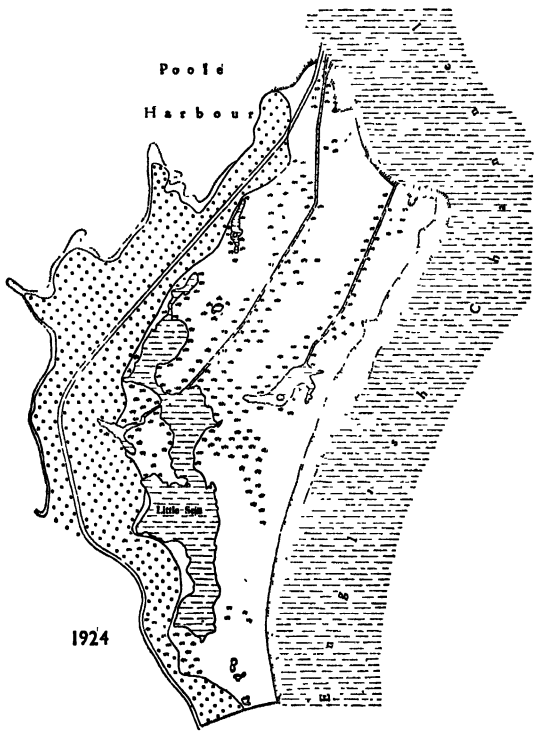


FIG. 6D
Formation of the Little Sea, *c.* 1924
Scale, 2 inches = 1 mile

ground mines and tunnels sometimes cave in and cause at the surface a depression which fills with water.

These are some of the main ways in which bodies of fresh water have originated. There are others, less important in the British Isles, but a catalogue of them would serve no useful purpose here. Our main

interest is with the plants and animals of water, and the next stage is to notice how lakes may be classified according to the biological processes going on within them.

One of the best-known limnologists, Professor Thienemann, has applied the word "eutrophic" to lakes in which the hypolimnion, that is the lower layer of cold water (Fig. 1, p. 20), becomes depleted of oxygen during the summer, and the word "oligotrophic" to those in which it does not. The oxygen in the hypolimnion is used up by the decay of organic matter which falls from the upper layer or epilimnion, and all of it is used up only when there is a copious production of life in the epilimnion. A eutrophic lake is, therefore, a rich lake. The inflowing waters will be richest in nutrient salts where they flow through flat or gently undulating country with a fertile soil which will almost certainly be cultivated, and so eutrophic lakes are generally found in such country. The waters will be at least moderately calcareous, for, without calcium, decomposition does not proceed very far. Oligotrophic lakes on the other hand are "little nourishing," to translate the name literally, and exist mainly in wild rocky regions where the water is soft.

Mortimer, whose work on the bottom mud was mentioned in Chapter 2 (p. 24), showed that, when oxygen is used up completely in the hypolimnion, changes take place which lead to a great increase in the nutrient salts in solution. The process is partly reversible and there is a decrease in concentration when the hypolimnion is oxygenated by mixing with the epilimnion in the autumn overturn. But some of the salts probably remain in solution to become available to plant life in the following spring. A eutrophic state, therefore, leads to a process whereby the water is still further enriched, but in an oligotrophic lake this does not happen. The distinction between the two types is fundamental. It is also (and this is unusual when an attempt is made to parcel up Nature into categories) quite clear-cut. The criterion is whether or not the surface of the mud attains an oxygenless, or in technical parlance, a reduced, state. But there are some lakes in which this happens in a good summer and not in a bad one; the path of the classifier is never quite smooth.

We do not propose here to follow up the elaborations of this scheme associated particularly with the names of Einar Naumann in Sweden and Kaare Münster Strøm in Norway, but we must notice one modification proposed by G. E. Hutchinson of Yale University. Obviously

a given amount of organic matter, that just requires for its decomposition all the oxygen in a hypolimnion, will not use up all the oxygen in a larger hypolimnion. Eutrophic lakes are in fact always shallow and accordingly have a small hypolimnion. There is, therefore, a difference between the lake which is oligotrophic because there is little production in its surface waters, and one which is oligotrophic because it is deep and has a big hypolimnion. In the latter, although there is vigorous production of life in the epilimnion, the oxygen of the hypolimnion is never used up because there is so much of it. Hutchinson described the first type, which is fundamentally poor, as edaphically oligotrophic, and the second, which is rich but not eutrophic because of its depth, as morphometrically oligotrophic. It may be remarked here that scientists do not produce names like these as a display of virtuosity, nor to earn a reputation like W. S. Gilbert's singularly deep young man. Such names translate into other languages with no more than a change of termination and their identity remains quite clear; an existing word given a meaning more precise than that ascribed to it in the ordinary dictionary would only cause confusion when translated into a foreign language.

Certain lakes do not fit into either the eutrophic or oligotrophic categories. They are rich in organic matter, but this consists of undecomposed plant fragments which may conveniently be referred to as peat. There has been little decomposition because of a deficiency of calcium and, as calcium is also very scarce in the water, little decomposition takes place when the peat material is washed in. The result is a considerable accumulation on the bottom of a characteristic deposit, but a scarcity in solution of nutrient salts on which plant life might be supported. Such conditions are known as dystrophic. Dystrophic waters are often stained brown, and extreme examples may resemble beer or even stout. Eutrophic waters are not very transparent owing to the teeming life which they support and extreme examples resemble pea-soup. Oligotrophic waters have those clear transparent qualities which delight poets and waterworks engineers.

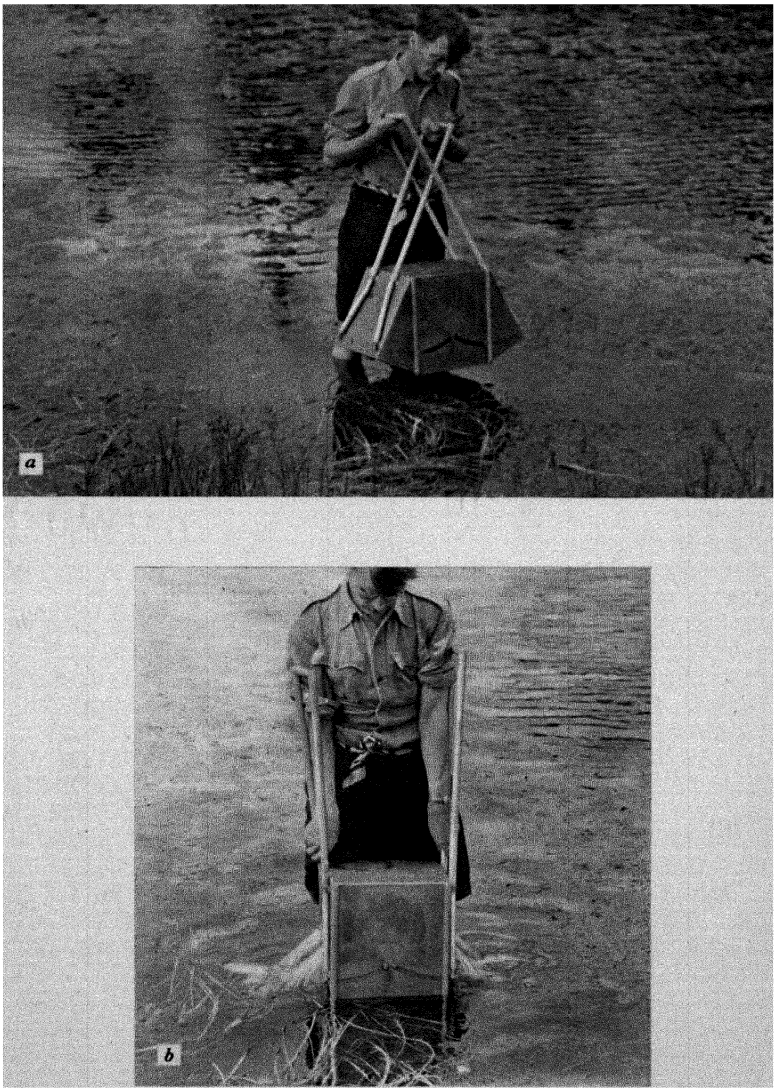
The British lakes fall clearly into these three categories. Those which lie in glacial rock basins and those which are made artificially in mountain regions may be expected to be oligotrophic. Most are, but the generalization is not without exception, and the subject is examined further in the rest of this chapter. Any of these pieces of water may be dystrophic if surrounded by deep peat which is undergoing erosion.

Theoretically glacial lakes on a plain may be oligotrophic or eutrophic according to the nature of the soil which the ice sheet left behind. If it is a barren sand or gravel, the lakes will be oligotrophic, but in fact the examples quoted are in rich calcareous soil and are eutrophic. Strictly the classification should go no further than this, for it is based fundamentally on the oxygen concentration in the hypolimnion and is therefore applicable only to large and at least moderately deep bodies of water, since small ones or very shallow ones do not have a hypolimnion. But the terms have been applied to ponds, and this usage has been sanctioned by Thienemann himself. If this loose application be allowed, the advantage of the words " eutrophic " and " oligotrophic " over words such as " productive " and " unproductive " becomes open to question ; it may be said in favour of the more recondite words that they are established and that they are likely to be transposed from one language to another, whereas a word like " productive " is translated. A corrie tarn high up in the mountains or a pond in a poor sandy area, for example the Little Sea, is typically oligotrophic. A peat pool is dystrophic, and a farmyard pond provides an extreme example of eutrophy. The nature of a small piece of water is influenced more by slight local factors, such as pollution by cattle, or manure on the surrounding land, and less by the geology of the whole drainage basin than is that of a large lake.

Comment has just been made on the difficulties of those who seek to classify natural phenomena into discrete categories. Professor W. H. Pearsall has avoided this difficulty by arranging the Lake District lakes in an evolutionary sequence. All the basins were formed at the same time, during the Ice Age, and all the lakes came into being more or less contemporaneously as the ice sheet retreated. But, in the intervening odd twelve thousand years between that event and to-day, some have changed or evolved more rapidly than others, so that they may now be arranged in a series with the least changed or " primitive " lakes at one end and the most changed or " evolved " lakes at the other.

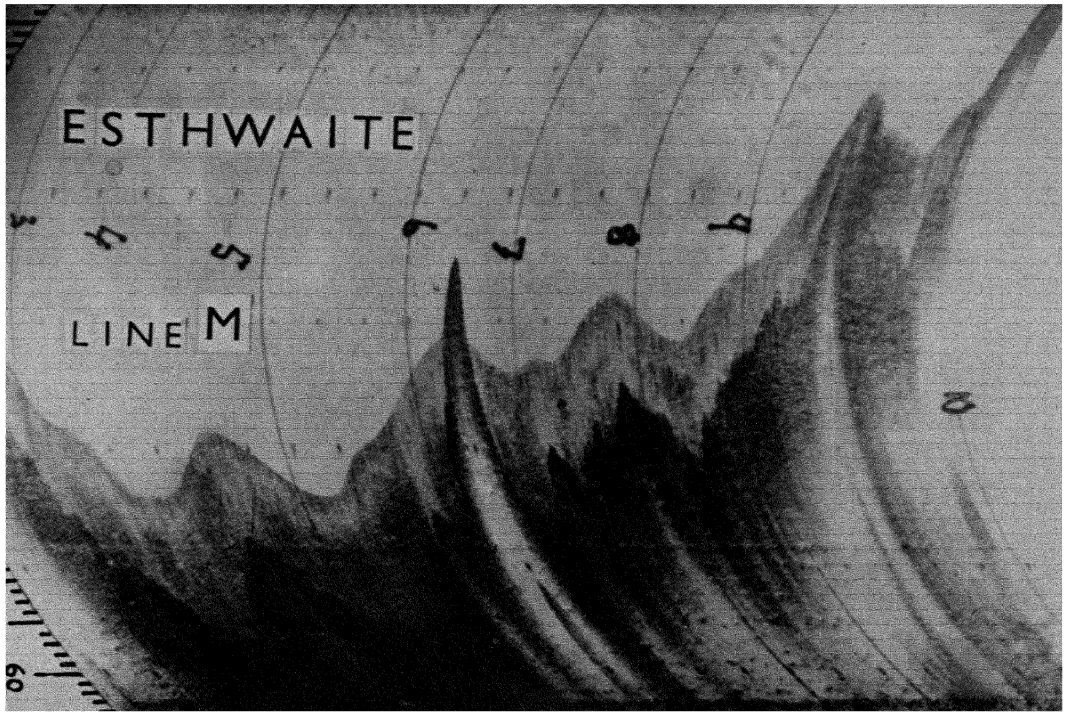
Wastwater and Ennerdale Water (Plate VII, p. 58) are the two most primitive lakes ; the latter has been selected as the standard example. It lies in a central band of hard volcanic rocks, the Borrowdale Series, which have weathered little since the Ice Age, and so Ennerdale Water to-day receives its water from a wild and desolate gathering ground which yields very little in suspension or solution, and has not attracted man to settle down and farm.

PLATE V



Photographs by John Clegg

a. **Hand Grab open**
b. **Hand Grab closed**



C. H. Mortimer

Portion of an Echo Sounder Record. Esthwaite Lake, Lake District. The upper lighter part represents mud, the lower darker rock. The projection of a ridge of bare rock is clearly visible between lines 6 and 7

Windermere and Esthwaite Water are the two most evolved lakes. They lie in the south of the district in a zone of Bannisdale slates, which, though hard rocks, are softer than the Borrowdale Volcanics and have weathered more. Much of the drainage area is floored with the products of weathering and is relatively flat. Obviously rain-water seeping through soil will dissolve out more than water trickling over solid rock, and so the streams and rivers entering Esthwaite and Windermere bring with them a higher concentration of nutrient salts than those flowing into Ennerdale. But the flat land also attracts the farmer and the cultivator who seeks to improve the soil by adding manures to it. Some of these find their way into the lake, and so the difference between primitive and evolved is enhanced. Within the last century Windermere, particularly, has become a residential resort. The result is that much human sewage enriches its waters and makes still greater its difference from Ennerdale.

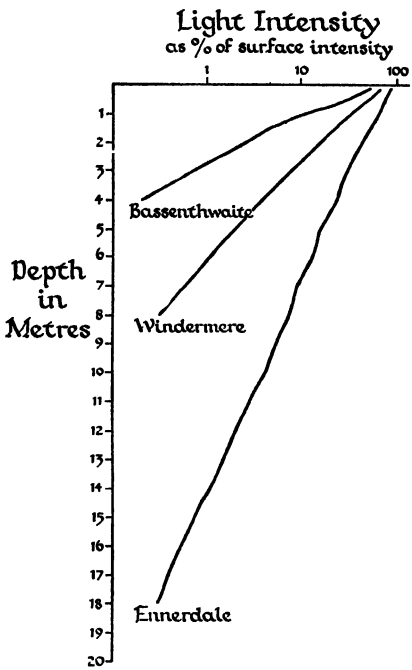


FIG. 7
Penetration of light into three Lake District lakes

Esthwaite Water is a relatively shallow lake and, in some years at least, all the oxygen in its hypolimnion is used up. It is, therefore, eutrophic.

The stage of evolution may be gauged by three factors, first the percentage of the drainage area which is cultivated, second the percentage of the shallow water region which is rocky, and third the transparency. The first two factors are fundamental; the third is partly fundamental and partly a result, because the transparency of

the water depends both on the amount of mineral matter in suspension and on the quantity of life present, provided there are no extraneous factors like staining from peat or pollution by mine washings. In the Lake District none of the larger lakes except Bassenthwaite contain peat-stained water, and pollution from mine washings, though it does occur, is fortunately rare. Table 2 shows the Lake District lakes arranged according to these three factors. The figures in the last column show the depth at which a white disc, 7 cms in diameter, could just be seen.

TABLE 2

Evolutionary sequence of Lake District Lakes (Pearsall, 1921)

Lake	*Percentage of catchment area cultivable*	*Percentage of lake shore to depth 30 feet rocky*	*Relative transparency of water (metres depth)*
Wastwater	5·2	73	9·0
Ennerdale	5·4	66	8·3
Buttermere	6·0	50	8·0
Crummock	8·0	47	8·0
Hawes Water ..	7·7	25	5·8
Derwentwater ..	10·0	33	5·5
Ullswater	16·6	28	5·4
Bassenthwaite ..	29·4	29	2·2
Coniston	21·8	27	5·4
Windermere ..	29·4	28	5·5
Esthwaite	45·4	12	3·1

On the whole there is a serial increase or decrease in each of the three columns. The most notable anomaly is the low transparency of Bassenthwaite, occasioned by its being the only lake of which the water is stained with peat. The amount of light at different depths in Bassenthwaite, Windermere and Ennerdale is shown in Fig. 7, p. 55, expressed as a percentage of the intensity at the surface.

Pearsall, in this classic study, envisaged a slow and steady change, but recent work on cores of mud from the bottom of Windermere has suggested that the evolution has had a step-like character, periods of

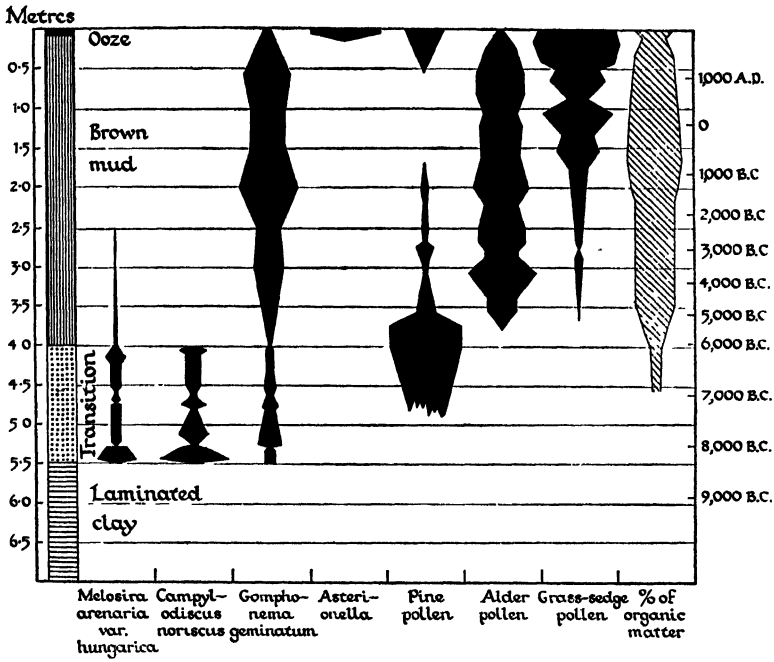


FIG. 8
Some salient features of a core of mud from deep water in Windermere

rapid change alternating with long periods of stability. At the left-hand side of Fig. 8 there is a diagrammatic representation of a core of mud taken from the bottom of Windermere. At the lower end it consists of clay which, on examination, proves to be made up of alternating layers of very fine and coarser particles ; it is accordingly referred to as laminated clay by Dr. Winifred Pennington (1943), who has described the cores. Above the laminated clay is a zone called the transition zone in which bands of pink clay, of varying thickness, some being quite large, are separated by grey zones in which there is a fair amount of organic matter. Overlying the transition zone is a thick column of brown mud which extends nearly to the surface ; it is capped by a fourth kind of soil, a black deposit which Pennington refers to as ooze.

The laminated clay contains very little organic matter and few

remains of plants, and was almost certainly formed towards the end of a glacial period, for similar deposits are being laid down to-day in certain glacier-fed lakes. During the summer both coarse and very fine particles are washed into the lake. The coarse particles sink almost immediately but the fine particles remain in suspension for a long time. When winter comes the inflowing streams freeze, and so no particulate matter is brought into the lake, but fine particles left over from the summer are still settling. The result is a summer layer of coarse and fine particles and a winter layer of fine particles only.

The low organic content of this deposit and the scarcity of plant remains indicate that there was little life in the lake when the laminated clay was being laid down. In the transition zone era living organisms were much more abundant, for the skeletons of minute floating plants known as diatoms have been found and identified, and the grey mud is evidently composed to some extent of the remains of plants and animals. It is likely that this part of the core was laid down during a period when the ice was retreating and conditions were unstable. It is suggested that the layers of pink clay were brought in as a result of landslides, the washing out of ice-dammed lakes, and similar adjustments of the landscape which might be expected at such a time. Production in the lake was probably increasing throughout this period.

There is an abrupt change from the pink and grey deposits of the transition zone to the brown mud. There are physical and chemical differences between the two zones and, as may be seen from Fig. 8, some of the common diatoms were different. *Melosira arenaria* var. *hungarica* and *Campylodiscus noricus* flourished during the transition period and disappeared during the brown mud era, whereas *Gomphonema geminatum* is abundant in the latter and scarce in the former. Although other species show no great changes in quantity with the transition from one type of deposit to the other, evidently some radical change took place in the lake when the deposition of brown mud started. At present there is no exact information about the nature of the change.

To-day not much is known about the natural conditions under which different kinds of diatom thrive, and advances in this field will contribute towards the interpretation of mud cores in terms of past climatic and other changes. *Melosira arenaria* var. *hugarica* is now extinct. It is possible that the change to brown mud was contemporary with an amelioration of climate.

The transition to ooze is equally abrupt; there are physical and

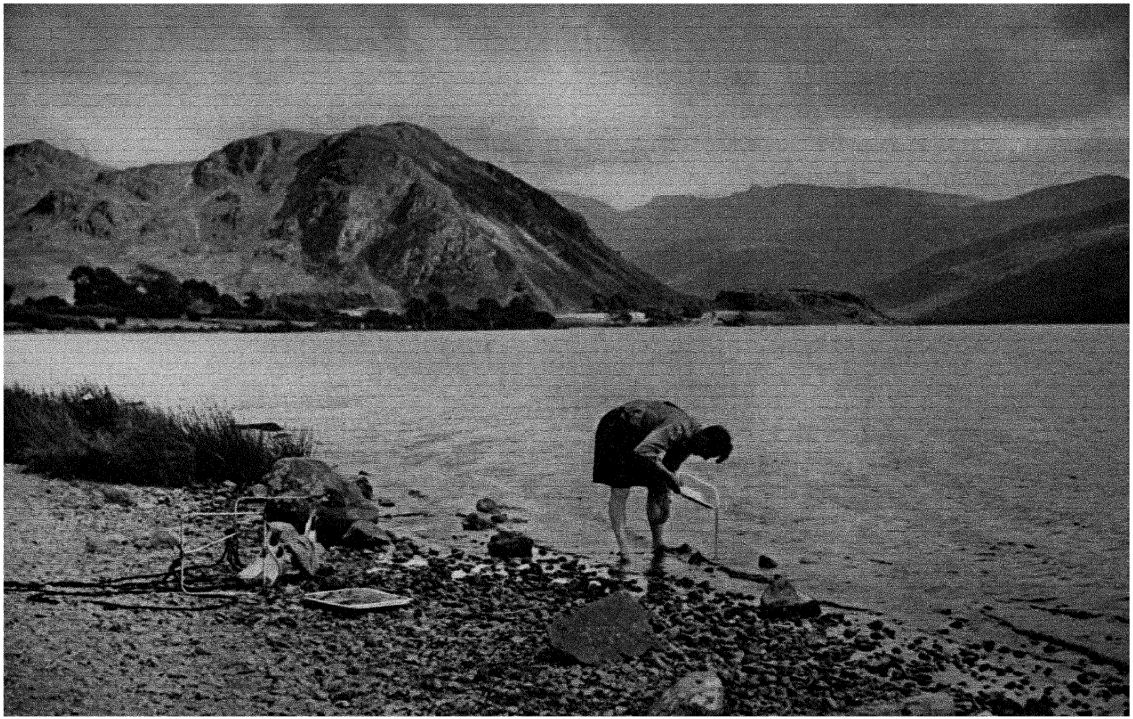
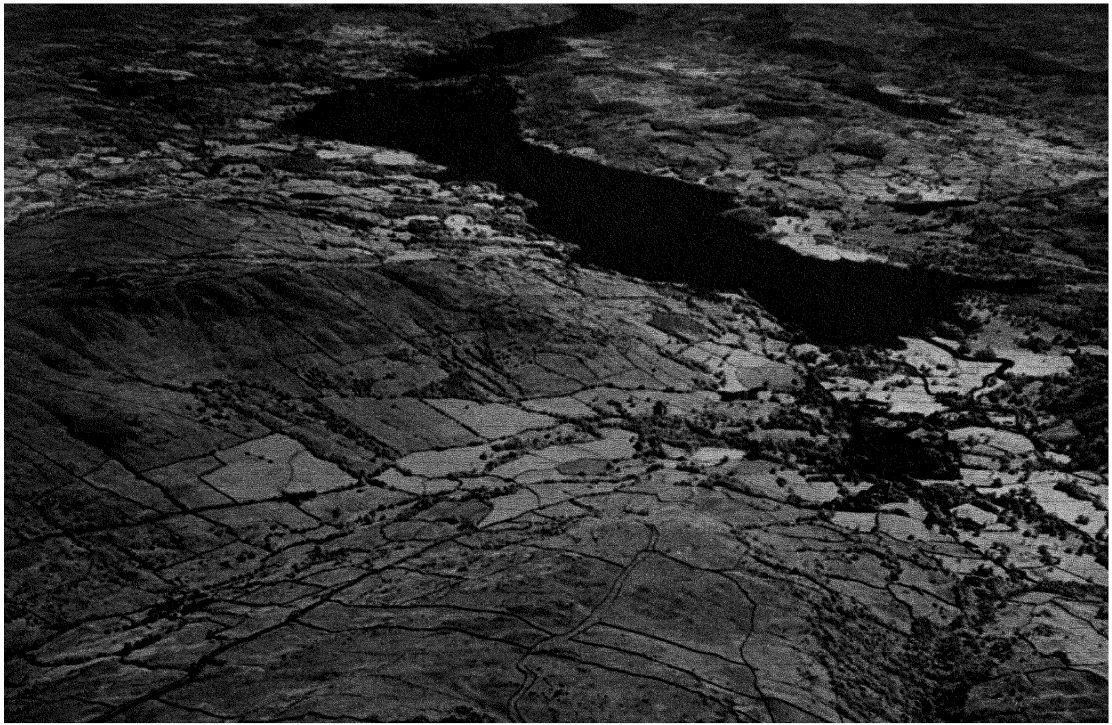


PLATE VII

John Clegg

Ennerdale Lake, Lake District



C H Wood

Aerial view from the north of Windermere, Lake District

chemical differences and also a difference in the diatom flora, for, with the appearance of ooze, *Asterionella* quite suddenly becomes very common. There is good reason to believe that this change took place about one hundred years ago when, owing to the influence of Wordsworth, Stephenson, and other writers and engineers, the Lake District became a popular place in which to live, and the lake waters began to receive appreciable amounts of sewage.

There appear then to have been four phases in the history of the lake and all, except perhaps the second, were long periods of little or no change. The transition from one to the other was abrupt. In this respect there is no reason to suppose that Windermere is unusual, because evidence that lake evolution has proceeded in a series of jumps, so to speak, and not gradually, has recently been brought forward by American as well as British limnologists.

Though not directly germane to the substance of the present chapter, it is interesting here to continue with the bottom deposits, and describe how Pennington (1943) and Pearsall and Pennington (1947) have endeavoured to put a date to the various events just described. Pennington started with the assumption that the deposition of mineral matter had been going on at a constant rate throughout the ooze and the brown mud eras. It was a comparatively simple matter to measure the rate of deposition in a year at the present time, and this gave data from which to establish the time-scale shown on the right of Fig. 8. The laminations of the laminated clay represent a year each, if the explanation of the method of formation of this deposit given above is correct. The transition zone, however, proved more difficult and it was not possible to do much more than guess. Clearly a check was desirable if one could be found, because the assumption that the rate of deposition of mineral matter had not changed might or might not be correct. Furthermore, as Pennington points out, small annual variations in the amounts of deposit to-day would lead to a big error when calculations of thousands of years were based on them.

Accordingly Pearsall and Pennington examined the data in the light of what was known of the past history of the Lake District. The data, besides those already mentioned, consisted of the identification and measurement of the amount of pollen at different depths, and also the estimation of the percentage of organic matter. Some of the more important items are shown in Fig. 8.

Before about 2000 B.C. nothing is known of the history of man in

the Lake District, and so the evidence about to be discussed refers only to a rather small part of the core. Nevertheless, if it shows that the interpretation of that part agrees, it will prove that the initial assumption was not far out. About 1800 B.C. the Lake District was invaded by a neolithic people who inhabited the hill-tops, where their stone circles and other remains may be found to-day. There is no trace of any colonization of the lower slopes of the valleys, and it is doubtful if the invaders could have cut down enough trees to make settlement at these lower altitudes possible, since all their cutting tools were of stone. There is evidence that these people had sheep and cattle, and it may be assumed that they did a certain amount of felling of the thin woodlands near the upper limit of tree growth. Pines would be the dominant trees at this altitude. Grazing by livestock would prevent regeneration of the woodland, and the deforestation would probably result in soil erosion. Grasses and sedges might be expected to grow where the trees had previously been. The initial invasion took place about 1800 B.C. and the population was well developed by 1000 B.C. It will be seen from Fig. 8 that at about this time pine pollen disappeared from the bottom deposits completely and the amount of grass and sedge pollen increased. Further, there was an increase in the amount of organic matter in the mud, and this is to be expected if there were increased erosion of the peaty soils of the drainage area. And so certain changes in the mud reflect changes which might be expected to result from the occupation of the hill-tops by primitive man, and the provisional time-scale adopted for the mud synchronizes with the known historical dates.

The Stone Age people were not greatly affected by the Romans, for whom the Lake District was but a line of communication, and none of the later invasions affected the district till the Norse came in about A.D. 1000. They infiltrated up the valleys, clearing and draining as they went; and so it is satisfactory to find that the point where A.D. 1000 has been set in Fig. 8 coincides with the beginning of a marked decrease in the amount of alder pollen, for alder thickets doubtless covered much of the valley bottoms before the Norsemen cut them down. The coincident reappearance and increase of pine may be attributed to the establishment of this tree on mosses which had been drained; it thrives in such places to-day. The increase of grass-sedge pollen is also to be expected.

From this time onward clearing of woodlands from the lower parts of the Lake District was a continuous process, first in the interests of

sheep-grazing and later to procure wood for iron-smelting. In 1556 iron-smelting was forbidden in order to prevent further destruction of woodlands, but the enactment does not seem to have achieved its aim, and there was no real halt to deforestation till about 1800. This, the beginning of the romantic period, saw the start of amenity planting. Oak and hazel pollen, which are not shown in the figure, decrease from a point 800 or 900 years ago ; but the reduction of oak is not continuous and this tree is increasing at the finish, so here also known historical events corroborate the dating system which has been applied to the cores.

Corresponding with the ooze era there is an increase in the percentage of organic matter, and this might be expected, as the period is one in which sewage begins to enter the lake in significant amount. But, on the other hand, it is not known how far down into the mud decomposition of organic matter extends. Undoubtedly breakdown goes on for some distance below the surface layer, and so it is to be expected that the later layers nearer the top should contain more organic matter than those below. The rise in the last few centimetres may, therefore, bear no relation to any external change. But if, as seems likely, *Asterionella* is associated with the enrichment of the lake waters, its appearance fits the time-scale.

It need hardly be pointed out that there is some conjecture in the fitting of the Pennington time-scale to historical facts, but it is possible to make a coherent story, and Pearsall and Pennington conclude that the time-scale arrived at by measuring the rate of sedimentation to-day is at least of the right order.

CHAPTER 5

RIVERS

IT WOULD be convenient to introduce this subject by referring to a typical river, as we have done in Chapter 2 for lakes. But to do so would be about as profitable as to describe the habits and way of life of the people of Britain in terms of the typical man or woman. A lake usually owes its existence to one definite geological event and this puts upon it a stamp which the biologist can make valuable use of in his schemes of classification. A river, on the other hand, may traverse many geological strata and receive some moulding of its general facies from each.

Professor Dudley Stamp in *Britain's Structure and Scenery* in this series writes on p. 39 : " It is a common generalisation in most books on physical geography that the course of a river may be divided into three parts. The upper or mountain course is that in which swiftly flowing water, especially after rain, is able to move stones of considerable size, to roll them along, to rub them one against the other and so to reduce angular fragments such as those broken off the mountains by frost action into rounded pebbles. . . . At the same time the river deepens and widens its own valley so that its valley has a typical V-section with unstable banks. The middle course of the river is that over the foothill belt where it has lost some of its velocity but is still moving rapidly enough to carry sand, silt and mud in suspension, and to roll pebbles along its bed. Its main work there is transportation ; its valley has a broad open section and has stable sides so that the erosive power of the river is strictly limited. The lower course is that in which the river meanders lazily across a plain ; though sweeping much mud out to sea or into the lake into which it empties, it has lost much of its velocity and so much of its power of transportation. It lays

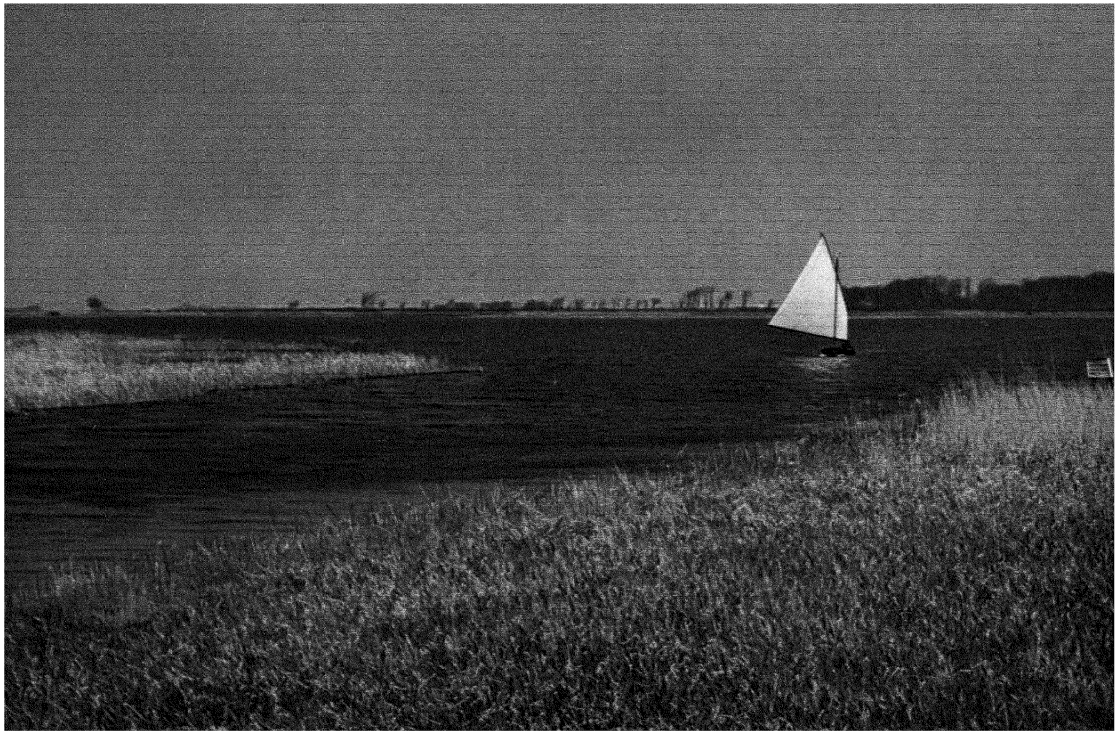


PLATE II

John Markham

Horsey Mere, a Norfolk Broad May



John Markham

Calthorpe Broad, Norfolk July

down part of its load as shingle beaches or sandbanks but especially builds up large flat plains of deposition by spreading alluvium over a wide flood plain or a delta."

Not all rivers have these three courses. The first obviously depends on the existence of hills which are fairly high and not permeable to water as, for example, chalk hills are. Or the later ones may be missing, and, for example, a torrent may run into the sea with no slackening of current. Rivers change during the passage of time and the changes are in the direction of shorter and less torrential mountain courses and longer and more meandering lowland courses. It is convenient to speak of a young or primitive and an old or evolved river, applying those terms, as they were applied to lakes, not as an indication of the tale of years but as an indication of the stage of development which has been reached.

Speed of current and corresponding nature of the bottom are the factors which affect the animals and plants of a river most, so this geological background is important to the biologist. But for most animals and plants small local variations, such as the difference in current at the edge and in the middle of a stream, are more important than the general conditions. Further, a quiet stretch may often be found near the head-waters of a river, or a torrential reach near the mouth, and with each will be associated certain animals and plants which, from a general point of view, are out of place. Even a weir in the meandering sluggish part of a river may harbour certain species typical of torrents.

Dr. Kathleen Carpenter (1928) has adapted for British waters the continental scheme of dividing rivers into main zones. It is based on the species of fish, the only animals of which the distribution is related to the general average nature of the river and not to the peculiar local conditions of some microhabitat. The scheme divides British rivers into four zones :

1. The Headstreams and Highland Brooks are small, usually though not necessarily torrential, and nearly always with a rather uniformly low temperature. A typical example is shown on Plate 18, facing p. 87. There are almost no fish.

2. The Troutbeck (Plates 19, 20, 21, 22) is larger and more constant than the headstream. Torrential conditions are typical and the bottom is composed of solid rock, stones and boulders, with perhaps some gravel. The trout is the only permanent fish of the open water though

the miller's thumb (*Cottus gobio*) is found sheltering among stones. These first two zones together correspond roughly with Stamp's upper or mountain course.

3. The Minnow Reach (Plate 23, p. 108) is still fairly swift and patches of silt and mud are only to be found in a few places protected from the current, but higher plants, notably the water crowfoot, *Ranunculus fluitans*, are able to gain a foothold. This is roughly the middle course of Stamp. It is the *Thymallus* (grayling) zone of the continental workers, but Carpenter rejects this name because the grayling is not a widespread species in Britain.

4. The Lowland Reach (Plate 24, p. 109) is slow and meandering, with a muddy bottom and plenty of vegetation. Coarse fish are characteristic, and on the continent of Europe it is known as the bream zone.

Tansley (1939), in *The British Islands and their Vegetation*, devotes a chapter to rivers, and begins it with a table showing the relation between current speed and the nature of the bottom. But it is worthy of remark that this information, repeated here in Table 3,

TABLE 3

Relation of current speed and nature of river bed

Velocity of current per second	*Nature of bed*	*Habitat*
More than 4 ft. (1·21 m.)	rock	torrential
„ „ 3 ft. (0·91 m.)	heavy shingle	torrential
„ „ 2 ft. (0·60 m.)	light shingle	non-silted
„ „ 1 ft. (0·30 m.)	gravel	partly silted
„ „ 8 in. (0·20 m.)	sand	partly silted
„ „ 5 in. (0·12 m.)	silt	silted
Less than 5 in. (12 cm.)	mud	pond-like

is taken from a text-book on river and canal engineering, and that data of this sort on paper and measurements in the field are very different things, especially if the observer is seeking for a correlation with species of animals or plants. Current speed will vary quite a lot according to the depth at which the measurement is made ; it will vary even more according to the distance from the bank ; and rainfall is yet another factor which will cause variation. Percival and Whitehead (1929),



PLATE IX

C. H. Wood

Glacial lakes in the Lake District. Thirlmere is the lake in the middle distance, Rydal Water is nearest the camera, and Grasmere lies between them



PLATE X

Corrie Tarns, Lake District. Low Water and Levers Water with Coniston Old Man in the foreground *C H Wood*

whose studies of river faunas are referred to in a later chapter, admit frankly that they could make little sense out of their current measurements and discarded them as ecological factors in favour of direct records of the nature of the bottom. The present writers salute them as honest men ; though obviously the broad outlines of any scheme of classification must depend on current speed.

Tansley classifies rivers into five zones, basing his system very largely on the work of Butcher (1933).

Zone 1 is described as very rapid. Where vegetation is present at all, the important plants are mosses and liverworts ; higher plants are often absent altogether and never dominant. This class includes all Carpenter's headstreams and highland brooks and part, at least, of the troutbeck.

Zone 2 is moderately swift with a bottom of stones and boulders, but with occasional patches of finer material in which a small number of higher plants can gain a foothold. *Ranunculus fluitans* (or sometimes *R. pseudofluitans*) the water crowfoot, is the most important.

Zone 3 has a moderate current with a gravelly bed. The list of higher plants is much longer. The water crowfoot is still the most important, others are the simple bur-reed, *Sparganium simplex*, several species of *Potamogeton*, and the Canadian pond-weed, *Elodea canadensis*.

Zones 4 and 5 are medium to slow, and very slow or negligible respectively. The list of higher plants is long and, as it varies a good deal from river to river, confusion rather than clarification would be the result of reproducing it here ; but it may be noted the water crowfoot is usually *not* an important constituent. It is impossible to equate this classification exactly with that of Carpenter, but Zone 2 and part, at least, of Zone 3, correspond with her minnow reach, and Zones 4 and 5 and perhaps part of Zone 3 correspond with her lowland coarse fish reach.

Against this background the few British rivers which have been studied in detail may now be examined. Nearly all the surveys were carried out by the staff of the Ministry of Agriculture and Fisheries, either acting directly for the Ministry or in collaboration with the Water Pollution Research Board.

The River Tees may be taken first, for it is the most primitive or youngest of the rivers surveyed, and was investigated more thoroughly than any of the others (Butcher, Longwell and Pentelow, 1937).

The Tees rises in the Pennines and flows to the North Sea, with a course of about one hundred miles. The gathering ground drained by the headstreams is fairly large, it is high above sea level, it receives a relatively heavy rainfall of about 60 inches a year, and the rock is impermeable. The result of these four factors is a severe scour in time of flood, and this has carved out a deep bed. Consequently the energy of a flood is not dissipated in inundating the surrounding country and the effect is concentrated on the river-bed. On one occasion some carts were being filled with gravel at the water's edge when the river rose so suddenly that the carts had to be abandoned and were swept away. This illustrates a most important condition affecting the plants and animals of the river.

The small town of Croft is about 45 miles from the mouth and about 65 miles from the source, travelling by river, and is a convenient dividing point. Above Croft all the river is rapid with little rooted vegetation and few fish except trout, grayling, and minnows. The river downstream is still moderately swift but there is much more rooted vegetation and various coarse fish are plentiful. After flowing for 20 miles from Croft the river reaches the head of the estuary, which is some 25 miles long.

The Tees rises on Cross Fell at a point about 2,500 feet above sea level. Many small tributaries also rise just on the eastern side of the Pennine watershed, and some of them originate in thick peat beds. One, for example, drains the peat pools which were mentioned in Chapter 4. These little streams run down the hillside with a fairly though not extremely rapid flow, because the eastern slopes of the Pennines are not steep. About six miles from the source three main tributaries have coalesced and the river is some 12 yards wide with a fair flow over a bottom of stones and boulders. Then it enters a quiet stretch and for three miles the current is sufficiently slow to allow the deposition of some fine sediment, which provides a foothold for a few higher plants, *Potamogeton alpinus*, the alpine pond-weed, *Callitriche intermedia*, the water starwort, and *Sparganium simplex*, the simple bur-reed. The only other attached plants are the mosses, *Fontinalis antipyretica*, and *Eurhynchium rusciforme*, and, at certain seasons, the algae *Lemanea fluviatilis* and *Cladophora glomerata*.

This slow stretch provides a pretty example of the sort of exception to the general plan which is to be found in almost any river. It is caused by a stratum of hard rock, and at the end of it there is a fine

waterfall. A little farther on, some 16 miles from the source and 1,000 feet above sea level, the river strikes a road and some human habitations, and comes to the end of what may conveniently be taken as the first part of its course. A chemical station was set up just here and the results obtained are shown in Table 4.

TABLE 4

Some dissolved substances in the Tees near the end of the first part, that is above any pollution

	Maximum value	*Minimum value*
Calcium carbonate ..	57	12 parts per million
Calcium oxide ..	33	5 ,, ,, ,,
Magnesium oxide ..	8	0 ,, ,, ,,
Sulphate	12	2 ,, ,, ,,
Chloride	10	5 ,, ,, ,,
Dissolved oxygen ..	95	86% of saturation value

The average amount of calcium is about 12 parts per million, and so the water is soft although the river has been flowing over limestone. But there are big fluctuations in the concentration of all the substances except oxygen, which is plentiful at all seasons and at all times of day and night.

Trout occur in this part of the river and may be taken almost up to the source. They are plentiful but of small size, the average length being but six inches.

The next part of the course extends all the way down to Croft, which is at the point where the river changes in character. The river crosses several geological formations, which affect its nature, but it remains rapid throughout with a bottom of bare rock or stones. There is hardly any rooted vegetation.

The main difference between this and the preceding part of the river is that it receives sewage effluents from towns along its route. The first place of any size is Middleton-in-Teesdale, some 22 miles from the source, and the biggest is Barnard Castle, about eight miles farther on. The population connected with the sewage systems of the two places was 1,700 and 5,000 respectively when the survey was made. Below the outfalls there were changes in the flora, and there can be no doubt

that these changes were directly attributable to sewage and the products of sewage decomposition. Below some of the larger works the dominant organism on the river bed was the sewage fungus. Farther downstream there was a characteristic association of algae, but this finally gave place to the same association as was found in the upper waters, where there was no pollution. Below the smaller sewage outfalls there was no sewage fungus, but there was the characteristic change in the algal community encrusting the stones and boulders. In all this part of the river the amount of sewage was small compared with the volume of water into which it was discharged and pollution was not great. Oxygen concentration in the summer was lower than in the first part of the river (Table 4) but it never reached a seriously low level. Chloride rose, probably as a result of the sewage. The amount of calcium also increased and an average figure just above Croft was 24 parts per million ; this rise was probably mainly due to the limestone over which the water had flowed.

Trout occurred throughout this part of the river and reached a greater size than in the first part, $\frac{1}{4}$ to $\frac{3}{4}$ lbs. in weight with a few specimens of 3-4 lbs. It contained minnows almost throughout, and grayling in the lower half ; thus, although there are no marked physical changes, the river enters the third of Carpenter's zones in this part of its course.

At Croft, 100 feet above sea level, there are several important changes in the river. It enters a great clay plain, laid down during the Ice Age, and flows across this in a meandering course, though with a fair flow. The stretch is too fast for a typical lowland course judged on purely physical grounds, and it is probably in the third of Butcher's five zones, for *Ranunculus fluitans* is one of the commonest plants ; but it is in the last of Carpenter's four classes since coarse fish abound. Other changes are due to the confluence of the River Skerne, a large tributary, which is more calcareous and much more heavily polluted than the Tees. These three factors, different kind of bed, more calcium, and more sewage products, all influence the biology of the river below Croft, but it is not possible to measure exactly how great a part each one plays.

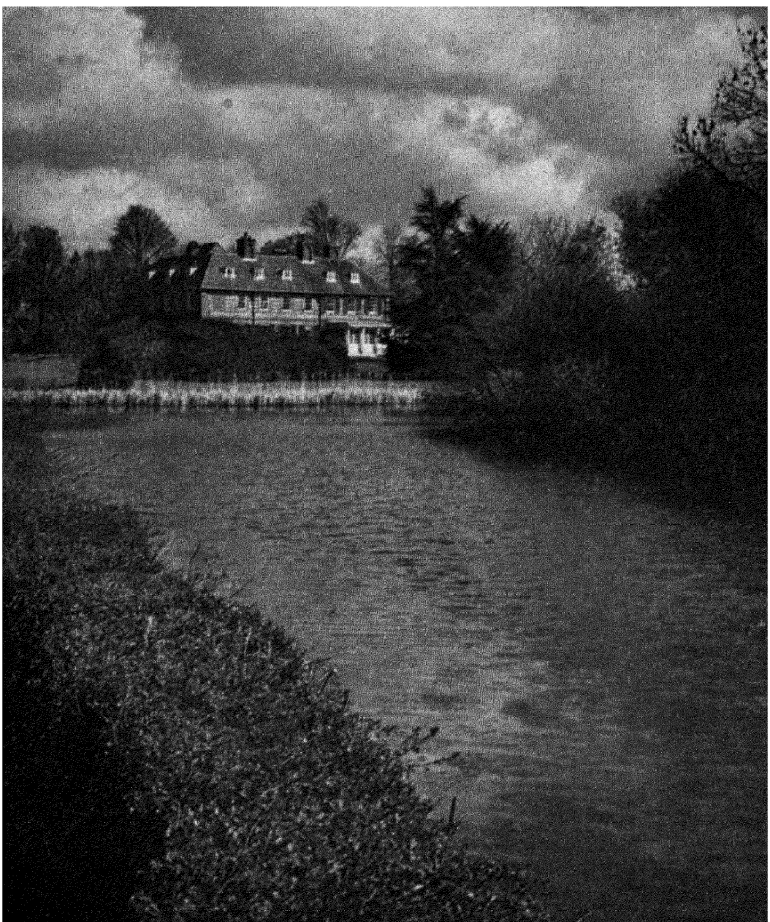
Most of the bed of the river is of medium-sized stones and gravel but there are occasional patches of sand. In water shallower than five feet typical plants are the water crowfoot, *Ranunculus fluitans*, and various species of pondweed, *Potamogeton*. These plants can colonize



PLATE 13

Robert Atkinson

Dewpond on Inkpen Hill, Berkshire April



Robert Atkinson

South country ornamental water, Hampshire April

the gravel and sand, and when they have formed a large patch they cause a stagnant area on the downstream side. Silt settles here and accumulates rapidly if there is heavy pollution upstream. It is colonized by such plants as *Nitella*, the stonewort, *Elodea*, the Canadian pondweed, and *Potamogeton crispus*, the curly pondweed.

There was usually sufficient water in the Skerne to dilute the sewage it received to below the danger point, but in one summer there was a long hot dry spell as a result of which all the oxygen was used up, and the toxic products of decomposition without oxygen were liberated into the water. The Skerne itself had a thick coat of sewage fungus on its bed, and this organism extended for some distance down the Tees below the confluence of the two rivers. Its range varied widely according to the season of the year. In winter when, owing to the low temperature, the rate of decomposition of sewage is slow, it extended a long way downstream from the mouth of the Skerne, but in summer, when decomposition is more rapid, its range was less.

A green filamentous alga, *Cladophora glomerata*, is also dependent on sewage, though apparently it finds conditions most favourable where the organic matter has undergone the initial stages of decomposition. It appeared in the Tees towards the end of May and grew rapidly to form a thick carpet in the shallow water a long way down the river from Croft. Then the first flood in July would usually sweep it all away, and it would be seen no more until the following year. If it lasted long enough, it trapped a deposit of silt and enabled rooted plants to grow in places where otherwise the flow was too fast. Before the estuary was reached the algal community typical of the upper, unpolluted reaches had become re-established on the stones.

Nitrogenous compounds and other products of decomposition were brought into the Tees by the Skerne, and the calcium concentration was increased to some 30 parts per million. There was less oxygen in this stretch during the summer than there was farther upstream, and the lowest value was reached during the time when the development of *Cladophora* was at its height. The dense growth of this plant, respiring in the hours of darkness, used up much of the oxygen and reduced the concentration to between 50 and 60% of the saturation value. This is well above the point at which deleterious effects on fish are likely, and trout flourished in this, the last fresh-water reach of the Tees, not uncommonly attaining a size of 1-1½ lbs. Coarse

fish, chiefly dace and chub, were abundant, and fishing was a popular pastime.

In the estuary, surveyed by Alexander, Southgate and Bassindale (1935), the most important natural phenomenon is the salinity. The fresh water tends to float on the sea-water and the result is a marked stratification. Fig. 9 shows the average conditions at high tide and at low tide, but it gives rather a distorted picture because it is necessary to use such different scales. Horizontally an inch represents about three miles, but vertically it represents only about 50 feet. The surface

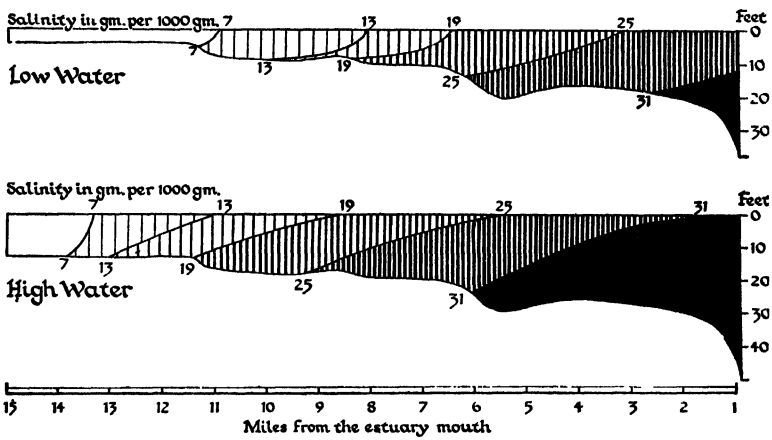


FIG. 9
Longitudinal section of the Tees estuary showing the salinity at high and low tide

current of fresh water draws up some water of higher salinity from below it, and to replace this there is an upstream creep of water of high salinity along the bottom. The whole mass moves up and down with the tide as shown in the figure. It is estimated that the mean time for all layers of a body of water to pass through the estuary is about six days in dry weather, decreasing to about two and a half under average winter conditions.

The estuary has been much changed by the hand of man and changed for the worse in the eyes of the naturalist. It must be admitted with regret that the Tees is typical rather than otherwise of larger

British estuaries. From about midway nearly to the sea there is an extensive industrial conurbation. This requires a navigable channel so that its products may be removed by sea, and accordingly the natural tendency of the river to drop silt where it is checked by its meeting with the sea is counteracted by the continual activities of dredgers. The river is a convenient main drain and, at the time of the survey, the sewage from rather more than a quarter of a million people was discharged into it untreated. So were a variety of industrial waste products, of which the most important were tar acids and cyanides. Both these decompose gradually in the water.

Much water is taken in to cool condensers and machinery, and this results in a slight rise in the temperature of the estuary. Oxygen, it need hardly be said, is not plentiful in solution in the water. The amount used up depends on the temperature and also on the salinity, being greatest at salinities of between 15 and 25 parts per 1,000. The lowest concentration of dissolved oxygen recorded during the survey was 9% of saturation.

The curly pondweed, *Potamogeton crispus*, the starwort, *Callitriche stagnalis*, and the two mosses, *Fontinalis antipyretica* and *Eurhynchium rusciforme*, which are abundant throughout almost the whole length of the fresh-water part of the river, penetrate a little way into the brackish water. A few seaweeds penetrate a short distance from the sea but only four extend beyond the fringe of the brackish water region. *Fucus vesiculosus*, one of the brown bladder wracks, extends to beyond the middle point of the estuary, growing on wharves and piles between tidemarks ; and three species of filamentous green algae occur throughout the brackish region.

It is difficult to determine exactly which fish dwell permanently in the estuary, as so many of the species recorded are migrants passing through, or casual invaders, but the three-spined stickleback appears to be a regular inhabitant, extending down to at least the upper reaches of the polluted part. The effect of the pollution on the fish, particularly the regular migrants, and on the lower animals is described in Chapter 14.

Reviewing the River Tees in the light of the classifications put forward at the beginning of the chapter, we find that it includes all of Carpenter's classes, for the lowest reach, immediately above the estuary, is dominated by coarse fish. On the other hand the last two classes, numbers 4 and 5, of Butcher's botanical classification are not

represented, for the current is nowhere so sluggish that the water crowfoot ceases to be the dominant plant.

A great contrast to the Tees is provided by the south country rivers rising in the chalk downs. Butcher has surveyed the plants of the Itchen, and there was a fisheries research station on the nearby Avon for several years before the war. Much of the gathering ground is chalk down. Rain falling on this sinks in and percolates relatively slowly so that it may not reach a hill-foot spring for months. The effect of heavy rain is, therefore, dissipated and it will not produce a marked flood wave as in the Tees. The other effect of the chalk is, of course, to render the water highly calcareous, and Butcher quotes a figure of 92 parts per million of calcium in the River Itchen.

Then the slope is not so steep. Moon and Green (1940) give a profile of the Avon and show that between Christchurch, which is at the mouth, and Salisbury the fall is about 150 feet in 39 miles, which is a little less than 4 feet per mile. The river rises some 20 miles from Salisbury at an altitude of about 350 feet, so this upper reach, for which we have not been able to find accurate data, is somewhat steeper, and the figure for the whole river will be greater, but still far below that of 30 feet per mile for the Tees.

The springs giving rise to the Avon headwaters are usually at the foot of the chalk and often flow in wide valleys floored with gravel. Sometimes the streams have been broadened so that they flow over wide areas in which water-cress is cultivated (Plate 25, p. 118). In dry weather the water-table often sinks below the surface of the gravel covering the impermeable stratum which is the true valley floor and the stream disappears. Sometimes, owing to the time which rain takes to seep through the chalk, there may be a long interval before the effect of a dry spell or a wet spell is manifest in the river.

Below Salisbury the Avon has been put to a variety of uses by man. One of the characteristic features are water meadows, although the method of farming under which they were engineered is now obsolescent, if not obsolete. The principle is to take water from the river in a main canal, which can be filled by the manipulation of sluices across its mouth and a barrage across the river. From this main canal the water is led into many subsidiary channels, from which it eventually runs over the land. It is gathered up in a complementary series of collecting channels and led back to the river at a lower level. The advantage

of this system was that the grass could be watered at certain critical times of the year, and the farmer was independent of the capricious rainfall of this country. The significance of water meadows in the economy of the river to-day is that a great deal of flood-water finds its way on to them and runs back to the river slowly. This is a second reason why the effect of flooding is much less fierce in the Avon than in the Tees.

Dams and weirs are thrown across the Avon not only to deflect water for irrigation purposes but also to pen up a head of water to provide power for mills. Weirs and side channels to take excess water when the level of the river is high are usually to be found in connection with mills, and the result is that the river does not flow in a simple single channel but in a maze of anastomosing channels.

The water is rich in nutrient salts and, since there is no great scouring by floods, the rivers flowing from the chalk are heavily overgrown with a variety of aquatic plants. Butcher records that the commonest plants of the River Itchen are: *Ranunculus pseudofluitans*, water crowfoot, *Sium erectum*, the lesser water parsnip, and *Apium nodiflorum*, where the current is fastest; *Hippuris vulgaris*, the marestail, and *Sparganium simplex*, the simple bur-reed, where it is somewhat less rapid; and *Elodea canadensis*, the Canadian pondweed, and *Callitriche stagnalis*, starwort, in the slowest reaches.

These rivers are noted for their fishing. Too much vegetation and good fishing are not compatible, and so a considerable amount of time and energy is expended annually in cutting and removing weed.

Besides the game fish, for which these rivers are famous, there is a plentiful and varied population of coarse fish.

The Avon has no torrential head-stream region nor a typical meandering lowland reach. The whole river occupies a place somewhere in between these two, but it cannot be made to fit exactly into any of the various schemes of classification. There is no steady loss of gradient from source to mouth, as there is in the theoretical river, but a mosaic of faster and slower reaches due to the various artificial obstructions which man has thrown across the river.

A third river worthy of notice is the Lark, another of those surveyed by the Ministry of Agriculture and Fisheries team in connection with pollution (Butcher, Pentelow and Woodley, 1931). It is quite a small river rising in the East Anglian heights and flowing in a west

by north direction to join the Ouse. The water is highly calcareous like that of the River Avon.

Only a comparatively small portion was surveyed, but this stretch is fraught with interest because it illustrates yet another effect of human interference. It may be remarked here that no south country river of any size is in a " natural " state, and any account of it must dwell at some length on the modifications imposed by man.

The River Lark was once navigable as far up as Bury St. Edmunds, though the last few miles were kept open with difficulty because the gradient was rather steep and the amount of water available was small. Eventually river traffic ceased to pay, and the locks fell into disuse. They are now derelict and the river flows in a bed which, having been widened to take barges, is too large for the volume of water which flows down it. This disproportion is particularly marked in one stretch which is now heavily overgrown with two emergent reeds, *Glyceria aquatica*, reed poa, and *Sparganium erectum*, the branched bur-reed. These plants probably established themselves first on beds of silt in shallow water. Their gradual spread would impede the current still more and result in further deposition of silt, and the process has continued and was still active at the time when the survey was made. The dense growth of reeds tended to deflect the current to the side, where it encountered and eroded a soft sandy bank, and so made yet bigger the area in which conditions were suitable for reeds. A stage had been reached where, when the reeds began to grow up early in the summer, above them the river flooded even though there had been no unusual rainfall, and below them a miller was hard put to it to obtain sufficient head of water to drive his mill.

Beyond this stretch overgrown with reeds there is a stretch overgrown with submerged pondweeds. In parts of it the current is sufficiently strong to keep a gravel bottom clear of silt and the water crowfoot is the dominant plant. Elsewhere the current is sluggish, the bottom is muddy, and the chief plant is usually *Potamogeton lucens* (Plate 32, p. 145), the shining pondweed. In some places it is replaced by a community in which *Sparganium simplex* and *Sagittaria sagittifolia*, the arrowhead, are the dominant species. There was no evident difference in the river to account for these two distinct communities and they provided something of a puzzle. But a study of the activities of the human beings interested in the river at length provided the

clue, and it was noticed that the bur-reed-arrowhead community was found in those parts where weed-cutting was most frequent.

Finally the river runs through a stretch of fenland before joining the Ouse, but unfortunately the survey stopped at the head of this stretch. The fenland river offers the extreme example of the lowland course. Left to itself it would follow a tortuous channel beset with marshes and stretches of open water. Changes of course might occur and the stream might split up and lose its identity in a number of small channels as does the River Euphrates to-day. Figure 5 (p. 46) shows the lower part of the Euphrates and the Tigris, and gives a good picture of a lowland course which has hardly been interfered with. In Britain no fenland river is left to itself. The fen soil is valuable for cultivating and the rivers are important as the means whereby the water pumped up out of the fens is got rid of. Vegetation, which would impede the flow of water, is removed and the channels are constantly dredged. Flood-banks are raised on either side, often at some distance from the river's brim, so that an expansion in width is possible when the river rises above its natural banks. Water left behind by a flood stands for a long period in this land between the river and the flood-bank, and the resulting " washes," one of which is illustrated in Plate 9 in *Britain's Structure and Scenery*, are characteristic features of the fenland landscape.

The schemes of classification put forward at the beginning of this chapter aimed to classify the different parts of one river. Butcher (1933), having described the ecological effect of current speed, offers a classification of entire rivers. He divides them into :

1. Those rising in high hills and mountains, e.g. Tees.
2. Those rising from springs and from drainage of low-lying land, e.g. Avon, Itchen and Lark, and
3. Those rising in low-lying marsh or fenland, e.g. Little Ouse and Waveney.

He subdivides each of these according to the amount of calcium in solution in the water, and finally draws attention to the important effects on plant life of human utilization of rivers for the purposes of drainage, water-supply, water-power, navigation, fish production, and refuse disposal. Of these factors, water-supply is the subject of a separate chapter in this book, and examples of how each of the rest may affect a river have been described in the preceding pages.

We may perhaps be forgiven for reiterating here that, although the kind of fish present depends on an average of the conditions over a fairly long stretch, the rest of the fauna, which cannot range to and fro in the same way, is restricted more narrowly to places where a certain combination of factors operate ; so are the plants. Most rivers are, therefore, a patchwork of different plant and animal communities and generalized groupings of these are not easy to establish.

One or two factors which influence the composition of the population of a river or stream require more detailed treatment than they have received so far. That important factor, nature of the bottom, has hitherto been discussed solely in terms of the size of particle which a given current will move off the bottom. But for a given rate of flow the material composing the bottom may vary within wide limits. A torrential current may flow over at least three main kinds of substratum. It may sweep over a smooth surface of rock ; this is not, as might be supposed, the most inhospitable type of substratum, because filamentous green algae or mosses may gain a foothold and cover the surface with a close mat in which a variety of animals can dwell. A more irregular outcropping of rock will weather to give stones and boulders. If these are large and flat, they will probably come to rest in such a position that only the most exceptional flood will shift them. They form what is known as a stable bottom and are usually covered with a thick growth of moss. The contrast, of course, is the rolling stone that gathers no moss. Smaller stones rounded by the attrition of the current may floor a considerable stretch of a river. Such a bed tends to shift, even though only slightly, whenever the current increases somewhat above normal, and the result is that conditions for plant and animal life are more rigorous than on a stable bottom.

Similarly in slow reaches the particles deposited may be of different kinds ; the major distinction is between inorganic and organic material, but within these two categories there can be much variation. The nature of the particles forming the substratum determines what plants colonize it. Exact relationships have not been worked out for rivers, but they have been worked out for the Lake District lakes, so it is more convenient to discuss this subject later in connection with the plant communities of Windermere (p. 103).

Another factor in flowing water is the oxygen concentration. References to it are frequent, though exact correlations of certain species with a given range of oxygen concentration are rather few.



PLATE 15

Robert Atkinson

Disused gravel pit, Oxfordshire March

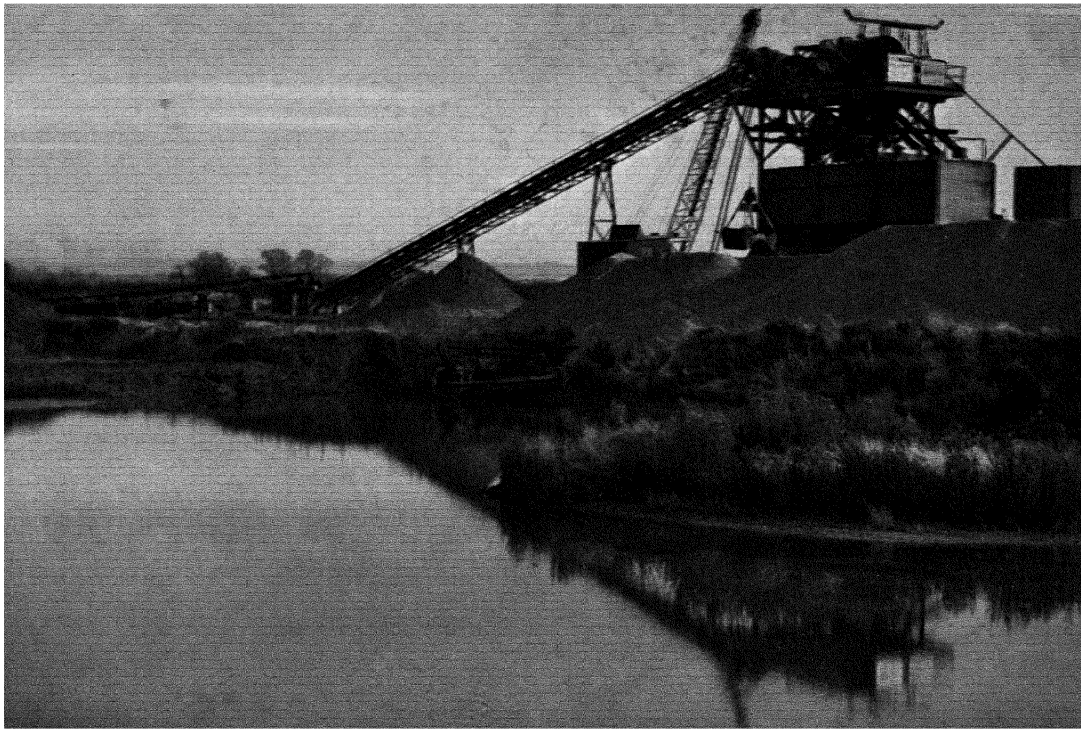


PLATE 16

Robert Atkinson

Gravel pit in use, Oxfordshire November

The concentration is intimately bound up with flow, vegetation, pollution and other factors, and it is difficult to make out the extent of the influence of each.

The French worker, Hubault (1927), has studied variations in the oxygen concentration of an unpolluted stream in greater detail than anybody else. He organized a team of helpers so that he was able to obtain simultaneous samples from different places along the length of the stream. Near the source in a torrential reach the most important factor influencing oxygen concentration was found to be temperature. During the afternoon when the stream was at its warmest there were 6·4 ccs. of oxygen per litre of water, and this is 85% of saturation value. During the small hours of the morning, when the temperature had dropped from its maximum of 13·5° C. twelve hours earlier down to 7·8° C., the concentration of oxygen reached 7·9 ccs. per litre, 89% of saturation value. Lower down, where the stream was sluggish and there were thick beds of water-weeds, exactly the reverse was found, and the oxygen concentration was highest by day, on account of its production by plants in sunlight. The figure ranged from a maximum of 5·4 ccs. per litre, 83% of saturation, to a minimum of 4·0 ccs. per litre, 60% of saturation value. The temperature was about 20° C. and the variation from the maximum, late in the evening, to the minimum, early in the morning, was a little less than 1½° C.

Butcher records that plants are much more efficient at oxygenating water than waterfalls. Under still conditions they may produce during daytime a concentration of oxygen in excess of the saturation value. In the dark plants use up oxygen and, though their removal on this account from hospital wards each night is a ridiculous precaution, dense beds of water-weeds may make a significant reduction in the concentration of dissolved oxygen.

We pass on from rivers taking with us an impression of many a hunting ground of the naturalist and many a haunt of the angler ruined by commerce and industry; but there is something on the credit side, for, without commerce, there would have been no canals. The Exeter ship canal was built in the sixteenth century and a few artificial waterways persisting to this day date from even earlier times. But the title of "father of inland navigation" is usually bestowed upon the third Duke of Bridgwater, at whose instigation a canal from Worsley to Manchester was built and opened in 1761. The commercial possibilities of this new means of transport were quickly

exploited, and in the next forty years nearly 4,000 miles of canal were put into operation. After about 1800 the activity began to wane as the challenge from rail and road became ever greater. To-day some of the canals have disappeared and others, though still containing water, are no longer used.

Even a used canal is surprisingly rich in animal life and an unused one is highly productive (Plate 26, p. 119). Canals are almost confined to the lowlands and so their water is usually hard and rich in nutrient salts ; there is sufficient flow to keep these replenished ; but there is no danger of excessive flow after heavy rainfall of the kind which may wash away so much plant and animal life from the canal-like stretch of a river.

Furthermore canals link up all the main river systems draining central England. Boycott (1936) writes : " And about the middle of last century a snail could start in the Thames at London and travel in uninterrupted water to Norfolk or Leeds or Kendal or Newtown in Montgomery or Hereford or Trowbridge, or by slipping into the upper waters of the Avon in the Vale of Pusey even to Christchurch or Southampton."

CHAPTER 6

ANIMALS AND PLANTS

THE environmental background having been sketched, it is necessary to devote this chapter to an account of the different kinds of animals and plants which occur in fresh water.

We start with four paragraphs written for those naturalists who have not had a biological training, and who have studied only vertebrates. The number of different kinds—or species to use the proper term—is usually much greater in an invertebrate than in a vertebrate group and, since the animals are so much smaller, the differences are less obvious, and sometimes undetectable by the naked eye. Many people are surprised to learn that the word mosquito, for example, covers in Britain no less than 40 different species. We have endeavoured to give some idea of the scope of the fresh-water fauna by mentioning the number of known species in each group.

Latin names are unavoidable, since only a few species have an English name. Invertebrates are usually referred to by two names, and the first of these, the genus or generic name, corresponds to the surnames in the human community ; though the Smith difficulty has been avoided by making a rule that the name of every genus must be different. The second name is the species name, and, like our Christian names, many are used over and over again ; for example, *lacustris*, which means pertaining to a lake, will be encountered often in the following pages applied both to animals and plants. Sometimes a third name denotes a small, usually geographical, variation.

Anything of which there are many kinds must be grouped into higher categories for the sake of convenience ; pennies grouped into the higher categories of shillings and pounds provide a familiar example. Animal species are grouped into genera, genera into families,

and so on through orders, classes, and phyla, with sub-divisions interpolated if necessary. The classification is based on structure and anatomy. The names of all these groups have a Latin form but, particularly in a work of this sort, they are frequently anglicized. Thus "Insects" is more usual than "Insecta," or "Vertebrates" than "Vertebrata"; and the midge family, for example, is referred to in the following pages as the Chironomidae or the Chironomids indifferently.

One of the main difficulties of a book of this nature is not so much to impart what is known, as to leave the reader with a fair impression of what is not known. Students of vertebrates or of one of the few well-known invertebrate groups, e.g. the Lepidoptera, may be surprised to find that, of the 61 species of water-bug in Britain, no less than 6, or 10%, were discovered in the decade before the war. The water-bugs may be taken as an average group, not as well-worked as some nor as neglected as others.

Most of the phyla are represented in fresh water, the total number of species is great, and it is not possible in these pages to do much more than indicate which of the main groups occur. As each group is mentioned, it is followed by figures in brackets. The first, sometimes the only, figure is the total number of species known from the British Isles, and the second the number which has been recorded from Windermere and the tarns and streams around it. The total for the British Isles is taken from the recent check-list of British insects by Kloet and Hincks (1945) and, for other groups, from the most recent available check-list or monograph.[1] Some of the figures lay no claim to exactness; their purpose is to give an idea of the size of the group. The totals for Windermere district are taken from the files of the Freshwater Biological Association, and are given only for groups which have been studied fairly intensively.

It is convenient to begin this summary account of the fresh-water fauna with the most advanced phylum, the Chordata, which includes all those animals with a backbone. In it are the fishes (45 British species, 15 recorded from the Lake District), and various amphibians, birds, and mammals which, although not fully aquatic, live in close association with water, and are noticed in Chapter 10.

The phylum Arthropoda derives its name from the fact that its

[1] The names used are taken from the same sources; those of plants from Professor Clapham's check-list in the *Journal of Ecology*, vol. 33, 1946.

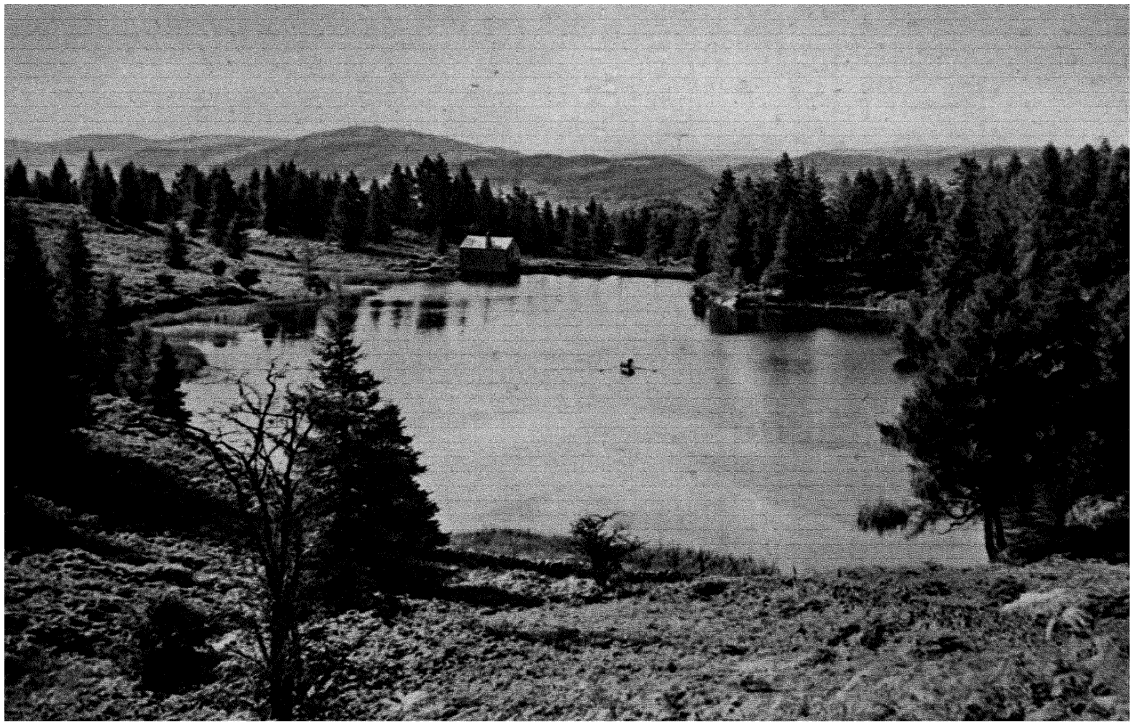


PLATE XI

John Clegg

Three Dubs Tarn, an artificial fishpond, Lake District

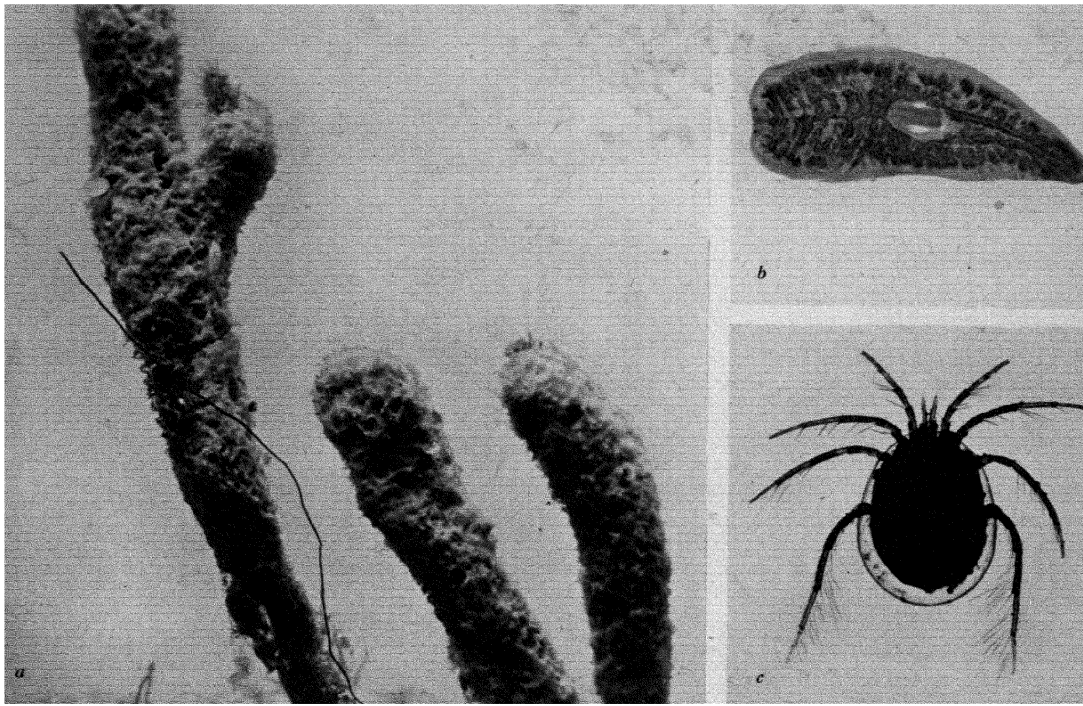


PLATE XII

Photographs by John Clegg

a. Fresh water sponge, *Spongilla lacustris* (×3). *b*. Flatworm, *Dendrocoelum lacteum* (×2½).
c. Mite, *Limnesia maculata* (×14)

FRESH WATER ANIMALS

members have an external skeleton and jointed limbs, the lobster being an example. A large number of aquatic animals belong to this phylum. Of the classes in it, the first, the class Crustacea, includes the Cladocera (90 British and 59 from Lake District) (Plate XIV a, b, p. 83) or water-fleas, and the Copepods (105) (Plate XIVc, p. 83) two groups of small animals. The plankton, that is the inhabitants of the open water of lakes and ponds, consists largely of members of these two groups, though some of them dwell among weeds. The creature known as the fish-louse (*Argulus*) (Plate XIIIb, p. 82) is a degenerate Copepod. Another group is the Ostracoda (88 and 25), small animals to be found mainly among plants or in vegetable debris. At first sight it appears that the small, kidney-shaped seed of some plant has been taken, but, if left undisturbed, the object is discovered to consist of two valves, which open sufficiently to permit the extrusion of limbs with which the creature propels itself. Larger Crustacea are *Gammarus* (3 and 1) (Plate XIIIa, p. 82), the fresh-water shrimp, and *Asellus* (5) (Plate XIIIc, p. 82) the water hog-louse, both of which are common, and *Cheirocephalus* (1 and 0) the fairy shrimp, which is rare and usually to be found only in muddy pools which dry up. Larger still is *Astacus* (1 and 1) (Plate 27a, p. 122), the crayfish, which is the largest British fresh-water invertebrate.

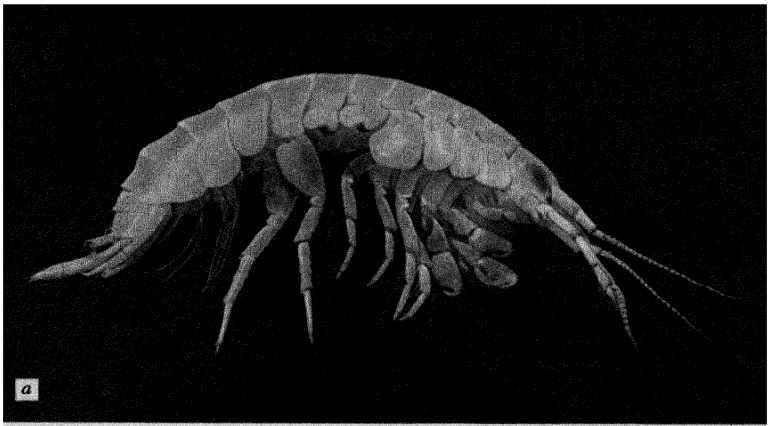
The class Arachnida, comprising Arthropod animals with eight legs, includes the water-spider and the water-mites or Hydracarina (234) (Plate XIIc, p. 81), small, round, often highly coloured creatures to be found in any habitat in fresh water. Many of the adults have long hairs fringing the legs and are able to swim; the immature stages are parasitic on insects and may often be found on the adults of such creatures as mosquitos, having attached themselves while the perfect insect was emerging from the pupal skin.

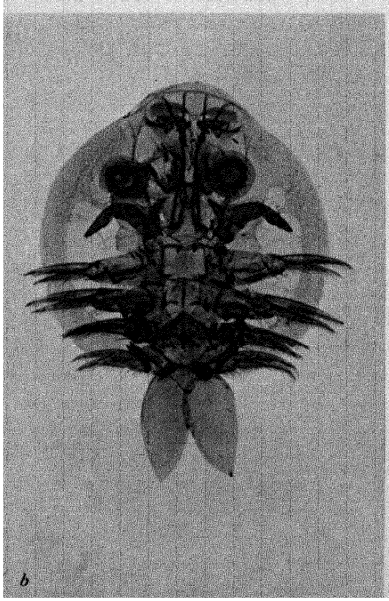
The class Insecta is characterized by the possession of six legs, and usually one or two pairs of wings as well, and it must be noticed in more detail as so many fresh-water animals belong to it. The young stages in some orders have the same general build as the adults, and differ from them only in their smaller size, and lack of complete wings and genital organs; they are known as nymphs. The stoneflies, order Plecoptera (31 and 24) (Plate XVIIIe, p. 97), the mayflies, order Ephemeroptera (46 and 25) (Plate XVIIIc, p. 97) and the dragon-flies, order Odonata (43 and 13) (Plate XVI, p. 95) all have aquatic nymphs, but the adults (Plates 28 and 29, pp. 123 and 128) live out of

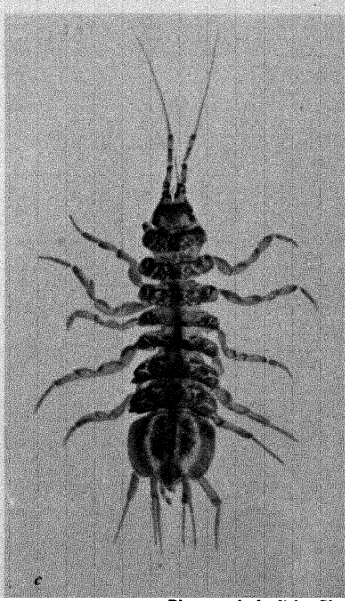
the water. The word " mayfly " is employed, as it is commonly used by naturalists, to cover the whole order ; fishermen restrict it to one stage of one genus (*Ephemera*) (Plate XVIIId, p. 97), and leave the whole order and many of the species in it nameless. The bugs, order Hemiptera, are mostly terrestrial, but a certain number (61 and 40) live in or on (Plate XIX, p. 112, and Plate XVIIIa and b) the water throughout life, though they may occasionally take to the wing and fly from pond to pond.

The young stages of other orders of Insecta are quite unlike the adults and go by the name of larvae. A larva does not give rise directly to an adult as a nymph does, but enters a quiescent stage, the pupa (known as a chrysalis in butterflies) in which its tissues are broken down and reassembled into those of the adult. Orders with larvae are the caddis-flies, Trichoptera (188 and 108), all of which are aquatic in the larval, and terrestrial in the adult stage ; the beetles, Coleoptera (270 and 65), of which a few families are aquatic throughout life (Plate XVIIc, p. 96), like the bugs ; and the flies, Diptera, of which several families have aquatic larvae. The family Culicidae, mosquitos (37 and 7), is important because of its relation to disease, and the family Chironomidae, biting and non-biting midges (507), is important to students of lakes because its members are so widespread and numerous ; lakes have been classified according to the kinds of Chironomid occurring in them. A few species in the orders Lepidoptera (butterflies and moths), Neuroptera, and Megaloptera have aquatic larvae (Plate XVIId, p. 96), and a small number of Hymenoptera (ants, bees, and wasps) parasitize aquatic larvae.

This ends the Arthropods and we come next to the phylum Mollusca ; it has many marine representatives, but some, both " snails " (43 and 16) and " bivalves " (26 and 15) occur in fresh water (Plate XV, p. 94). The Annelida, or true worms, are also marine, terrestrial, and fresh-water (about 200), and the phylum includes the leeches (11 and 9). Other phyla are the Rotifera, wheel-animalcules (Plate XIVd, p. 83) (just over 500), all fresh-water ; the Platyhelminthes, mostly parasitic but with two groups, the little-known Rhabdocoeles (about 200) and the Planaria (8 and 6) (Plate XIIb, p. 81) occurring free in the water ; and the Nematoda, round-worms, mostly parasitic, but with some members wholly fresh-water and others with one stage in a complex life-history in fresh water. Finally the simplest animals of all fall into three phyla ; the sponges, Porifera



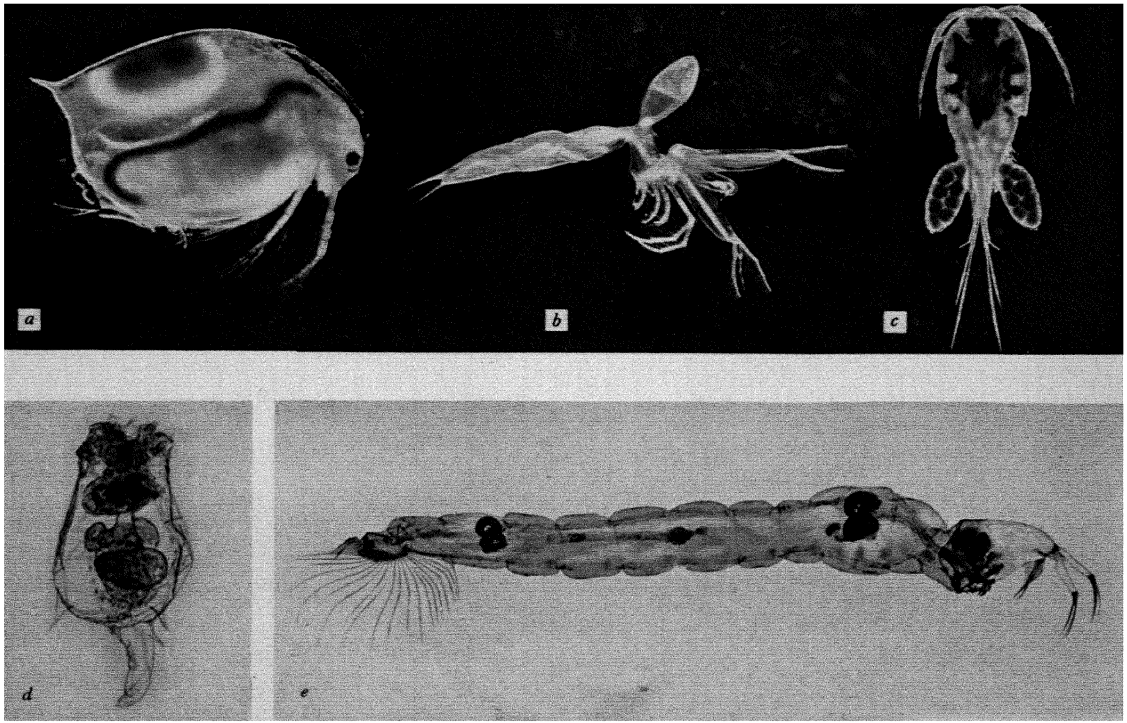




Photographs by John Clegg

a. Fresh water shrimp, *Gammarus pulex* (×5) *b*. Fish-louse, *Argulus coregoni;* male, dorsal aspect (×5). *c*. Water hog-louse, *Asellus* sp. (×3)

FRESH WATER CRUSTACEA



Photographs by John Clegg

a. Water-flea, *Daphnia atkinsoni* (×20). *b*. *Leptodora kindti* (×4½). *c*. *Cyclops* sp. (×22)
d. Rotifer, *Brachionus calcyflorus* (×80). *e*. Phantom larva, *Chaoborus* sp (×8)

PLANKTON ANIMALS

(5 and 2) (Plate XIIa, p. 81); the Coelenterata (6 and 3), which include the marine anemones, corals, and jellyfish, but which in fresh water are represented by simple polyps only, though there is one medusa (jellyfish form) which is found very rarely in British inland waters; and the Protozoa, or single-celled animals, which abound in fresh water. The Bacteria, assigned definitely neither to the plant nor to the animal kingdom, play an important, though as yet little understood role in the economy of all fresh waters. Most kinds are far too small to see except with the aid of a high-powered microscope, but some cluster in such vast numbers that the organisms themselves or their products become obvious. The sewage "fungus," for example, is really one of the Bacteria, and the evil-looking reddish or yellowish substance often to be seen in springs and seepages is a product of innumerable iron bacteria.

The main divisions of the plant kingdom are the flowering plants, the ferns, the mosses and liverworts, the fungi, and the algae. Animals living at the water's edge, either just in it or just not in it, can move up or down as the water level rises or falls. There is, therefore, usually little difficulty in deciding whether they are aquatic or not. Plants cannot move, and there are many which grow at the water's edge in the zone which is sometimes flooded and sometimes dry; and so it is difficult to state exactly how many flowering plants come within the province of the fresh-water biologist, but the number is probably not far short of 200.

Isoetes (the quillwort), *Pilularia* (the pillwort), *Azolla*, and *Equisetum fluviatile* (the horsetail), are the only aquatic representatives of the ferns (using that term in its widest sense). Mosses and liverworts often form extensive swards where the substratum is rocky or stony, and they profoundly influence the fauna by providing a foothold for animals which otherwise would be swept away by the current. Fungi are well represented, though by small and inconspicuous species only; they play an important part in decomposition, and some cause disease among higher forms. Included among aquatic fungi is a group called Chytridiales, the members of which are small and simple (Plate XXII, p. 115), but important in the general scheme because of their effect on the algae, which they parasitize. The least evolved group, the algae, lives mainly in the water, and in fresh water the green algae are rich both in species (over 2,000) and numbers, and of great importance as primary producers of living material. Some of

the main groups are mentioned by name in subsequent pages, and require brief description here, though it is beyond the scope of this book to notice all of them and the differences by which they are distinguished. Diatoms (Plate XXa, p. 113, XXI, p. 114, XXIV, p. 127) are contained within a case of siliceous material, the flinty substance of which glass is made, and the case is in two halves which fit together like a box and its lid. There is often a delicate and beautiful sculpturing, and it was therefore the shell which caught the attention of the early microscopists, and led to the name. The individual is usually a single cell, but one of the commonest, *Asterionella*, is made up of a number of cells, loosely joined together at one end and radiating like the spokes of a wheel (Plate XXa, p. 113). Desmids are also usually single-celled, and each cell is commonly symmetrical about a central constriction, and of a characteristic and frequently beautiful shape (Plate XXb and c, p. 113, XXIV, p. 127). The individual blue-green alga is usually a number of cells in a common mucilage sheath (Plate XXf, p. 113, XXIII, p. 126). The colour of some of the species has a bluish tinge, and a discrete nucleus is absent. Some of the algae have small lashing filaments or flagella by means of which they progress, and these forms may be single (Plate XXe, p. 113), or united in spherical colonies. Certain of them occupy the border territory between the plant and animal kingdoms. Other algae consist of a row of cells joined together in a filament (Plate XXI, p. 114, XXIV, p. 127), and it is this type which will be most familiar to the observer who does not possess a microscope, since it produces the tress-like growth often to be seen on rocks and other objects in the water.

(The scheme of classification which has been briefly outlined above is based on structure, and on the probable evolutionary relationships of organisms.) It is fundamental, but, in a work concerned chiefly with the organism in relation to its environment, a grouping based on this relationship has a wider practical significance. There are five main groups in lakes and rivers, and it is not possible here to do much more than mention the main components of each ; but it is hoped that the illustrations will give an outline picture of the groups discussed. The groups are :

(Surface forms,
Stone- and weed-dwelling forms,
Floating forms,

Swimming forms, and
Burrowing forms.

Of the Greek names which biologists apply to these groups the only one which cannot conveniently be ignored is "plankton" for the floating forms.

The *surface dwellers* include the pond-skaters or water-striders, the water-measurer, some smaller bugs (Hemiptera) which have no English names, and the whirligig beetles. The pond-skaters or water-striders (*Gerris*) are rather narrow bugs with the middle and hind pairs of legs greatly elongated. These legs end in small pads which support the insect on the surface film, and the claws are displaced from the usual terminal position. The fore legs are used for seizing food. *Hydrometra*, the water-measurer (Plate XVIIIa, p. 97), also known as the water-gnat, rather unfortunately since it has no relationship at all with the true gnats, is very slender, has a remarkably elongated head, and uses all six legs for walking. The piercing and sucking mouth parts are also used to secure the prey, and the extra movability which this entails is stated to be the reason for the elongated head.

The whirligig-beetles (*Gyrinidae*) are small steely-black oval insects which are nearly always found in swarms, and which spend their time whirling rapidly around upon the surface of the water. The eyes are divided into an upper and lower portion, and the beetles are said to be able to see objects above and below the water surface simultaneously. The legs are shortened and flattened to serve as paddles. The larvae are truly aquatic. The adults live upon the surface but disappear into the water with surprising suddenness when alarmed.

Certain larvae of the Diptera, notably the mosquitos, live in the water but attach themselves to the surface by a projection at the hind end of the body where the openings of the breathing tubes are situated. Some of them do not leave the surface unless they are scared, but others spend long periods feeding on the bottom of the pools which they inhabit.

The *stone- and weed-dwelling forms* are numerous and diverse. All the stonefly (Plecoptera) nymphs, of which the largest are known to fishermen as creepers, belong here. They are crawling forms, somewhat reminiscent of an earwig in general appearance though instead of forceps at the end of the body they have two long tapering "tails"

known as cerci (Plate XVIIIe, p. 97). Most are found under stones in streams or along exposed lake shores, and only a few small species are found in typical pond conditions with a thick growth of rooted plants. The mayfly nymphs (Ephemeroptera) are similar but more diverse in " tails." They have paired flaps down each side of the body, and structure, and they may be distinguished at once by their three these are commonly known as gills, though, as will be shown later, as an indication of function this is a misnomer. Some of the stone-dwelling species are flat (Plate XIXa, p. 112), well adapted to cling to a stone in a current, but ill-equipped to swim ; the typical weed-genus, *Cloëon*, on the other hand, is a good swimmer and propels itself by undulations of the body made more effective by the row of close-set hairs down each side of each tail.

All the dragon-fly nymphs belong to this community. The appendages at the hind end of their bodies also number three but are otherwise quite unlike the cerci of the mayflies. In the small dragon-fly nymphs (Plate XVIa, p. 95) they are flattened and commonly, though again erroneously, known as gills, and in the large dragon-fly nymphs (Plate XVIb, p. 95) they are no more than triangular prolongations of the end of the body. The most characteristic feature of all dragon-fly nymphs is, however, the " mask " or hinged labium, which can be extended suddenly in front of the head to seize some prey, which, unsuspecting, passes within reach of the hiding-place where the nymph is lurking. The larger ones can, on occasion, make a short but rapid dart in pursuit of some quarry just out of reach by suddenly contracting an enlarged chamber near the end of the alimentary canal. The smaller forms swim rather ineffectively by undulating the body from side to side.

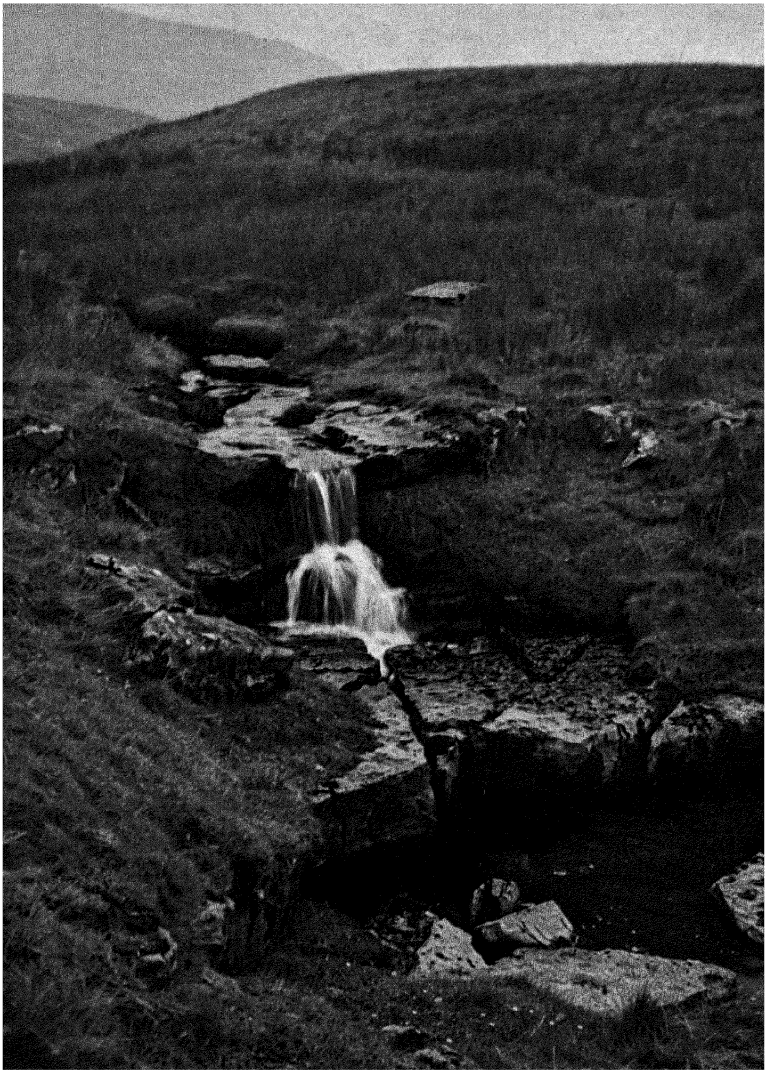
Caddis larvae (Trichoptera) can usually be distinguished at a glance because all the body, except the head and the part bearing the legs, is protected by a case made of vegetable fragments, stones, grains of sand, or other suitable material, and the whole body is withdrawn inside the case if danger threatens. At the hind end of the larva there are two appendages known as false legs, and it is by means of these that the insect keeps hold of its case. These organs are characteristic of the whole order although some larvae do not have a case at all, but live free among stones or weeds, where most of them spin a net to catch their prey. Most of the case-bearing caddis-worms can do no more than drag their cumbersome houses behind them, but



PLATE 17

Robert Atkinson

Malham Tarn, Yorkshire May



John Markham

Headstream in the Pennines Simon Fell, Yorkshire July

some (*Triaenodes*) make a neat slender case of pieces of leaf stuck together into a flat-surfaced cone. Their hind legs are elongated and fringed with hairs so that they can be used as swimming organs.

The animals so far mentioned obtain oxygen from the water. Most have extrusions of the body wall of one kind or another, and these structures have been known for many years as gills. There is good evidence that many play no special role in the absorption of oxygen from the water and their real function is not known; though the "gills" of certain mayflies keep a current of water flowing over the surface of the body and, since this is the seat of oxygen absorption, a current over it is valuable when the concentration of oxygen in the water is low. The so-called gills of mosquito larvae, which have a respiratory system open to the atmosphere, play a part in the maintenance in the body fluids of a higher concentration of salts than exists in the water inhabited by the animals. The bugs and the beetles are dependent on atmospheric oxygen and must swim up to the surface periodically to renew the bubble of air which they always carry about with them. The hind legs of both are elongated, flattened, and fringed with close-set hairs, modifications which have converted what was once a walking organ into a highly efficient paddle. The very youngest stages of the bugs depend on oxygen in solution but otherwise the immature forms of both groups require oxygen in gaseous form like the adults. The young bug is like the fully grown bug in general shape and build, but the young beetle is totally different. The familiar larva of *Dytiscus* is a spindle-shaped creature with six well-developed legs, two small appendages at the hind end of the body where the breathing tubes open, and a pair of large sickle-shaped jaws, possession of which immediately distinguishes it from any other larva (Plate XVIIc, p. 96). Other species have different forms and no single obvious feature is characteristic of the whole group.

Some other genera of beetles, the best known of which is *Donacia*, are terrestrial as adults but have larvae which dwell in the water. They are quite different from those just described, being grub-like and inactive. These larvae cannot utilize oxygen dissolved in water but they do not require to come to the surface for air, as they possess a modification whereby they can tap the air-containing tubes in the roots of plants. The same habit is found in a genus of mosquitos and in two other families of flies.

Dipterous larvae contribute prominently to the stone- and weed-

dwelling component of the fauna.) They are diverse in form, but one common feature is the absence of jointed legs such as all other larvae possess. (The Chironomid family is almost ubiquitous in fresh water, but, as it is more typical of the burrowing fauna,) description of it is deferred. Other dipterous larvae are grub-like creatures which may belong to the daddy-long-legs (*Tipulidae*), horsefly (*Tabanidae*), or one or two other families. There is an interesting series in the first, from the larva which dwells in the comparatively dry soil of lawns (where incidentally it is a notorious pest on account of its habit of eating grass roots) through one which dwells in the damp mud of marshes, to species which are truly aquatic. The larvae have occupied these quite different types of habitat without any great modification of structure.

An interesting adaptation is seen in the rat-tailed maggot which, when full-grown, becomes one of the hover-flies (*Eristalis*). The body is grub-like but provided on the underside with pad-like projections known as false legs or pro-legs. With these it walks about on the bottom of highly polluted localities, obtaining oxygen meanwhile through a remarkable long telescopic tail at the end of which the breathing tubes open.

(In streams and rivers, particularly where the current is strong, larvae of *Simulium*, the buffalo gnat, are often abundant.) The larvae have a characteristic dumb-bell-like shape and there is a pro-leg just beneath the head. This pro-leg and also a big round pad on the bottom of the animal is provided with hooks. The larva spins a web over the surface of some rock or stone, and then fixes itself by means of its basal attachment organ, allowing the head to trail free in the water. The mouth-parts are provided with a rake-like arrangement of bristles by means of which minute particles carried down by the current can be secured. When the animal desires to move, it attaches itself by the pro-legs and swings the body to a new position, and so, holding fast by the front and back alternately, it proceeds rather like a " looper " caterpillar or some of the leeches.

(These are the more important insects dwelling among the weeds or on stones.) Many other invertebrates inhabit this part of the fresh-water environment. *Gammarus*, the fresh-water shrimp (Plate XIIIa, p. 82), is very widespread and often numerous.) It is flattened from side to side and arched from head to tail. It can swim quite effectively, but spends most of its time in the debris on the bottom. Characteristic

is the male habit of carrying a female around with him almost permanently. The sand-hopper, found beneath piles of sea-weed on the seashore, is a relative of *Gammarus* likely to be familiar to many. *Asellus*, the water hog-louse (Plate XIIIc, p. 82) is also widespread. It is a more sedate creature, and a not very rapid walk is the only form of locomotion of which it is capable. It is clearly related to the "slaters" or wood-lice of the land, but is more slender. (Some smaller Crustacea also belong to this community) but, except for the Ostracods, they are more typical of the plankton, and are described there. (Mites also inhabit this part of the fresh-water environment,) and there is scarcely any type of bottom which will not yield some of the many different species.

(All the fresh-water snails belong to this group.) Though varying in size and shape, most of them are "snail-like" and require no description; but there are two species which have lost the coiled form and come to resemble the familiar limpets of the seashore both in aspect and way of life, though, like most fresh-water animals, they are much smaller than their marine counterparts. (Some snails (e.g. *Viviparus*, Plate XVb, p. 94) have gills which may or may not protrude from beneath the shell,) and they have invaded fresh water from the sea. One well-known little species, *Hydrobia* or *Paludestrina jenkinsi*, has invaded fresh water from estuarine conditions within the last century, and quite detailed information about its progress is available. But nothing is known about the physiological peculiarity which has enabled this species to make this change, while almost every other is restricted rather narrowly to a certain range of salinity. Many fresh-water snails (e.g. *Limnaea*, Plate XVa, p. 94) breathe by means of a lung, and are descended from land-living ancestors.

(Most of the Annelida or true worms belong to the burrowing group, but all the members of one order, the Hirudinea or leeches, dwell among weeds or stones.) A sucker at the head end and another at the tail end of the body is characteristic of the leeches. By using these suckers they can progress from place to place rapidly, "looping" like a Geometrid caterpillar, but most can also swim quite effectively with an undulating motion. They are nearly all blood-suckers, and a single meal is usually very large, and therefore not digested for a long time. Perhaps for this reason leeches are usually to be found motionless attached to some solid object.

(The flatworms or Planarians (Plate XIIb, p. 81) are flat but they

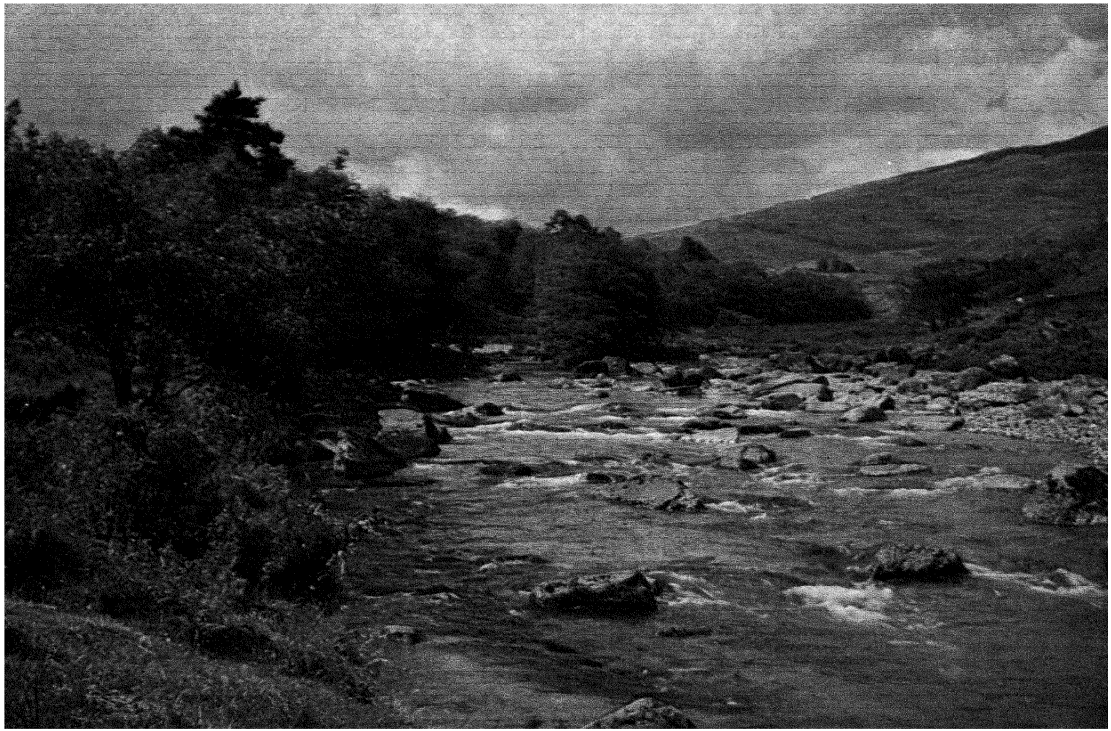
are not like ordinary worms at all, since they are unsegmented. The body is long and narrow and seldom more than half an inch from the front of the head, which is usually rather square, to the tip of the tail, which is pointed. The creatures are coloured black, brown, or white, and they are familiar objects gliding about on almost any type of substratum except, perhaps, soft mud. There is something rather mysterious about their progress for the organs of locomotion are too small to be seen with the naked eye.

Sponges are not uncommon encrusting stones or branches submerged in the water. Close examination reveals that they are perforated with holes of various sizes (Plate XIIa, p. 81) and that they also resemble in texture the bathroom object, though much smaller. The Coelenterata are represented commonly in fresh water by *Hydra*, which is like a sea anemone in general build but much smaller, relatively more slender, and with longer tentacles. It is a frequent object hanging from submerged plants but, as it is quite small, no thicker than coarse thread when fully extended and rarely as much as an inch long, it is overlooked except by those who know exactly where to search for it.

(Protozoa abound upon the surface of stones and weeds, but hitherto they have not received much attention.)

(The *plankton* is remarkable because it includes only a single insect, the "phantom larva," *Chaoborus*, more familiar to many under the now obsolete name *Corethra* (Plate XIVe, p. 83). This larva, which gives rise to an adult closely resembling a mosquito, though it does not bite, has several peculiar features. The body is almost transparent and the only conspicuous parts of it are the eyes and two pairs of air-sacs, one in the thorax and the other near the end of the abdomen. These sacs can be expanded and contracted, apparently by some substance which is secreted into the body fluid as a result of nervous stimulation, and by means of them the animal can rise, sink, maintain its position in the face of changing atmospheric pressure, or remain level when the front end is weighed down by some organism which has been captured for food. The organs with which the prey is secured are the antennae or feelers, and this modification of these organs is unusual among insects.

All the other larger (this is a relative term, they are all small animals) members of the plankton belong to the Crustacea, and fall into two groups, the *Cladocera* and the *Copepoda*. The Cladocera are



John Markham

Troutbeck with bed of stones and boulders River Glaslyn, North Wales July

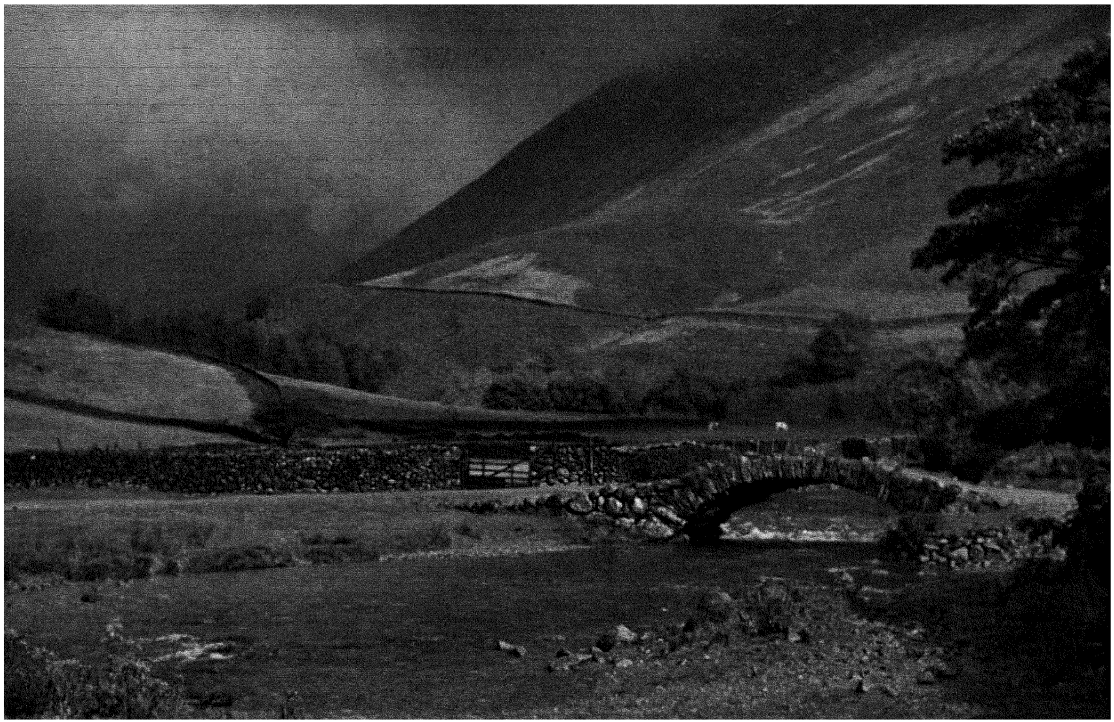


PLATE 20

B A Crouch

Troutbeck with stony bed Mosedale Beck, Cumberland September

often called water-fleas because some kinds resemble real fleas in size and shape, and progress in a series of jerks ; they do not, of course, bear the slightest true relationship to fleas. Both Cladocera and Copepoda have been called floating forms and distinguished from the swimming forms, though actually they are capable of a fair amount of locomotion. This, however, is mainly in an up-and-down direction and they are not capable of any considerable progress in the horizontal plane. The organs of locomotion in both groups are the antennae or " feelers," but here resemblance ceases. The Cladocera have typically two " shells," not comparable with the shells of a bivalve mollusc but not unlike them in the way they enclose the body, except for a narrow groove along the ventral surface of the animal. Within the shells a series of hairy limbs move constantly to and fro and maintain a current of water in which minute animals, plants, and particles of debris are conveyed to the mouth. Where the shells join along the back there is a chamber in which the embryos are kept. Some species have the shell much reduced and the antennae more developed (e.g. *Leptodora*, Plate XIVb, p. 83), and are carnivorous, preying on other planktonic forms.

The Copepods are pear-shaped and without shells (Plate XIVc, p. 83). Many of them also feed on fine particles but the current which brings these is set up by the antennae, and the animals feed and move by means of the same action. The eggs are attached to the hind end of the body, usually in two oval masses projecting on either side, though sometimes there is but one in the middle.

Also important in the plankton are the Rotifera or wheel animalcules. They are of rather simple structure and small or very small size. Their characteristic feature, giving origin to the name, is a crown of small hair-like excrescences called cilia, which by continual beating give the appearance of a rotating wheel and maintain a current of water which conveys minute particles of food to the mouth (Plate XIVd, p. 83).

Protozoa, or single-celled animals, are abundant in the plankton and the number of different species is large. Some (Ciliata) have cilia like those of the Rotifers and may indeed resemble a rotifer closely ; others have one or two longer locomotory organs ; these are known as flagella, and the group as the Flagellata. Finally there are the Heliozoa or sun-animalcules, which have long immobile threads of protoplasm radiating in all directions.

The *swimmers* in fresh water include only the fish (Plate 30, p. 129), and the higher vertebrates, amphibia, birds, and mammals, which need no description here, and so we reach the last group, the *burrowers*. In this group insects are represented by a great many species of the fly (Diptera) family Chironomidae. The adults are midges but most of them do not bite and are larger than the small black fly which is such a pest in the evening in some parts of the country. Superficially these larger ones are not unlike mosquitos, but, whereas it is the hind legs of mosquitos, it is the front legs of Chironomidae which are longer than the other pairs. The larvae are elongated, somewhat worm-like creatures with a pair of unjointed legs just behind the head and another at the end of the body. The head is of a characteristic shape and there is a variable number of sausage-like protuberances, known as gills, on the last or the last two segments. Some Chironomid larvae contain haemoglobin, the red pigment of vertebrate blood, and are known as bloodworms. Most species live in tubes made from the mud which surrounds them, but all can swim, although not very effectively, by lashing movements which throw the body into a figure of eight. This method of progression is diagnostic of the family.

The larvae of the alder-fly, *Sialis*, and the nymphs of the mayfly, *Ephemera*, dwell in burrows in mud or fine sand. The two are not dissimilar superficially but *Ephemera* (Plate XVIIIc, p. 97) has the three tails characteristic of its order, whereas *Sialis* (Plate XVIId, p. 96) has but one. *Ephemera* has feathery " gills " curved over its back and *Sialis* has simple filamentous " gills " projecting from the sides. When teased, *Sialis* opens its jaws, elevates its tail and goes backwards, a syndrome which is quite characteristic. The powerful jaws are a clear indication of the carnivorous propensities of this larva. Pupation is believed to take place always on land, and, if this is invariably true, some larvae in Windermere must migrate two hundred yards or so to find suitable conditions.

The Annelid worms are important among the burrowers. Some are not unlike the familiar earth-worm, but most are smaller and more thread-like. Finally there are the bivalve molluscs, ranging from the swan-mussel (Plate XVc, p. 94), which may be as much as seven inches long, down to the pea-mussels (*Pisidium* and *Sphaerium*), some of which are only about the size of a capital " O " on this page.

Protozoa and other microscopic animals are probably important but at present neglected members of the mud fauna.

These are the five groups into which fresh-water animals may be classified on habit, and their most important members. Distinction between them is, on the whole, clear-cut. Some of the surface dwellers may occasionally dive beneath the surface, and sometimes a snail or a flatworm may be seen crawling along the underside of the water-surface, but there is no doubt about the group to which these animals really belong. Some of the stone- and weed-dwellers are good swimmers but they spend most of their time attached and are never found out in the open water far away from their substratum. Cladocera and Copepoda are found both in weeds and far out where they must spend all their lives clear of anything to rest on, but, in general, the species found in the two types of habitat are not the same.

Certain stone-dwellers provide the only instance where there may be some doubt. For instance, the nymph of the large black and yellow dragon-fly, *Cordulegaster boltonii*, is found buried in gravel, and nymphs of the genus *Agrion* (more familiar to most under the old name *Calopteryx*) may lie buried in mud. But neither make any sort of real burrow, and in feeding habits both belong clearly to the stone- and weed-dwellers, so it is to this group that they have been assigned here.

The plants may be treated in a similar, though not identical manner, and divided into surface dwellers, species attached to the substratum, and plankton. Though some of those which possess cilia or flagella may be seen passing across the field of a microscope at what appears to be high speed, none can make such progress in a lake that it is not at the mercy of the slightest current, and it may be said that there are no true swimmers in the vegetable kingdom. Nor does any plant qualify as a burrower though many have a root-system embedded in the substratum. The surface dwellers float at the surface with no attachment to the bottom of the pond or lake. The total number of species is small but they are drawn from widely different parts of the plant kingdom. There are two liverworts, *Riccia* and *Ricciocarpus*, the water "fern," *Azolla* (Plate 31, p. 144), and, among flowering plants, the frogbit, *Hydrocharis morsus-ranae* (Plate 33, p. 148), and five species of duckweed, *Lemna*.

Almost any substratum, provided it is sufficiently well illuminated, is colonized by vegetation. Rock faces, boulders and large stones are covered with algae which may trail in the water in hair-like tresses or form a thin coating of slime. Several species of moss and liverwort also attach themselves in such places, and in a stony river, provided

the stones are large and not too liable to shift in a flood, there may be extensive and dense beds formed by *Eurhynchium rusciforme*, *Fontinalis* spp. and others. Sandy and muddy bottoms are colonized predominantly by higher plants, though mosses and algae may occur, and the peculiar stoneworts, *Chara* and *Nitella*, which are algae though their form resembles superficially that of more advanced plants, may cover wide areas. It is convenient to divide the rooted plants into those which are submerged (Plate 32, p. 145), those which have floating leaves like the water-lilies (Plate 33, p. 148), and those which are emergent, that is the reeds (Plate 12, p. 63), rushes, and sedges. There are some plants which have both submerged and floating leaves (Plate 34, p. 149), or both floating and emergent leaves, but on the whole this classification is a useful one. It is usual to find the emergents in the shallowest water, the submerged plants in the deepest water and the floating-leaved plants in a zone between. The floating-leaved species must not of course be confused with the floating species, or surface-dwellers, mentioned on the previous page.

The planktonic forms of plant life are numerous and diverse but all belong to the Algae.

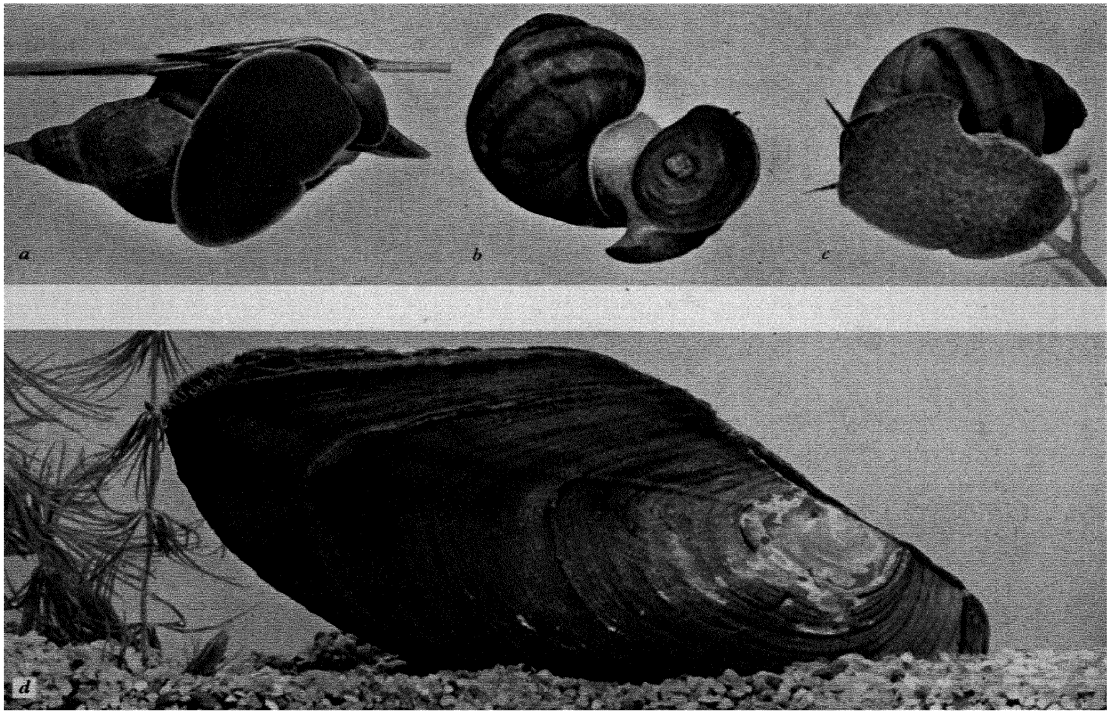


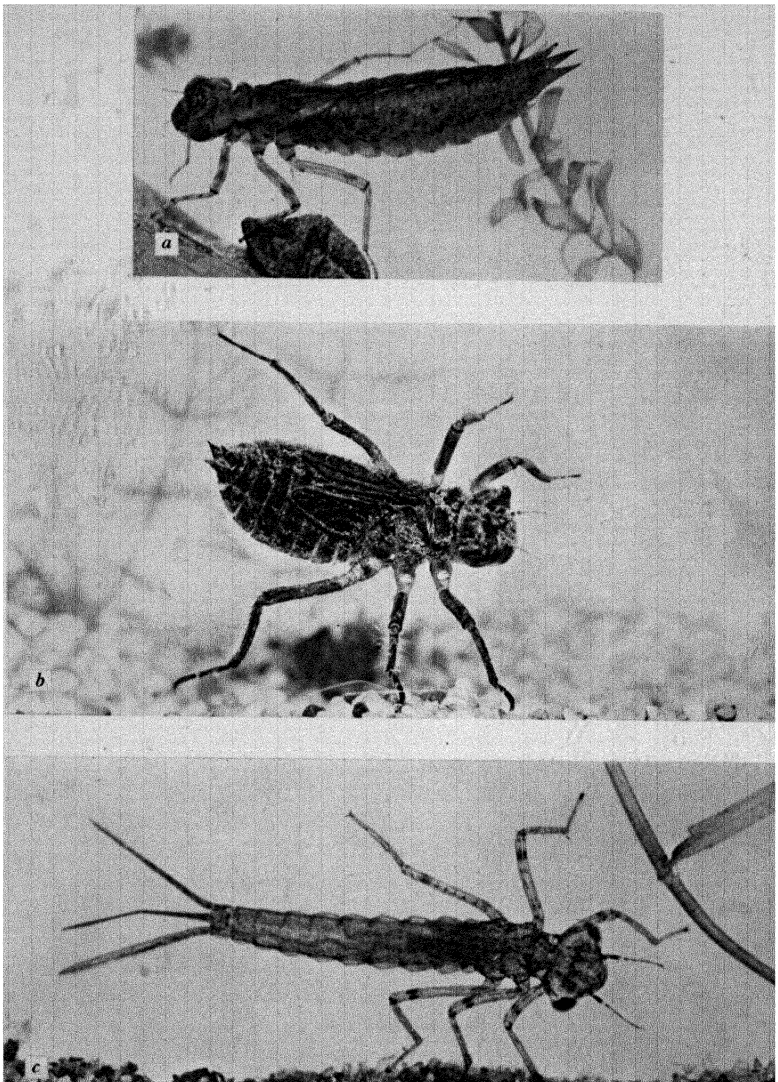
PLATE XV

Photographs by John Clegg

a. Great pond snail, *Limnaea stagnalis* *b*. and *c*. River snail, *Viviparus viviparus*
d. Swan mussel, *Anodonta cygnea*

FRESH WATER MOLLUSCA

PLATE XVI



Photographs by John Clegg

a. Aeshnid (×1½). *b*. Libellulid (×1½). *c*. Agrnid (×4)

DRAGON-FLY NYMPHS

CHAPTER 7

THE ORGANISM IN ITS ENVIRONMENT

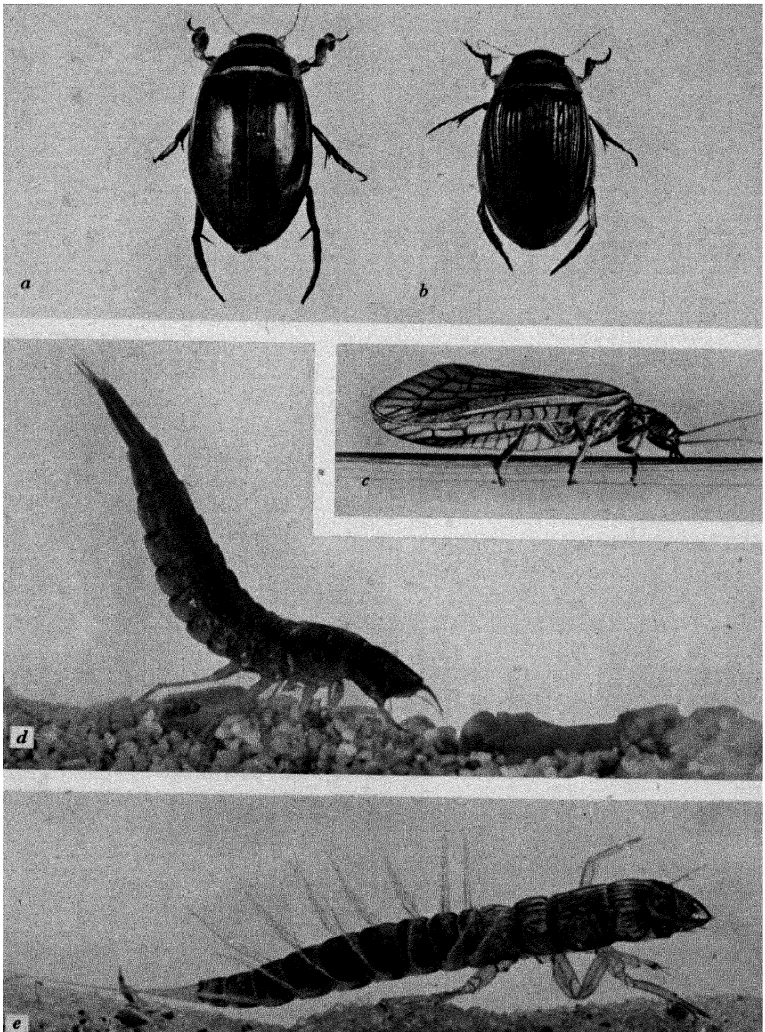
THE purpose of Chapter 6 was to give a picture showing the different kinds of organisms to be found in fresh water, setting them out first according to the classification based on structural affinity, and then according to a grouping based on their relationship to the environment. The present and subsequent chapters take different kinds of fresh-water habitats and describe the animal and plant communities which dwell in each. The communities are treated very generally, because a work of this sort is not the proper place to give long lists of species ; and, if it were, there are not many long lists to be given. Much of the fauna consists of the nymphs and larvae of insects, and means of distinguishing many of these, though they probably exist, have not yet been worked out. Consequently almost any publication describing the survey of a lake, pond, or stream will give a list in which mayfly, stonefly, and dragonfly nymphs, and caddis and true fly larvae are identified to the genus and no further ; and even these imperfect lists are not very numerous. This chapter is not a considered selection from a wealth of material, but approximates more to a summary of all the available information.

Windermere, being the best known biologically, is a convenient standard with which other lakes may be compared. It is, to recapitulate some of its salient features, 10½ miles long and about half a mile in breadth, so that, although the biggest in England, it is not a large lake as lakes go ; but it is of such a size that the wind can raise waves of sufficient magnitude to erode any shore on which they beat. The greatest depth is 219 feet (67 metres) and the average depth is 73 feet (22·3 metres). Important data for the biologist are that the greatest depth to which sufficient light for rooted-plant growth

penetrates is about 16 feet (5 metres), and 25% of the lake bottom is covered by less than this depth of water; and that, if 32 feet (10 metres) be taken as the approximate average depth of the thermocline, then the volume of water below it, that is the hypolimnion, is twice the volume of water above it, that is the epilimnion. All the rocks in the drainage basin are relatively hard and deficient in lime, but most of the land immediately surrounding the lake is under cultivation, and there are fairly large human settlements at Ambleside, near the head of the lake, and at Windermere Town near the centre of the lake. The result is that, though the waters of Windermere are soft, the amount of nutrient salts is fairly high, and the lake is moderately productive. But, owing to the large size of the hypolimnion relative to the epilimnion, the oxygen in it never becomes depleted or even approaches depletion, and Windermere is morphometrically oligotrophic.

There are no surface plants in Windermere and the population of surface animals is poor. In extremely sheltered places, such as boathouses, one of the larger species of pond-skater, *Gerris najas*, occurs in congregations, and there are also colonies of the whirligig beetle, *Gyrinus*. Some of the smaller water-bugs occur in the reed-beds.

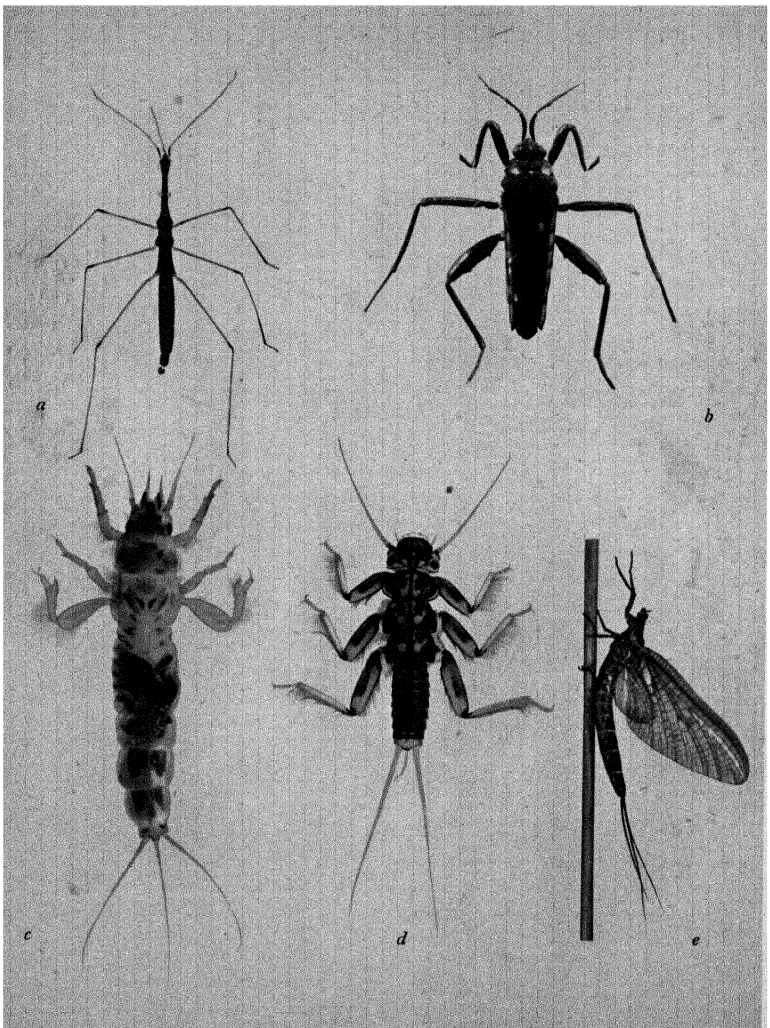
The only published list of minute floating plants or phytoplankton (Wailes, 1939) enumerates 67 species, but it does not include the very small species known as the nannoplankton or net-passing plankton, and there is no doubt that the total number is much greater than this. During the winter all forms are scarce, and some over-winter in a special resting stage. Species belonging to the Desmids are relatively numerous during the months of November, December, and January. In February or March a diatom, *Asterionella* (Plate XXa, p. 113) begins to reproduce rapidly and, as has been described in Chapter 2, p. 22, its numbers rise to a peak in early summer and then decline as certain salts in solution are used up (Fig. 2, p. 22). In July phytoplankton is scarce but, as the salts in the water are replenished, both from the inflowing streams and rivers, and by the decomposition of dead plankton organisms, there is another increase, though now the groups most strongly represented are the blue-green and the colonial green algae; they seem to be associated with the high amounts of dissolved organic matter present in the lake at this time of year owing to the decomposition already mentioned. Diatoms increase again in September and October. The end of this outburst happens sometimes



Photographs by John Clegg

a. Male (smooth) and *b*. female (furrowed) nat. size, and *d*. larva (×2) of the water beetle, *Dytiscus marginalis*. *c*. Adult (×2) and *e*. larva (×3) of the alder fly, *Sialis lutaria*

WATER INSECTS



Photographs by John Clegg

a. Water measurer, *Hydrometra stagnorum* (×3). *b*. Water cricket, *Velia currens* (×5). *c*. Nymph (×3) and *e*. adult (×1½) of *Ephemera danica*, the Mayfly. *d*. A creeper, the nymph of the stonefly, *Perla carlukiana* (×1½)

WATER INSECTS

when silicates, nitrates and phosphates are still present in relatively large amounts and its cause is unknown.

That certain dissolved substances used up during the growth of the phytoplankton may act as limiting factors is well established, and it is one of the most important phenomena taking place in fresh water. But the whole subject of the relationship between dissolved nutrients and plants is territory still largely unsurveyed. It is known that certain species are associated with nutrients in a certain proportion, and that other species come to dominate the scene when the proportions change, but how this comes to pass has not been discovered. Possibly it is sometimes, or even often, achieved by the production of some substance which discourages the growth of other species and prevents competition for the available nutrient salts. Such substances are known as " anti-biotics " and the celebrated example at the present time is penicillin. This is produced by the familiar green mould which is sometimes, to the vexation of the housewife, found growing on a pot of jam or an orange which has been left too long in the larder. The organism, known as *Penicillium*, having established itself on a nutritive substratum, produces this anti-biotic and prevents bacteria or other fungi from exploiting the same source of food.

A remarkable instance has been described quite recently. A small alga known as *Prymnesium parvum* suddenly became very abundant in some carp ponds in Palestine. The carp died rapidly, killed apparently by some substance produced by the *Prymnesium*. The sequel was even more remarkable, for a comparatively short and simple investigation discovered a simple and effective remedy. Nitrogen is essential for the organism, as it is for any other, but it must be in the form of nitrate; ammonium salts in low concentration kill *Prymnesium* in a short space of time. The whole subject of anti-biotics has recently been reviewed by Lucas (1947).

The recorded zooplankton, or animal floating forms, includes, according to the list published by Wailes, 7 species of Cladocera, 4 species of Copepoda, 24 species of Rotifera, and 13 species of Protozoa. This list also is likely to be augmented by future work, particularly more detailed attention to the nannoplankton. Of the Cladocera, four are of the familiar water-flea type, one is a peculiar form which lives within a gelatinous capsule, and the remaining two are modified, carnivorous species.

The animals of the plankton, like the plants, are present in small

numbers during the winter months, and some species have not been found at all. During the summer they abound, but the period of greatest abundance occurs somewhat later than that of the plants.

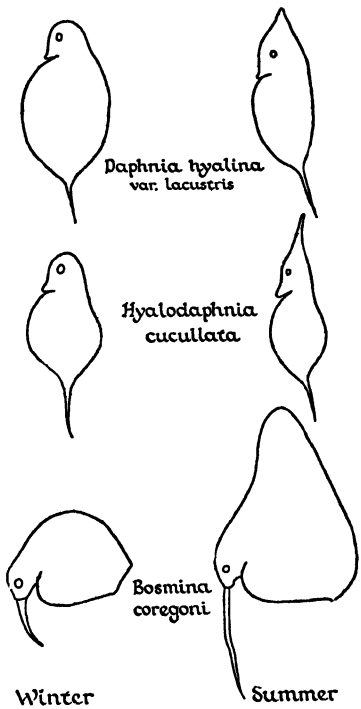


FIG. 10
Winter and summer forms of some zooplankton animals; the summer forms are extremes selected from a large number of examples (After Wesenberg-Lund, 1908)

Rather little is known about the zooplankton of Windermere, or indeed of any British lake, though Sir John Murray's Bathymetric Survey of the Scottish Lochs included zooplankton collections. In other countries the group is the centre of several major controversies, omission to make some reference to which would be an unpardonable parochialism, and the present juncture is suitable for some mention of the main points of disagreement.

Some species of water-flea reproduce asexually throughout the summer, and the offspring from this method of procreation are all females. In the autumn males are also brought forth, and then sexual reproduction ensues. The fertilized eggs have a hard resistant coat and lie dormant for a long period before undergoing further development. Of two rival schools of thought, one maintains that the appearance of males and sexual reproduction is a rhythmical phenomenon which takes place after a certain amount of asexual reproduction, and the other that it is a definite response to the onset of unfavourable conditions. Some recent work by Dr. C. H. Mortimer supports the latter view. He kept cultures of various species of Cladocera for 16 months and during that period there was no sexual reproduction as long as con-

ditions were kept at an optimum. Unfavourable conditions in which males were produced were a lower temperature, reduced food-supply, and overcrowding.

Some Cladocera of the water-flea type have in winter a round front end and a relatively short " tail " projection, but in summer a pointed front end and a longer " tail." The small round *Bosmina* may have in summer a hump which is lacking in winter, and a longer proboscis. Examples of these differences are shown in Fig. 10, which is taken from Wesenberg-Lund's (1908) big paper on the Danish plankton ; but it must be mentioned that, for the sake of illustration, extremes have been chosen from among his very numerous drawings. Some of the algae also show a greater development of spines and other projections from the body surface in specimens taken in summer. All

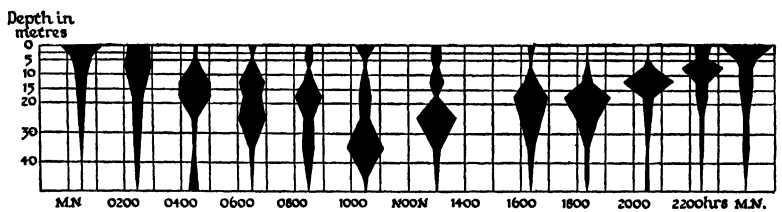


FIG. 11

The daily migration of *Cyclops strenuus* in Windermere. In the construction of the figures the catch at each depth has been converted to percentage of the total catch
(After Ullyott, 1939)

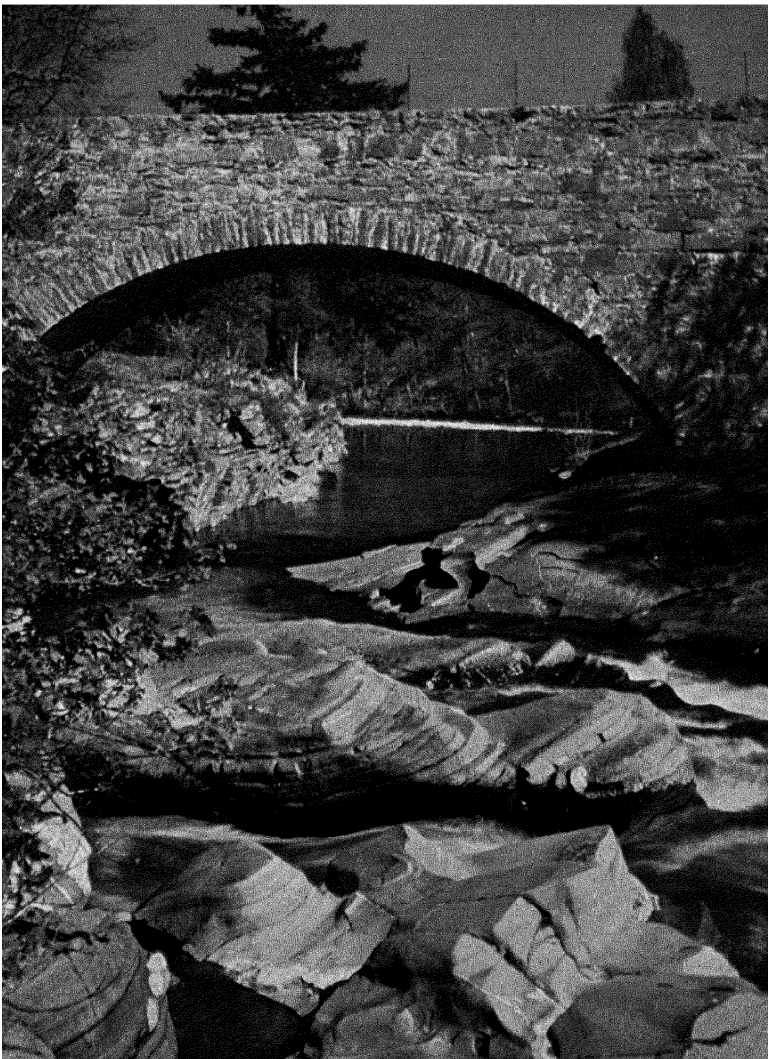
these summer forms have a greater surface area and therefore sink more slowly, since they offer more resistance to the water ; all plankton forms, except a few which have bubbles of gas in them and the insect, *Chaoborus*, which has hydrostatic organs, are slightly heavier than water and tend to sink. Water is more viscous at lower than at higher temperatures and, according to Wesenberg-Lund, the increased surface area of the summer forms is a definite response to the reduced viscosity of the water. But according to the rival school it does not always coincide in time or place with the conditions leading to reduced viscosity, and they attribute it to mere exuberance made possible by an abundant food supply and favourable conditions generally.

One of the most remarkable activities of the Crustacean members of the plankton is their constant movement up and down, a pheno-

menon which has been observed and investigated in many parts of the world. At midday the animals are in greatest abundance at some distance from the surface, and in the upper layers of the lake they are few. As the day draws on there is an upward migration, and round about midnight it is the surface layers of the lake which are most thickly populated. Then the return migration to the depths begins as night gives place to day (Fig. 11). The movements of the plankton and the movements of the sun are obviously related in some way, though whether the plankton organisms move to keep themselves in a zone where light of a certain intensity is always the same, or whether they react to some other stimulus as well is still a debated point. It has, for example, been suggested that the animals tend to move against the pull of gravity but avoid illumination above a certain brightness. There are, however, certain objections to this interpretation and recently a rather close correlation, illustrated in Fig. 12, has been shown between the depth at which the plankton is thickest and the depth to which rays of light at the blue end of the spectrum penetrate with a certain intensity. This work suggests that the movements are a reaction to light alone.

It is difficult to believe that this travelling up and down, which must use up a large amount of energy, is entirely functionless, though at present it is not possible to do more than speculate about what end it may serve. It has been pointed out that the water in lakes is always streaming in a horizontal direction, and so any animal which tended to stay at one level would get carried to the side of the lake. By constantly moving up and down the animals will pass from a current in one direction at one depth to its counter-current in the opposite direction at another depth, and the effects of the various currents will cancel each other. But the phytoplankton does not undergo vertical migrations each day like the zooplankton, so the problem immediately arises of how the phytoplankton meets the same contingency. Most of the algae sink steadily and some observations made in Windermere one year showed that under ice the upper layers of the water became quite devoid of algae. It must be assumed that under usual conditions swirls and eddies set up by various causes keep the upper layers of the water continually supplied with algae.

To resume the account of life in Windermere it is logical to pass on from the plankton to the animals which feed on it. Apart from the carnivorous members of the plankton itself, one of the most important



John Markham

Troutbeck with rocky bed. River Feshie, Inverness-shire. May

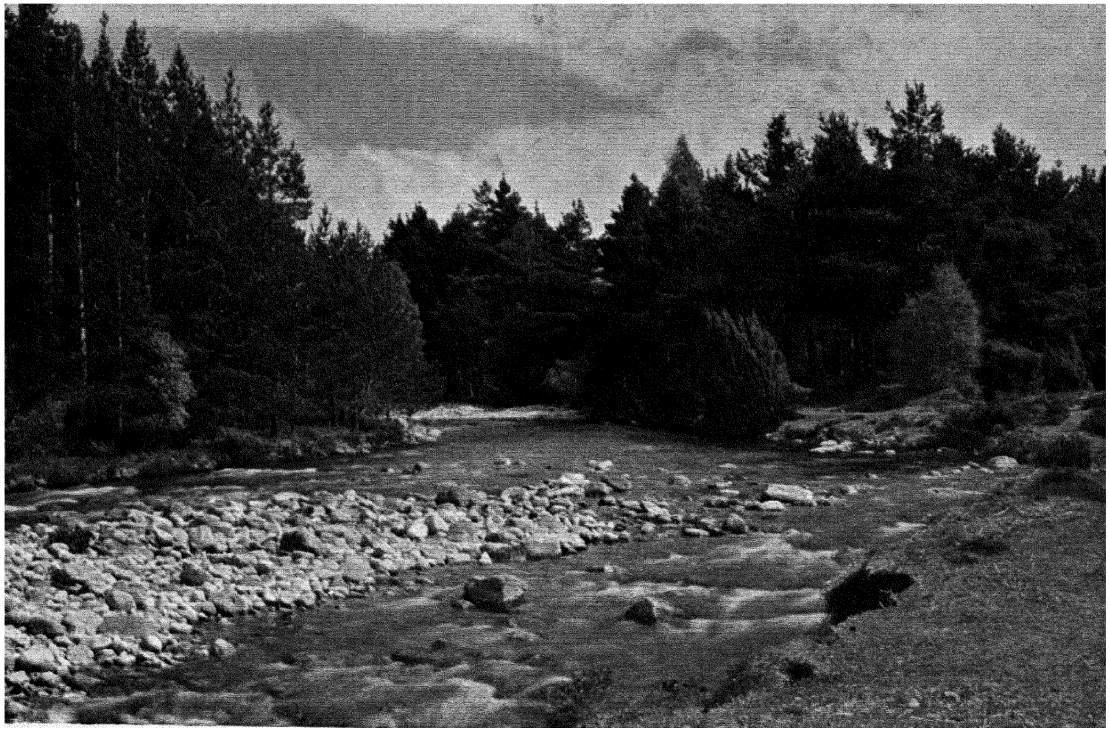


PLATE 22

Troutbeck with stony bed River Bennie, Inverness-shire June

John Markham

is the char (*Salvelinus alpinus willughbii*) (Plate 30, p. 129). This fish inhabits the deeper parts of the lake, but some specimens come into the shallow water in winter to spawn. Others lay their eggs in deeper waters, and the possibility that this difference in habit indicates two biological races is under investigation at the time of writing.

Also linked in the food-chain with the two preceding groups are the burrowers. In Windermere, Humphries (1936) records all the main types already enumerated with the exception of the large mussels. The nymphs of *Ephemera*, the Mayfly, represented by a single species, occur only where sand floors the lake, and have not been found at depths over 30 feet. *Sialis*, the Alder-fly, also represented by one species, is found in mud, but it, too, is limited in depth and does not occur beyond 40 feet. At this depth it may have to travel a considerable distance to reach dry land and, since it is believed always to pupate on dry land, it would be interesting to know more about this journey. At greater depths the fauna consists only of 8 species of midge larvae (Chironomidae), 2 species of true worms (Oligochaeta), 5 species of pea-mussels (*Pisidium*), and an occasional mite (Hydracarina). These figures are based on revised lists, except that relating to Chironomids, which is based on larval identifications and may, therefore, be too low. *Chaoborus*, the phantom larva, is also present.

The creatures found in the deepest part of the lake live perpetually in an environment which, though not comparable with the depths of the ocean, is none the less remarkable for its lack of variety; water movement is no more than an imperceptible creep, midday is scarcely less dark than midnight, and the temperature range throughout the year may be no more than from 4° C. to 6° C. (Fig. 1, p. 20). The inhabitants of Windermere have not to contend with a lack of oxygen in the summer, a physiological problem which dwellers in richer lakes have to solve. The Chironomids do not spend all their lives in the mud, but must make the long journey to the surface so that the adult may emerge and reproduce; it is a journey fraught with peril, for the ascending pupae are preyed on extensively by fish. It is interesting to note that within this family is found a phenomenon known as paedogenesis, in which the adult stage is abolished and sexual maturity is attained in the larval stage.

Finally there is the shallow region around the margin of the lake. Conditions are more diverse here than in any other part, and the fauna shows a corresponding richness in number of species and variety

of form. In order to avoid a controversy which generates much heat among continental workers, who disagree about the limits of the littoral and sublittoral zones in relation to the water level, it is proposed here to refer to this part of the lake as the zone of attached vegetation.

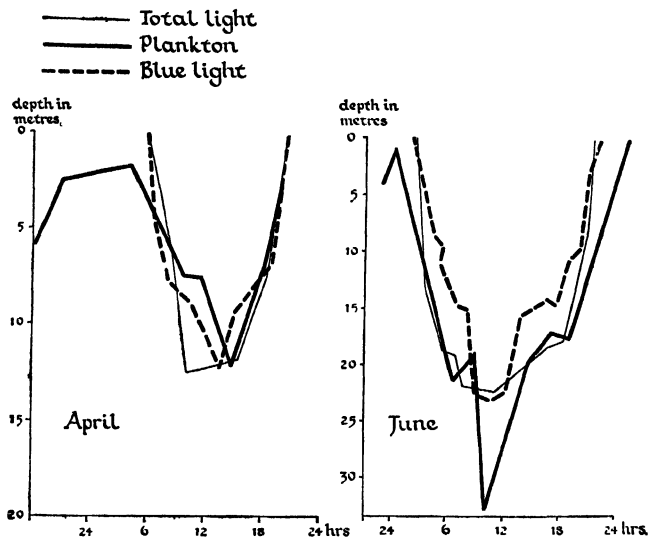


FIG. 12

Daily migration of *Cyclops strenuus* and the penetration of light in Windermere. The thick continuous line is obtained by plotting at hourly intervals the depth at which most specimens were caught (Fig. 11); the thin continuous line shows at hourly intervals the depth to which total light of an intensity of 32,800 erg/cm²/sec. in April and 108,000 erg/cm²/sec. in June penetrated; the thick broken line shows blue light treated in the same way, the intensity taken being 9600 erg/cm²/sec. in April and 305 erg/cm²/sec. in June

(After Ullyott, 1939)

The depth to which it extends depends on the depth to which light of a certain intensity can penetrate, and in Windermere this is about 16 feet. In this zone the substratum is the most important single factor affecting the plants and animals. This is clearly illustrated by the stretch of

Windermere shore which has already been described and which is shown in Plate 1 (p. 20) and Plate I (p. 36). We start at Watbarrow point, a smooth, steep, flat, rock face, and pass thence through the slates of the Bannisdale shore, and then the rounded stones and boulders of the Drift shore, to the sandy floor of High Wray Bay. Elsewhere in the lake there are other bays which can be arranged in a progressively more sheltered series (Fig. 4, p. 27).

The flora of the rock face and the Bannisdale shore is similar. Algae form a thin cover which makes the bottom slippery to walk on and, at certain times of year, there is also a zone of filamentous algae trailing in the water. These algae occur also on the Drift shore but there, in addition, rooted plants can gain a foothold in the patches between the boulders. The main species is *Littorella uniflora*, the lake-wort. This plant reaches its greatest abundance on sandy bottoms, where it forms extensive and compact swards.

In more protected bays beds of emergent vegetation occur. The first species to supplant *Littorella* is *Phragmites communis*, the common reed, and once it has become established it exerts a profound influence on subsequent developments. The changes which take place have not actually been observed in any one reed-bed, but there is good reason to believe that the more sheltered a bay the more rapidly will the vegetation in it develop or evolve ; and therefore from a study of the present-day flora of a series of reed-beds, each more protected from wave action than the last, the plant succession can be ascertained.

A thick reed-bed affects the environment in two ways ; first, by dying down at the end of each season it covers the bottom with organic matter, and secondly, it impedes the flow of water. Vegetable debris decomposes very slowly unless it is well mixed with silt. The details of the chemistry of the process are not known but there is evidence that one important element which comes in with silt and speeds up decomposition is calcium. A reed-bed which colonizes a sandy bottom will therefore, by dying down each year and impeding silt-bearing currents of water, gradually convert the substratum from one which contains little to one which contains much organic matter. Such bottoms are unfavourable to many species of plant, among them *Phragmites* itself, and the reed is gradually replaced by sedge, *Carex rostrata*. Bogmoss, *Sphagnum*, will enter the plant association later on and, as the continued accumulation of organic matter raises the soil, bog and then moorland plant communities will appear.

But it may happen that a reed-bed develops at the mouth of a river and silt is deposited upon each season's plant remains. The result is a greater degree of decomposition of the organic matter and the formation of a rich black mud. *Phragmites* can grow on this substratum and it will persist until, during spells of fine weather, it is growing on dry land. Sallows and other bushes join the plant community at this stage, and a fenland type of vegetation is produced. There is one such fen by Windermere where the stream draining Blelham Lake flows in, but the best-known example is the fen at the head of Esthwaite Water, a locality which Professor Pearsall has kept under observation for 35 years. His maps of the vegetation may be seen in Tansley's book (1939, pp. 640 and 641).

The deep-water plant communities in the particular stretch of lake under discussion have not been investigated but, since there is much detailed knowledge about the zones in other parts of the lake and in other lakes, we can postulate what occurs with considerable confidence. It has been known for a long time that the various species tend to occur in long narrow zones parallel with the shore, and one suggestion was that light might be an important agent in this zonation, as it is along the seashore. Pearsall, however, was able to demonstrate that, although light does play a part, a more important factor is the nature of the bottom. Waves, beating against a boulder-clay shore of the type frequent in the Lake District, carry off all but the coarsest material so that only stones and boulders are left behind. The particles carried away settle in deeper water, the coarsest coming down first and the finest travelling the greatest distance from the shore. The result is a graded series from shallower water nearer the land to deeper water farther out (Fig. 3, p. 25).

The platform itself bears usually but a sparse vegetation of *Littorella* and an occasional tuft of water-milfoil (*Myriophyllum*), but on the slope, where conditions are more sheltered owing to the depth, vegetation is thick. The top zone of coarse sand is usually colonized by the quillwort, *Isoetes*; below it there is typically a zone of *Nitella*, one of the stoneworts; and a community dominated by various species of pondweed, *Potamogeton*, is to be expected on the finest silts in the deepest water.

Sometimes the configuration of the shore-line is such that the particles are carried away at an angle to the edge of the lake and a spit is formed. Rivers also form spits, and an example laid down by

the main inflow into the head of Windermere can be seen in Plate VIII (p. 59). Rivers yield more material of all sizes than waves eroding a shore, particularly more of the finest particles.

It is essential that, if the relationships of the various plants are to be understood, the associations must be thought of as phases in an ever changing scheme and not as something fixed and permanent. Three variable factors influence the course of development or evolution. First there is the size of the particles of inorganic matter, second the rate at which these are accumulating, and third the quantity of organic matter. The first two factors, and to some extent the third, for remains of terrestrial plants may contribute a considerable amount of organic matter, depend on the nature of the land in the drainage area. The intensity of each one will vary considerably from one part of a lake to another according to the distance from the mouth of a stream or river and the size and nature of that stream or river. There are also overall differences between different lakes. The finest silts, for example, are found only in lakes lying in a drainage basin which has weathered much and given rise to big areas suitable for cultivation.

The plant successions start with species which are totally submerged throughout life. After a variable number of species in this stage floating-leaved plants become dominant. Further evolution and filling up of the water with solid material leads to the appearance of vegetation with an emergent habit. These three stages are almost invariably found, but the plants in them are quite different in the various successions, of which the following are some of the more important that have been described by Pearsall. A coarse bottom, where the substratum is accumulating rapidly, for example a bed of sand near the mouth of a beck, is colonized first by *Juncus bulbosus* forma *fluitans*. As the substratum is built up, and the depth of water decreases, *Potamogeton natans* gains a foothold and becomes the important member of the floating-leaf community. In its turn it gives way to the emergents, *Equisetum fluviatile* (horsetail) and *Carex rostrata* (sedge)

A coarse substratum where there is slow accumulation of inorganic sediments will be colonized by *Isoetes lacustris* (quillwort). In lakes such as Ennerdale this plant is common, and the only other species which attains any degree of abundance is *Nitella opaca* (stonewort). With the increase in the organic content of the soil as vegetable debris accumulates and does not decompose, *Isoetes* is gradually replaced by *Juncus bulbosus* forma *fluitans*, *Myriophyllum* (water-milfoil), and *Lobelia*

dolomanna in shallower water. The floating-leaved and emergent species are the same as in the preceding succession.

Where there is fairly rapid accumulation of fairly fine silt, the succession is *Nitella* → *Potamogeton perfoliatus* → *Elodea* (the Canadian pondweed), *Sparganium minimum* (the small bur-reed), and *Potamogeton alpinus* → water-lilies → *Phragmites*. Speaking generally, this succession is typical of Windermere.

In Esthwaite Water the rate of accumulation of fine silt is more rapid than in any other lake, and associated with this is a succession in which there are several species not known elsewhere in the Lake District. The first colonist is *Najas flexilis*, and this is replaced by *Potamogeton pusillus* and other species of the same genus having in common a long and narrow leaf so that the name linear-leaved associes is often used to refer to them. Water-lilies are the plants of the floating-leaved stage, but the emergent typical of richly silted conditions is *Typha*, the reed-mace.

These four successions take place when the three environmental factors remain constant. In the natural state they do not always remain constant; a rich silt supply may be cut off or diverted so that a rich silted mud becomes organic, or the reverse may take place, and an area where vegetable debris is accumulating and forming an organic substratum may come under the influence of silting which will bring about decomposition of the plant remains. The succession will be modified by such changes and, to take extreme instances, *Najas flexilis* may ultimately be succeeded by *Potamogeton natans* and *Carex*, or a place originally colonized by *Nitella* may eventually support water-lilies and *Typha*. The full story is complicated and the reader who requires more information is referred to Tansley (1939), where, if still further detail is desired, references to the original papers by Pearsall may be found. The underlying principles, on the other hand —the fineness of the inorganic particles, the amount of inorganic matter or silt, and the amount of organic matter or vegetable debris, with light playing some part—are simple.

The animal communities of the different parts of the attached plant zone of the lake may now be examined. The portion of the lake shore described earlier (p. 26) has been investigated by Moon (1934). On the bare rock face he found but two species; one of them, *Ancylastrum fluviatile*, the fresh-water limpet, is in fact like a miniature limpet (though not related to those of the seashore) and is

adapted to colonize just such a habitat as a bare rock face. The other is the ubiquitous *Limnaea pereger*, the wandering snail. Where there are cracks affording a slight degree of cover, the fauna is augmented by two species of caddis larvae.

On the Bannisdale shore there is a much greater degree of cover to be obtained underneath the slates, and the fauna is much richer in species. In addition to the two snails already encountered, occasional specimens of *Planorbis carinatus* (the keeled ramshorn), *P. contortus* (the twisted ramshorn) and *P. albus* (the white ramshorn) may be found. Flatworms, mites, leeches, *Gammarus* (the fresh-water shrimp), and *Asellus* (the water hog-louse) also occur in small numbers. The characteristic feature of the fauna is the variety of insect nymphs and larvae. There are 4 species of mayflies, 5 species of stoneflies, and about 18 species of caddisfly larvae ; subsequent workers having bred out the adults, it is possible to give precise numbers for the first two groups, but the total of the last must remain approximate until the adults of the order have been studied. Chironomid larvae are also present in fair numbers. These creatures are almost ubiquitous in fresh water, but little is known about the species of the different habitats on account of taxonomic difficulties. There are over 500 species in Britain ; the adults can be named only by a specialist, and the larvae cannot be named at all in the present state of knowledge.

Some members of this fauna possess obvious structural adaptations for life in this particular environment. The limpet shape of *Ancylastrum* has already been mentioned, and both *Ecdyonurus dispar* and *Heptagenia lateralis*, two of the Ephemeroptera, have flattened, spread-eagled bodies (Plate XIXa, p. 112) adapted for life on the surface of a stone. Other animals, as for example the stonefly, *Dictyopterygella recta*, do not occur in other types of habitat although there are no obvious structural reasons why they should not do so. The restriction to one type of habitat, for some species at least, is attributable to physiological adaption or physiological restriction, a subject which is discussed more fully later, on p. 127. The rest of the fauna may be described as adaptable, rather than adapted, and it occurs in a wide range of habitats ; *Limnaea pereger* and *Gammarus pulex* are two extreme examples. Many of the Trichoptera (caddis flies) make their cases of stones, and such cases are more compact and heavier than those made of plant material, and therefore less liable to be moved about by wave action. It is, however, rash to leap to the conclusion that this represents

adaptation ; species which build stone cases may do so because they have formed the habit of utilizing the material most ready to hand in a stony environment. In the genus *Silo*, however, a row of larger stones is attached to the sides of the case, and this may perhaps serve to prevent the case being turned upside down.

A general feature of the fauna is a scarcity of swimming forms, particularly those which have to come to the surface for air, though a beetle, *Platambus maculatus*, is a characteristic member of the community.

The fauna of the Drift shore is similar, but it is augmented by some of the burrowers. The next habitat in the series, bare sand, is inhabited only by the specialized burrowing species—various Chironomid larvae, pea-mussels (*Pisidium*), worms, the nymphs of the mayfly (*Ephemera*), and the larvae of the alder-fly (*Sialis*) ; the total number of groups represented is small.

Colonization of sand by reeds produces sheltered conditions in which a more varied fauna is to be found. It includes many of the Bannisdale shore species, but there are some notable absentees, and some species not previously encountered. To take the absentees first : they are *Ancylastrum fluviatilis*, *Ecdyonurus* and *Heptagenia*, the three animals with structural adaptations for life on a stony substratum ; all the Plecoptera ; and several Trichoptera. Among species encountered for the first time, there is another limpet, *Ancylus lacustris*, which lives on the stems of the reeds ; several species of water-beetle and the water-boatmen *Corixa* and *Notonecta*, all forms which are dependent on the air for their oxygen ; and *Enallagma* and *Coenagrion* (dragonflies), *Leptophlebia* (Ephemeroptera), and two stoneflies, *Nemoura variegata* and *Nemurella inconspicua*, all essentially still-water forms.

The fauna of the submerged vegetation has not been studied in detail, though Miss Carmel Humphries has made some observations in the course of a survey of the bottom fauna of the deeper parts of Windermere. In general it resembles that of the reed-beds, but the air-breathing beetles and bugs are absent, and the snails attain a greater abundance than in any other part of the lake. Several species of water-mite not found elsewhere are recorded.

Of the fish, trout, perch, pike, and eels are all abundant in Windermere, in addition to the char already mentioned, and minnows are numerous in the shallow water round the edge. Salmon occasionally



PLATE 23

John Markham

Minnow reach River Conway, North Wales September



PLATE 24

Robert Atkinson

Meandering lowland reach River Test, Hampshire May

pass through on their way to spawn in rivers flowing into the lake; *Cottus gobio*, the miller's thumb, has been recorded under stones; and another rare species is the roach.

Windermere thus presents habitats ranging from flat rock face on which waves may beat with all their force to reed-beds and weed-beds where animals may dwell free from the disturbing action of the waves. There are marked changes in the fauna between one end of the range and the other. The next step is to describe how the fauna and flora of other lakes differ from that of Windermere, and the first problem is to find examples in which faunistic studies have been made. There is some information, though it is not complete, for the other lakes in the Lake District. These can be arranged in a series from "primitive" to "evolved" as described on p. 54. For present purposes it will suffice to take, for contrast with Windermere, Ennerdale, which is one of the two most primitive lakes, and Esthwaite, which is the most evolved of all. But all these are soft-water lakes and it is desirable to take also an example of a hard-water lake, for it is among them that the most productive conditions of all are found. None of those in Britain have been studied and it is necessary to seek an example on the continent. Esrom Lake in Denmark, one of the "Baltic" lakes formed by an ice-sheet covering a plain, has been studied very thoroughly, and the work, carried out by Prof. Dr. Kaj Berg (1938), is quite recent. It may be added that Berg's account is in English and so Esrom Lake has many advantages as an example.

A few remarks on hard and soft waters may be interpolated here. It is unfortunate that, as a general rule, hard rocks should give rise to soft waters and vice versa, for the terms hard and soft used to denote respectively large and small amounts of calcium in solution are convenient. The waterworks engineer does not consider water hard unless it contains 60 parts per million of calcium; the housewife, eking out her soap ration, becomes aware of hardness at about 30 parts per million; and for snails, the only animal group for which detailed information is available, the critical concentration is about 20 parts per million.

Reverting to the comparison of different lakes, we may take the plants and animals group by group as was done for Windermere. There is little to be said about the surface-dwellers, for they are unimportant on large bodies of water, and in any case they have not been worked out.

Among the phytoplankton are found many of the so-called "indicator organisms." In Ennerdale the commonest forms are desmids; these occur also in Windermere, but diatoms and Chlorophyceae other than desmids are more important, and blue-green algae abound towards the end of the season; Esrom Lake is also characterized by diatoms and some blue-green algae. The zooplankton species—or at least the larger forms which are the only ones which have been investigated in detail—tend, on the other hand, to be the same in all lakes.

In Ennerdale Water trout and char are the principal fish, and minnows and sticklebacks are known to be fairly common; sufficient work to warrant a comprehensive list has not been done. In Windermere (Frost 1946), as already mentioned, perch, pike, and eels are common in addition to the two game fish, and the same association may be found in the hard-water lakes, though if a series with increasing shallowness and abundance of weed be taken, a progressive increase in the proportion of coarse fish will be found.

Nothing is known about the bottom fauna of Ennerdale Water, but, if it conforms with the continental lakes, which have been classified according to their Chironomidae, the commonest members of this family belong to the genera *Tanytarsus* or *Stictochironomus*. In Windermere *Sergentia*, and in Esrom Lake *Chironomus* is the important genus.

The rooted plant associations of the Lake District lakes have already been described. Rather little is known about the animals of the shallow water region of any of the English lakes except Windermere; no general surveys have been made and the available information relates to a few groups only. Of the larger Corixidae only two species, *Corixa striata* and *C. scotti*, have been found in Ennerdale Water. In Windermere *C. striata* is much more abundant, and *C. scotti*, which is characteristic of barren soils whether they be sandy and inorganic or peaty and highly organic, is found only in a few places. In silted bays two other species, *C. fossarum* and *C. distincta*, are numerous. A fifth species, *C. falleni*, is rather rare. In Esthwaite Water there are the same species but *C. falleni* is more important. In hard-water lakes, such as Loch Leven, *C. falleni* is one of the most common species, and the others are *C. striata* and *C. praeusta*.

The snail fauna of Ennerdale Water is poor and includes only the wandering snail, *Limnaea pereger*. In Windermere 13 species have been

recorded, 8 being abundant judged by Lake District standards, and there are also 11 species of pea-mussel (*Sphaerium* 2, *Pisidium* 9). In Esrom Lake there are 20 species of snail and 11 of bivalves, including one large one, *Dreissensia*, the zebra mussel. But the real contrast between the two is not apparent until the total populations are set side by side; there may be upwards of 6,000 molluscs per square metre in Esrom Lake, whereas a favourable patch of the same size in Windermere is unlikely to yield more than about 100 specimens. *Gammarus* and *Asellus* are both abundant in Esrom Lake, and so the commonest members of the fauna are not insects. In Windermere they are, and this is the great difference between hard- and soft-water lakes. The importance of the difference cannot be gainsaid, though how far it is reasonable to attribute it all to the concentration of calcium, as some authors do, is open to question.

Thus what comes into a lake exerts an influence on the plants and animals living in all the various habitats. The fact is well established, though the exact nature of the correlation remains obscure; it is not known, for example, why the coarse fish, perch and pike, flourish in Windermere, but do not occur in the more austere conditions offered by Ennerdale Water. The second important feature about a lake is its shape, particularly its shape in profile. Only a shallow lake is likely to be eutrophic. Further it will have more gently shelving shores and therefore a much greater area covered by attached vegetation, and this will affect its biology in comparison with a deep lake.

The most detailed work on the animals in running water in Britain is that of Percival and Whitehead (1929), who selected typical examples of different kinds of bottom and made careful counts of the animals on a given area. Four of their types, which may be taken because they illustrate the range of conditions in a rapid stony stream, were: typical unstable bottom; one which though more stable was not sufficiently so to support a growth of moss; stones and boulders with some moss; and lastly thick moss. The commonest members of the fauna were: on the typical unstable bottom, undetermined species of Chironomids, the flattened mayfly nymph *Ecdyonurus* sp.[1] and the similar *Rithrogena* sp., one caddis species, and the mayflies *Baëtis* spp; on the more stable bottom the same animals and, in addition, several more caddis species, the fresh-water limpet, and the wandering snail;

[1] This contraction denotes that the species was not identified; sp. is used when it is thought that there is only one species, and spp. when there are more than one.

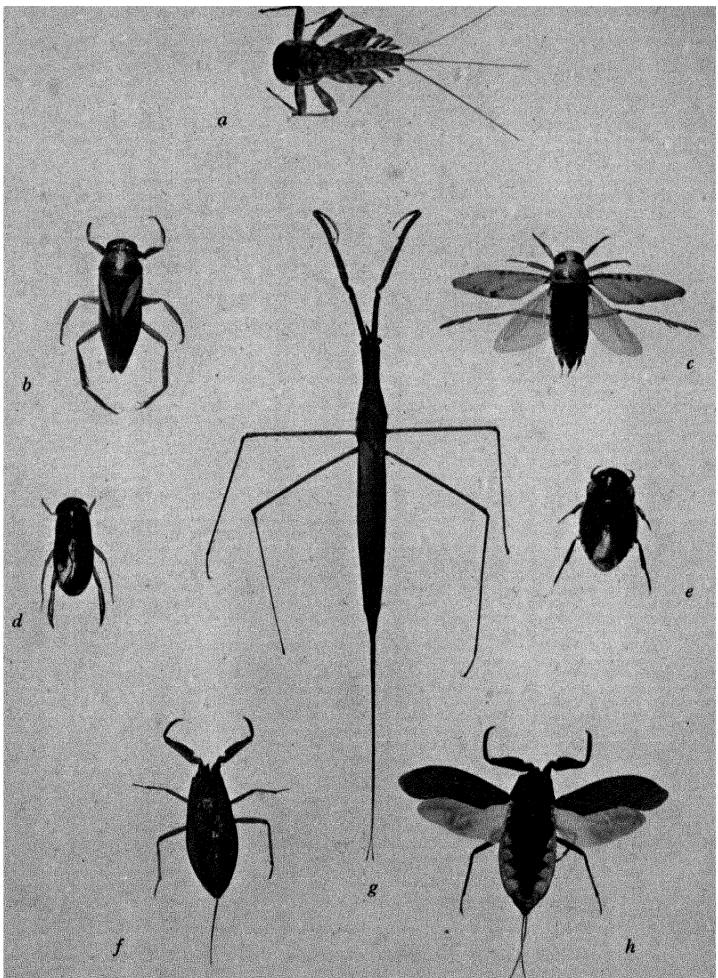
in the not-so-thick moss, *Baëtis* spp. in large numbers, another mayfly *Ephemerella* sp. (nymph of what the fishermen call the blue-winged olive), various stonefly nymphs, and the fresh-water shrimp, *Gammarus*, the flat mayfly nymphs being quite scarce; in the thickest moss, Chironomidae in great abundance and the other animals in smaller numbers.

In a stream where the temperature never rises above 17° C. flatworms are abundant on stony bottoms, particularly where there is not too much vegetation growing. There are some notes on them in the next chapter. Hynes (1941) has recently made a detailed study of the ecology of stoneflies, and his work adds considerably to knowledge about stream faunas. Some species, such as *Leuctra nigra*, *Protonemura praecox*, and *Amphinemura standfussi* are found only in small streams, and hardly ever in rivers. Others, such as *Leuctra geniculata*, are not found anywhere except in rivers. Within one stream or river there is a difference between the fauna of the stable and the unstable bottom. *Perlodes mortoni* and *Perla carlukiana*, two of the large creepers, and *Chloroperla tripunctata*, were taken only on an unstable substratum in the Lake District, whereas another large species, *Perla cephalotes*, and several small ones were almost or completely confined to the stable substratum. *Amphinemura standfussi* is found particularly in packets of dead leaves caught up among the stones and boulders of a stream bed.

In general the fauna is similar to that of the stony lake-shore, but there are two groups which occur in streams and rivers but not in lakes, the family Simuliidae (buffalo gnats), which are true flies, and the net-spinning Trichoptera. The larva of *Simulium* lives on the surface of a rock or a plant, in a situation exposed to the swiftest current, and obtains its food by filtering the water with its hairy mouthparts. The caddis larvae also subsist on particulate matter but catch it in nets which they build between stones or among plants. These creatures depend on a current to bring them their food, and so they cannot live on a lake shore where conditions may be still for a long period.

In the slow reaches of a river, where fine particles can settle on the bottom and rooted plants can grow, the assemblage of animals comes to resemble that of a pond or of a sheltered reed-bed in a lake.

The River Tees, a river with moderately soft water throughout its length, has been studied thoroughly by Butcher, Longwell and

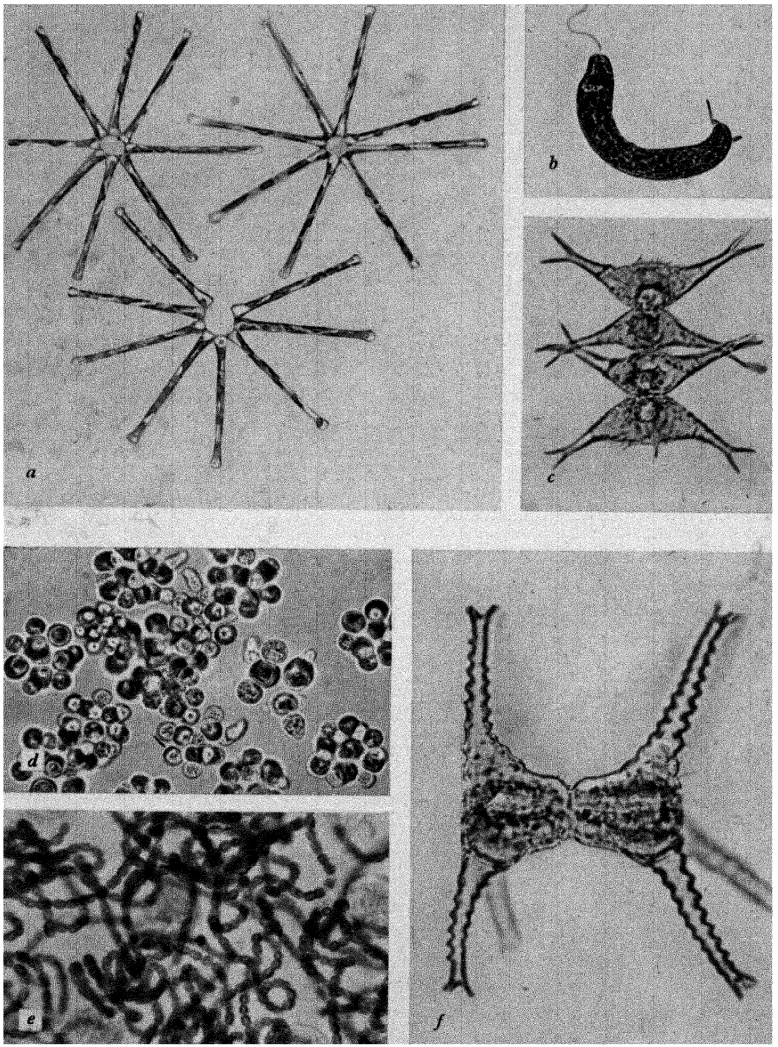


Photographs by John Clegg

a. *Ecdyonurus* sp. (Ephemeroptera). *b.-e*. Water boatmen; *Notonecta obliqua* (*furcata*), *N. glauca*, *Corixa punctata*, *Naucoris cimicoides*. *f*. and *h*. Water scorpion, *Nepa cinerea*. *g*. Water stick insect, *Ranatra linearis* (all nat. size)

A FLAT MAYFLY NYMPH AND SOME WATER BUGS

PLATE XX



a. Diatom, *Asterionella formosa* (×400). *b*. Flagellate, *Euglena spirogyrae* (×350). *c*. Desmid, *Staurastrum pseudopelagicum* (×500). *d*. Colonial green alga, *Sphaerocystis schroeteri* (×450). *e*. Threads of the blue-green alga, *Anabaena flos-aquae* (×300). *f*. Desmid, *Staurastrum gracile* (×720)

PLANKTONIC ALGAE

Pentelow (1937). They did not separate different types of substratum as Percival and Whitehead did, but their data covered the river from source to estuary. The fauna they encountered is similar, in broad outline, to that just described, and the animals which they record as more or less abundant at all stations are: Chironomid larvae; 3 net-spinning caddises, namely *Hydropsyche* sp., *Polycentropus* sp. and *Rhyacophila* sp.; 3 mayflies, namely the flat *Ecdyonurus* sp., *Ephemerella* sp. and *Baëtis* sp.; 1 stonefly, *Leuctra* sp.; and the limpet *Ancylastrum fluviatile*. It will be noted that only the last is not an insect.

The fishes of the Tees are the trout, dace, chub and minnow, which are common; the grayling, gudgeon and roach, which are fairly common; and the pike and perch, which are rare. But only the trout and the minnow are found in the upper reaches, and the rest are confined to the lower, slower, richer reaches. This fish distribution is not the same as that found in the Lake District lakes, but it is similar, with trout in the "primitive" conditions and coarse fish only in the "evolved" conditions.

Pollution of rivers and streams by sewage has a very great effect on the fauna and, unfortunately, pollution is so frequent in British rivers that this is an all too widely applicable piece of ecology. Immediately below a sewer with a big discharge the microflora of the river-bed is replaced by sewage fungus and the fauna consists largely of worms belonging to the family Tubificidae. They are jostled by red Chironomid larvae as conditions improve. With further purification, algae re-establish themselves, and there is a fauna in which the common animals are *L. pereger*, the wandering snail, *Ancylastrum fluviatile*, the fresh-water limpet, *Asellus*, the water hog-louse, and *Herpobdella octoculata*, a leech. This, it will be noted, is a typical non-insect fauna; it is associated with a rich nutrient supply, resulting from the breakdown of sewage, and not particularly with a big concentration of calcium. With further purification the algae and insects found in clean reaches gradually return.

When eventually it becomes possible to put specific names to all the insect nymphs and larvae, interesting differences in detail between one habitat and another will probably come to light. The Simuliidae is one of the few families of which the larvae can be named, and careful attention was paid to it during the course of the Tees survey. *Simulium monticola* and *S. variegatum* were found only in the more rapid parts of the river, where they lived on stones and boulders; in slower reaches

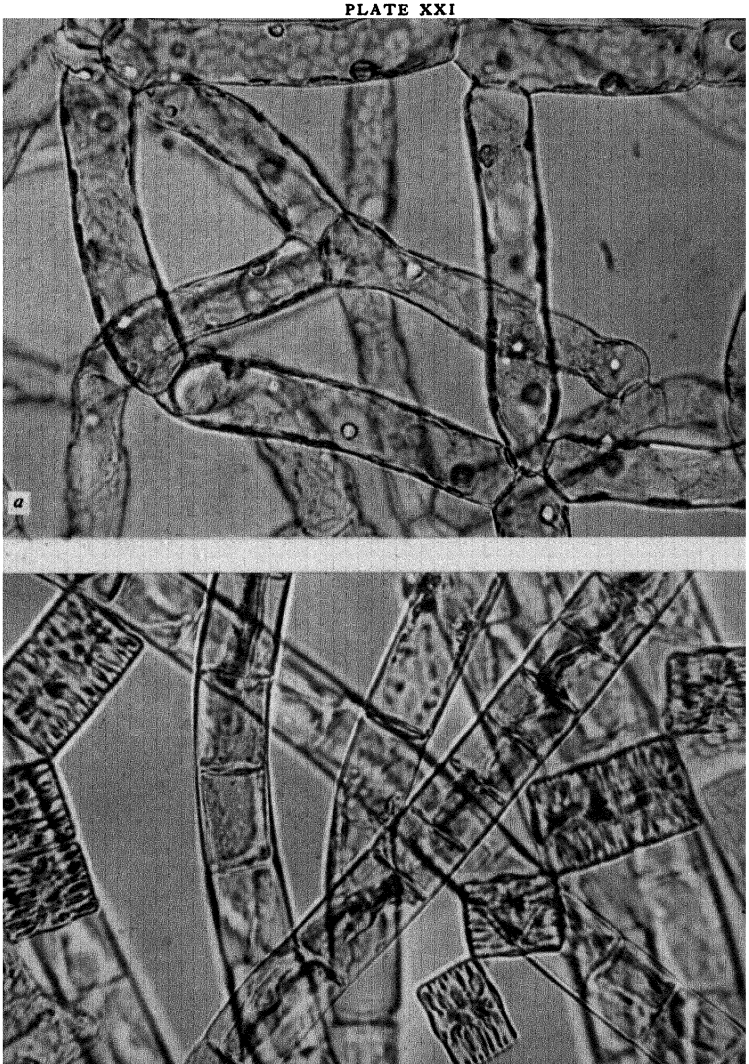
they were replaced by *S. reptans* and *S. equinum*, which attached themselves to the surface of plants. Of these four, *S. reptans* was the only one found in the River Skerne, a tributary which differed from the Tees in having hard water, in suffering heavier pollution, and in having a less steep gradient. *S. ornatum* and *S. aureum* were abundant in the Skerne but were not present in the Tees.

Some 25 miles from the mouth increased salinity due to sea-water first becomes detectable. Much of the fresh-water fauna stops abruptly, but a few species, the hog-louse *Asellus*, the worm *Tubifex tubifex*, the leech *Herpobdella atomaria*, and the snails *Limnaea pereger*, *Ancylastrum fluviatile* and *Hydrobia jenkinsi*, which last was originally a purely estuarine form, penetrate for a greater or less distance. They meet a few marine animals which can live in dilute sea-water. The number of true brackish-water species, which occur neither in fresh water nor in the sea, is small (Fig. 13). There are two shrimps, *Gammarus zaddachi* and *Gammarus duebeni*, a flatworm *Procerodes* (*Gunda*) *ulvae*, and a colonial coelenterate *Cordylophora lacustris*. The absence of all four species of snail which occur in estuaries is unexpected. There is also a brackish-water planktonic Copepod, *Eurytomora affinis* var. *hirundoides*.

Alexander, Southgate and Bassindale (1935), who surveyed the estuary, noted that the number of different kinds of animals and plants diminished towards the middle of the estuary, and they summarized their findings in figures which are reproduced here as Figs. 13 and 14. In Fig. 14 the fresh- and brackish-water species are shown as a percentage of the number occurring in a typical stretch above the estuary, and the marine species as a percentage of the number in the sea at the river mouth; in addition, the oxygen concentration is shown. It will be seen that the point where there were fewest species was also the point of maximum pollution as indicated by the amount of oxygen in solution. The workers decided, however, not to leap immediately to the obvious conclusion but to make first some observations on an unpolluted estuary, and they carried out a quick survey of the River Tay. The results are shown also on Fig. 14, and it will be seen that there is in the Tay a diminution in the fauna towards the middle of the estuary just as in the Tees. Salinity changes are, therefore, the factor concerned and not pollution. But certain marine species penetrate into regions of lower salinity in the Tay than in the Tees and this may be due to pollution.

The Bristol Avon, not to be confused with the Hampshire Avon

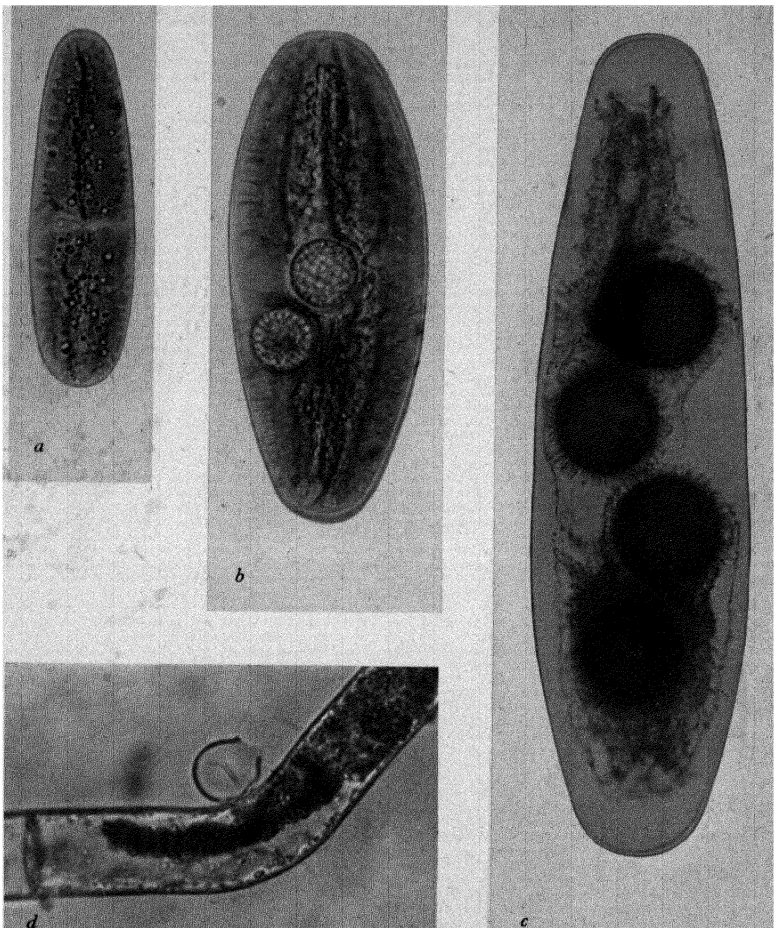
PLATE XXI



Photographs by H. M. Canter

a. Cells of the Water-net, *Hydrodictyon reticulatum* (×550)
b. Threads of the filamentous green alga, *Mougeotia* sp., and zigzag colonies of the diatom, *Tabellaria* sp. (×500)

ALGAE



Photographs by H. M. Canter

a. A healthy desmid cell (×400) *b*. A similar cell containing two parasite bodies (×380). *c*. A desmid cell with four parasite bodies now encysted in spiny envelopes among the remains of the cell contents (×430). *d*. A spore-case on the outside of a *Mougeotia* sp. filament (×700)

CHYTRIDIALES, FUNGAL PARASITES OF ALGAE

described in Chapter 5, was another of the rivers surveyed by the Ministry of Agriculture and Fisheries team (Pentelow, Butcher and Grindley, 1938), pollution in this instance being due to a milk factory. Attention was concentrated on a ten-mile stretch in which the river pursued a meandering course through meadows. It was not, however, completely sluggish, and there were stretches where the current was fast enough to keep a pebbly bottom free of finer particles. *Gammarus*; *Theodoxus* (*Neritina*) *fluviatilis*, a snail confined to hard waters with a fair flow; *Sphaerium*, a pea-mussel; worms of the family *Tubificidae*; Chironomid larvae; and the caddis *Goera pilosa*, are listed as the commonest animals. Various other Trichoptera and several Ephemeroptera were also present in fair numbers, but, as detailed species lists were not possible, exact comparison with the Tees cannot be made. It will be noted that in this, an example of a hard-water river, *Gammarus* and Mollusca predominate in the fauna.

Six species of *Simulium* were recorded. None of them were taken in the Tees, but three, *S. equinum*, *S. ornatum*, and *S. aureum*, were found in the River Skerne. The other three were *S. argyreatum*, *S. venustum* and *S. salopiense*.

At the most polluted station of the Avon 96% of the fauna was composed of Chironomids, Tubificids, Lumbriculids, *Asellus*, and the leeches *Herpobdella octoculata* and *Helobdella stagnalis*. This is a fauna of moderate pollution only.

The Lark is also a calcareous river but it represents a stage in development beyond the Bristol Avon. It is more uniformly sluggish, more silted (most of the bottom being of mud), and more heavily overgrown with plants. Among the weeds and under stones *Gammarus* is by far the most abundant organism. Other common stone- and weed-dwelling animals are the bladder snail, *Physa fontinalis*, the inevitable Chironomidae, mayflies of the genus *Baëtis*, and two species of leech. Corixidae, the small water-boatmen, occur in the weeds. Three species of *Simulium* are recorded; two, *S. ornatum* and *S. aureum*, occur in the River Avon and the River Skerne, but the third, *S. angustitarsis*, has not been encountered before in these pages.

In the mud of the River Lark occur all the typical mud-dwelling forms, *Sphaerium corneum*, a pea-mussel, being particularly abundant. *Asellus* and the leech *Herpobdella atomaria* are also numerous in the muddy regions. But in polluted mud, near a beet-sugar factory, the fauna is reduced to Chironomids and the worms *Tubifex* and *Limnodrilus*.

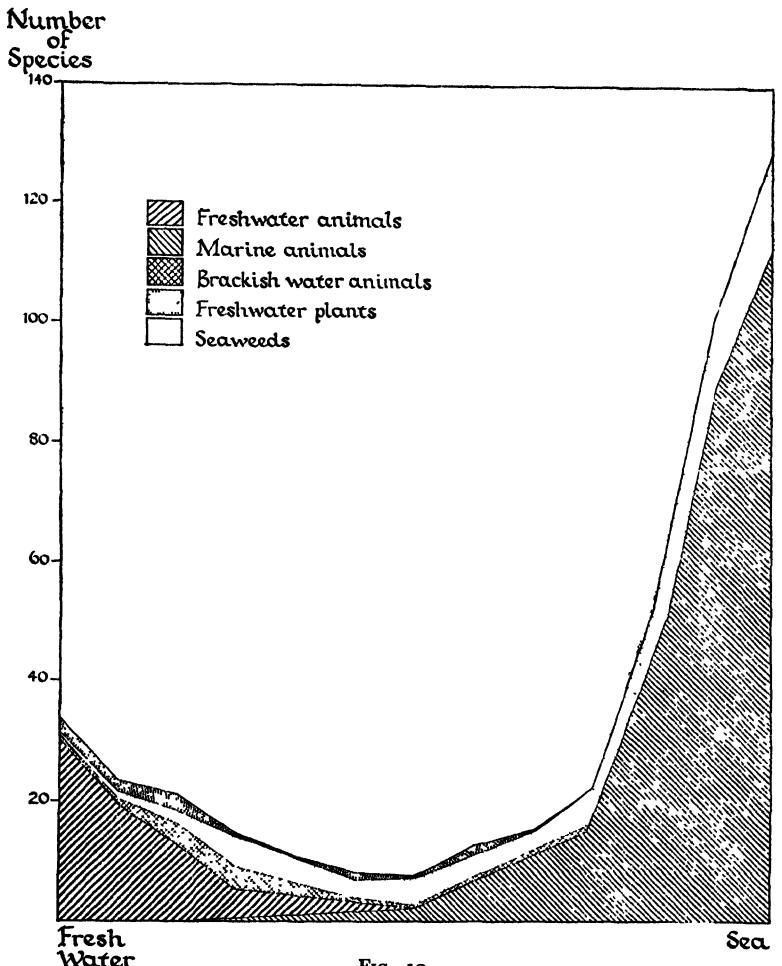


FIG. 13
Fauna of the Tees estuary

None of these three rivers had a true animal plankton, and it seemed that the phytoplankton was chiefly recruited from attached species which had been dislodged.

Before we leave running water we may notice another estuary of a rather different type, for one of its main inhabitants illustrates a point which comes up for discussion later. It is the estuary of a small stream flowing over a pebbly beach in Wembury Bay near Plymouth. Pantin (1931) writes that just above the level reached by the highest tides there is a pool and this contains a fauna typical of fresh water, apart from one estuarine animal, the snail *Hydrobia ventrosa*. Between roughly the level of high-water spring tides and high-water neap tides

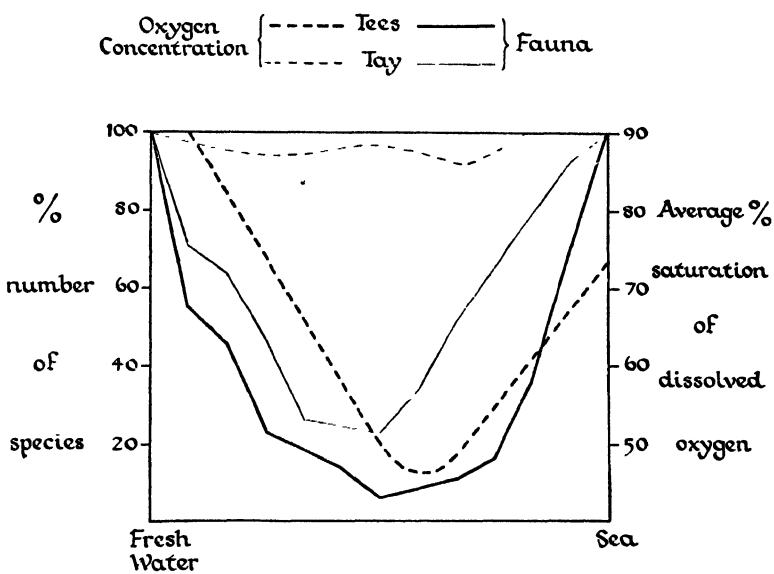


FIG. 14
Fauna and dissolved oxygen in the estuaries of the Rivers Tees and Tay

there is a stretch where no animals were found, and Pantin refers to it as a "desert." Below the level of high-water neaps to a point about midway down the beach, where the shingle gives place to rock, there were only three animals, a flatworm *Procerodes* (*Gunda*) *ulvae*, a related creature which was not named, and a worm called *Protodrilus flavocapitatus*. In the rocky region they were joined by a few marine species and beyond the level of low-water neap tides they ceased to occur.

Finally there are ponds, difficult to describe from a faunistic point of view, as they are so diverse and have not been studied much. A few generalizations are permissible. The still conditions of the surface favour surface-dwelling forms, both plant and animal, and, where there is a rich supply of nutrient salts, surface plants, chiefly *Lemna* (duckweed), may cover the whole area, thereby setting up conditions unfavourable for rooted plants and adverse for many animals. In most ponds, plankton, swimmers, burrowers, and weed-dwelling animals are all well represented ; among each there are a certain number of species which are confined to ponds and do not occur in lakes. The fauna has a general resemblance to that of quiet parts of a lake, though swimming forms which must come to the surface for air tend to be more numerous in a pond than in any part of a lake.

Small bodies of water tend to be subject to greater vicissitudes than larger ones. Decomposition of plant remains in hot still weather, or under ice, may use up all the oxygen in what is normally a well-oxygenated pond, and instances of the annihilation of a fish population from this cause are recorded from time to time.

Cattle visiting a pond to drink may foul it with their dung and produce a degree of pollution unknown in lakes. In such ponds the water has the appearance of green soup owing to the presence of myriads of a flagellate alga, *Euglena*, and a certain association of Protozoa and Rotifera is characteristic. The water-bug, *Corixa lateralis*, is commonly present as well, often in enormous numbers, and a dense population of red Chironomid larvae occurs in the mud.

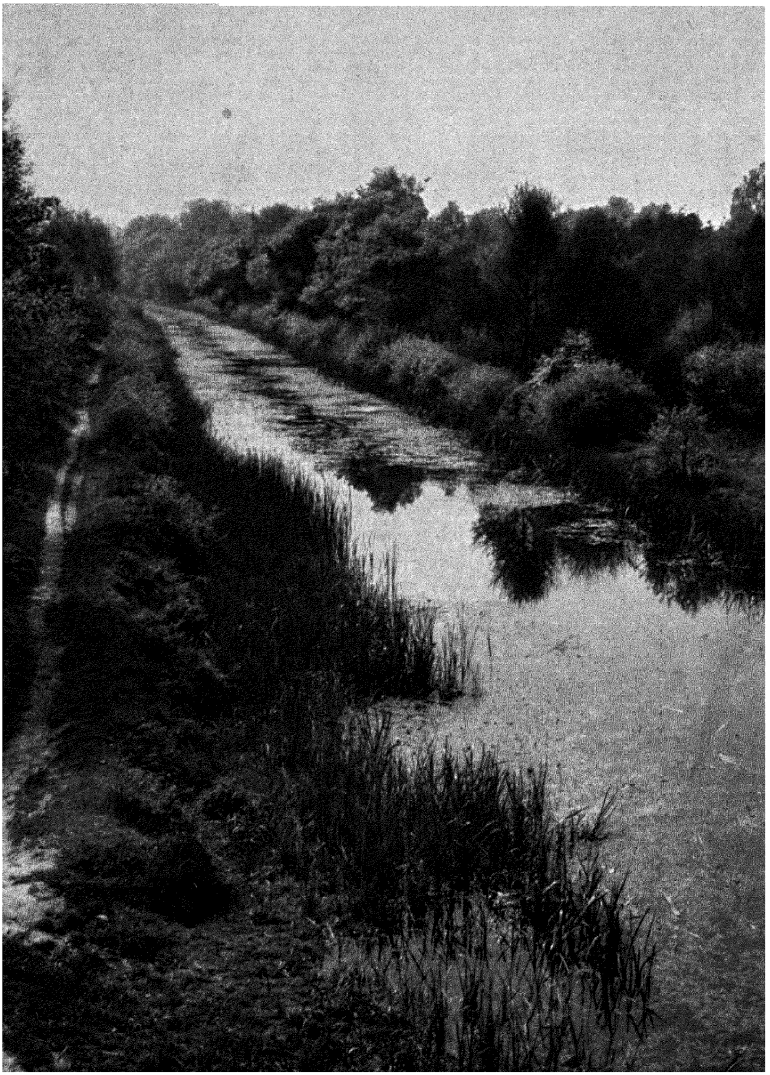
Some ponds dry up each year, and certain animals are found almost exclusively in such places. The fairy shrimp, *Cheirocephalus*, may occur in great numbers in small temporary pools while they hold water. It produces resting eggs which can withstand desiccation, and these lie dormant in the mud while the pond is dry, and proceed with development when it fills up. Certain mosquitos, notably those belonging to the genus *Aedes*, lay their eggs in early summer on damp ground in hollows which will be filled up with water during the winter and spring, and the eggs lie dormant until covered with water. Arctic regions, where pools form everywhere when the snow first melts because the ground beneath is still frozen, produce enormous numbers of these mosquitos.

Brackish-water ponds have attracted attention. Howes (1939) surveyed in 1934 and 1935 a creek which had been dammed at both



Robert Atkinson

Watercress bed St Mary Bourne, Hampshire April



John Markham

Disused canal Surrey May

ends so that it no longer had connection either with the river of which it was once a distributary, or with the sea. The salinity was about two-thirds that of sea-water, but the relative proportions of some of the salts were not the same as in the sea. He found about 50 species. Most were marine animals known to be able to live in slightly dilute sea-water. There was only one fresh-water animal, a beetle *Hydroporus planus*, but it was probably no more than a casual visitor, and there was no reason to believe that it bred in the creek. The rest was a characteristic brackish-water fauna ; most of the animals had marine affinities but there were four related to fresh-water species : *Phytia myosotis*, a snail, *Philhydrus bicolor*, a beetle, *Corixa selecta*, a water-boatman, and *Aedes detritus*, a mosquito. The last was rare, and scarcely to be expected in the open water of the creek, though it is abundant in brackish water in marshes and small pools.

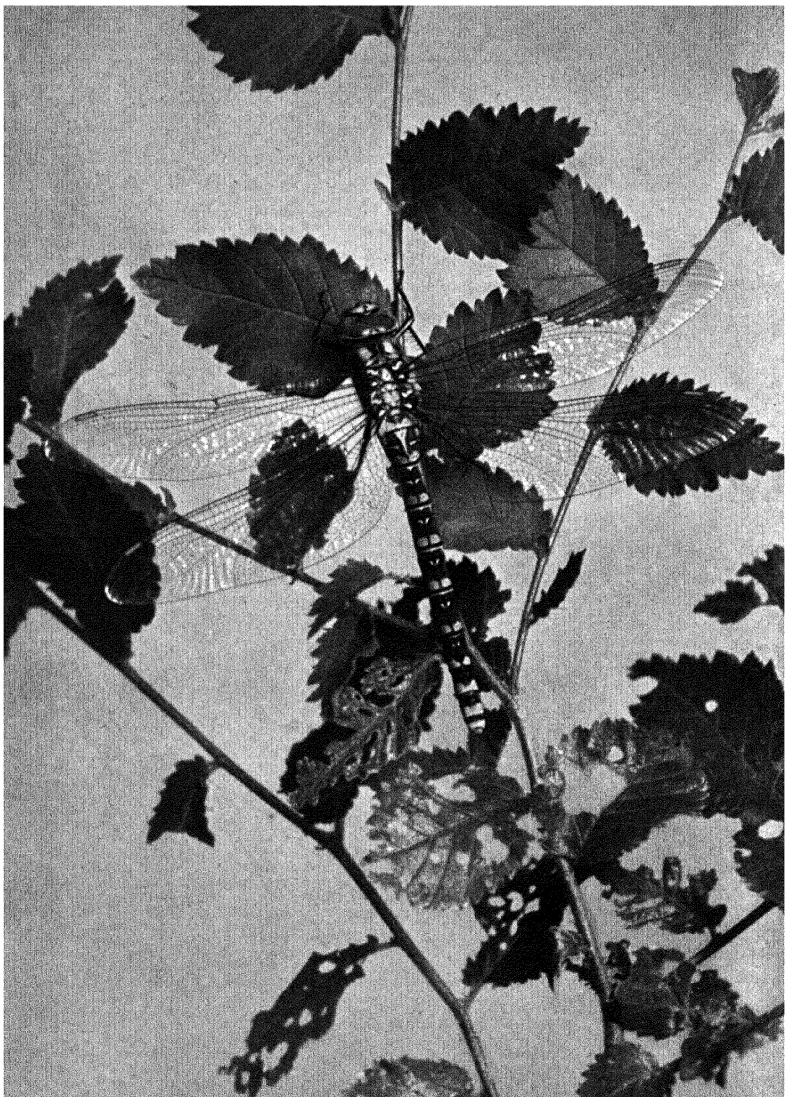
Nicol (1935) investigated a series of pools in a salt-marsh. The highest were reached only by the highest tides and the average salinity was about 3% that of sea water, though after an invasion by the tide the salinity would rise to half that of sea water. Six species of water-beetle usually found in fresh water were fairly constant inhabitants of these pools, but the rest of the fauna was typical of brackish water : four Crustacea, including *Gammarus duebeni*, one mosquito *Aedes detritus*, and one beetle. During periods of neap tides this fauna might be augmented by fresh-water species such as the mosquitos *Culex pipiens* and *Anopheles claviger*, and the pond-snail *Limnaea truncatula*, but these would not survive an inundation by the sea.

The rest of the pools were entered by most tides. There was considerable variation in the fauna according to the nature of the substratum and the amount of vegetation. The commonest animals were brackish-water species with marine affinities, but a few creatures also found abundantly in the sea were common.

In inland waters of high salinity two salt-marsh mosquitos, *Aedes detritus* and *Ae. caspius*, may be abundant, together with various other dipterous larvae belonging to families about which much less is known. Other brackish-water animals which have been taken in inland localities are the shrimps, *Gammarus chevreuxi* and *G. tigrinus* and the two water-boatmen, *Corixa lugubris* and *C. selecta*.

It has not been possible to write an even smoothly-flowing story, because the matter on which it is based is fragmentary and often unrelated. It is possible, as a central theme, to relate the fauna to the

amount of flow or wave action ; and at some levels down this series differences bound up with the hardness or softness of the water can be described, though not, in the present state of knowledge, explained. The effects of pollution have also been traced. But, beyond this, bare lists differing one from another are all that can be produced, and the differences cannot be linked up with any feature of the environment. The number of surveys of typical pieces of fresh water in Britain is very few. This is partly because the work is not easy. The investigator finds himself with specimens from many different groups, and it is only with the collaboration of a number of experts that a reliable species list can be produced. For a few groups neither an expert nor a modern handbook exists, and the immature stages of many insects can at present be named only by breeding out the adults. Some workers therefore maintain that a better line of approach is to take one group and, examining as many different habitats as possible, to find out the conditions under which each of the species belonging to it occurs. The results obtained by this approach are described in the next chapter.



S. Beaufoy

Dragonfly, *Aeshna cyanea*, female June

into two or more vice-counties. Most naturalists making regular records of captures use this scheme, but there are some variations. Uniformity will, it is to be hoped, be introduced by the forthcoming Ray Society publication defining and fixing the vice-county boundaries exactly. The usual practice, when making a map of the distribution of any species, is to black or mark in some other way each vice-county from which it has been recorded after the records have been examined critically and verified (Figs. 15a, b, c).

The vice-counties do not bear any relationship to natural regions such as chalk-down, fenland, etc. ; and it will be remarked that the blacking-in of a vice-county may mean that the species in question

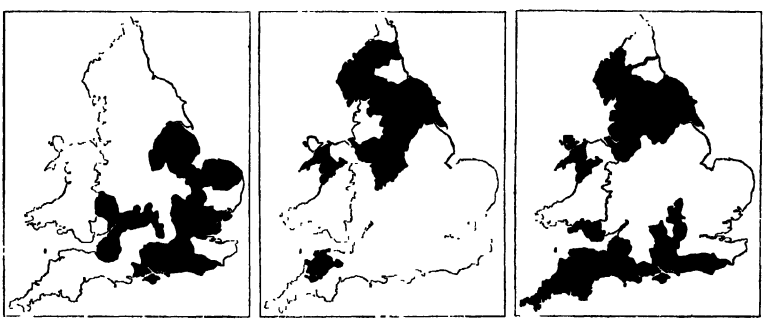


FIG. 15
Distribution maps of three British Corixids : a, *Micronecta scholtzi* ; b, *Corixa wollastoni* ; c, *Corixa scotti*

is common throughout the length and breadth of it, or merely that a single specimen has been recorded once. But, in spite of such departures from the ideal, any alternative scheme would involve considerable practical difficulties and also the discarding of many of the records which have been accumulating for the last hundred years or so. The ordinary ordnance survey maps are now issued with a national grid superimposed on them, and it is to be hoped that in future naturalists will adopt the habit of giving a grid reference to all their localities.

It is necessary to warn the reader again not to expect for any aquatic group information as complete as that which Ford was able to

give for the butterflies in the first volume of the NEW NATURALIST series. Two groups only of aquatic invertebrate animals, the molluscs and the beetles, have received detailed attention. Mollusc records are published by the Conchological Society in their journal, and they recognize no new vice-county record unless specimens are submitted for confirmation of the identification to one of their number who has been appointed to the post of Recorder. Maps are published, though the fresh-water naturalist will find it more convenient to refer to Boycott (1936) for the distribution maps and an account of the ecology of the species which interest him. The botanists have a similar system with appointed recorders to whom specimens are submitted. No beetle society exists, though the group is a popular one, but Professor F. Balfour-Browne (1940) has collected the records together and acted as a recorder. He has not, however, rejected all the records not confirmed by himself, but in his maps he shows them stippled whereas the rest are black.

A distribution map may give more information about the range of people interested in an organism than about the organism itself, but, when collecting has been fairly thorough, the map is of real value and conveys information which is an essential preliminary to ecological study. It is proposed now to illustrate distribution, not with the molluscs or the beetles, the two properly studied groups, but with the water-bugs, a group with which one of the authors is familiar. This makes it possible to illustrate at the same time the difficulties pertaining to a group for which records have not been systematically kept. The late Mr. E. C. Bedwell compiled from published notes and papers in entomological and other journals a list of county records for the British bugs (*Hemiptera-Heteroptera*) and it was edited after his death by Dr. A. M. Massee (Bedwell and Massee, 1945). For reasons which are not stated, but which may have been due to the nature of the material, records are by counties and not by vice-counties. Further, Scotland and Ireland are treated as whole units, and county distribution within them is ignored. But the most serious defect of the list is that there is no indication of what, if any, steps the authors took to check the reliability of the records of others. Most could doubtless be trusted to name their captures correctly, but some certainly could not. Separation of the sheep from the goats would, of course, be a highly invidious matter and one from which a compiler might well shrink.

However, with some personal knowledge, it is possible to extract from Bedwell and Massee's list sufficient accurate information about the distribution of water-bugs to illustrate the points which it is desired to make. Fig. 15a shows the counties in which the minute water-bug *Micronecta scholtzi* has been found. Professor R. Poisson (1938), who has monographed the sub-family to which this species belongs, gives its world distribution as Belgium, Holland, Germany, Hungary, Caucasia, Italy, Corsica, Spain, Portugal, Morocco, Tunisia, and Algeria. It has thus what is known as a Mediterranean distribution and presumably is favoured by a temperature which is high by European standards. Poisson notes that it occurs all over France but does not extend into the Alps, the Pyrenees, or the mountains of the central massif. In Britain it is confined to the south and east, that is the warmer half of England, and presumably its further spread has been checked by low temperature. The mapping of a distribution and its interpretation are, however, two different things, and a caveat must be entered here. South-east differs from north-west England in more than one important ecological feature; it is warmer on the average and definitely drier, and it is also that part of England which contains most of the soft calcareous rocks, the hard lime-poor ones being confined to the north and west. However, since *M. scholtzi* lives in water, it is unlikely to be affected by the humidity of the air, there is no evidence that it is a calciphile, and so the temperature explanation of its distribution is the most probable and may, for the time being at any rate, be allowed to stand.

Fig. 15b shows a different distribution; *Corixa wollastoni* is confined to the north and west. Unfortunately its distribution in England only can be shown; it is probably widespread throughout Scotland but details are not available. In England it is a species of high ground. In the Lake District, for example, it may be taken in almost any peat pool above 1,500 feet, but lower down it is hardly ever encountered. Such peat pools contain species in other groups with a similar distribution, examples being the beetles *Hydroporus morio* and *Agabus arcticus*, and the pea-mussel *Pisidium conventus*. *C. wollastoni* occurs on the Pennines and the mountains of Wales (in which country further collecting will assuredly reveal it to be more widespread than is shown in Fig. 15b), and extends as far south as Dartmoor. Mr. E. S. Brown (1945), in a paper on the fauna of the Faeroe Islands, records the world distribution outside Britain of *C. wollastoni* as Norway,

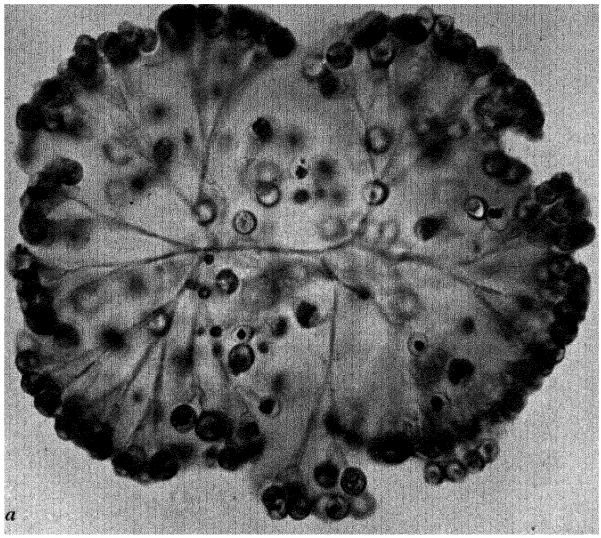
Sweden, and Finland with doubtful records from Holland and America. The only other species in the Faeroes, *Corixa carinata*, has been taken in Iceland, Norway, Sweden, Finland, Lappland, West Russia, Caucasia, the Alps, and the Pyrenees ; its British distribution cannot be mapped, as the records are inextricably confused with those of a closely related species. These two are northern in distribution and confined to high latitudes, or to high altitudes when they occur farther south. Again, in the absence of experimental evidence, it is to be presumed that temperature plays an important part in this distribution.

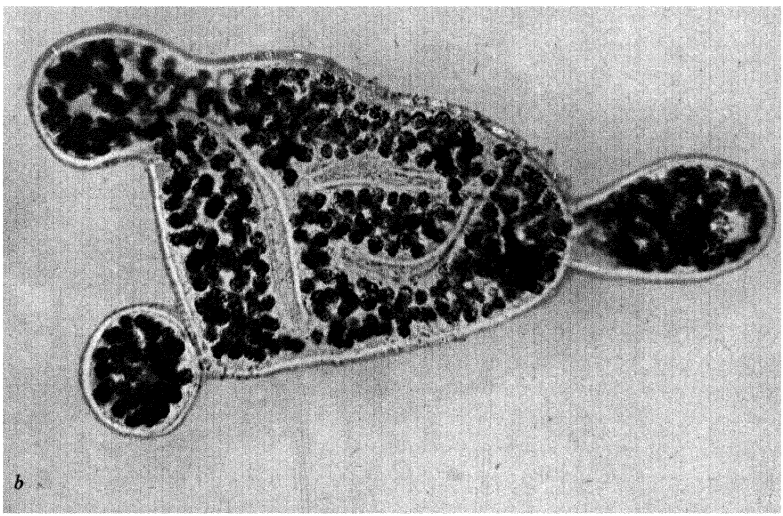
Fig. 15c shows a different type of distribution. *Corixa scotti*, like *C. wollastoni*, is undoubtedly widespread in Scotland but data for its county distribution are available only for England. It, too, is confined to the north and west, but it is not a northern species in Europe and it is not restricted to high ground. It is, for example, the most abundant species in Little Sea on South Haven Peninsula, Dorset. *C. scotti* is essentially a species of heath and moorland ; either it cannot live in calcareous waters or it cannot maintain itself there in competition with other species, and this is why it is confined to the south and west.

It is now time to discuss some group where the limitation of range by temperature is a proven fact and not merely a probable hypothesis. The stream-dwelling planarians or flatworms provide a clear illustration. *Planaria alpina* and *Polycelis cornuta* are two species which in Britain are found only in cold springs and the streams which flow from them. In a rapidly flowing stream *Planaria alpina* extends from the spring down to a point where the temperature is about 13° Centigrade (=55° Fahrenheit) ; beyond, it is replaced by *Po. cornuta*, which extends down to a point where the temperature is 16° to 17° Centigrade. No purely stream-dwelling flatworms are found at higher temperatures than this in Britain. The temperature relationship described is found all over Europe in torrential streams. As the low temperature region moves downstream in winter, the flatworms move with it, and it may happen that they reach a lake shore. If this is stony, they will live on it for a time, but in Britain they do not become permanently established in lakes because summer temperatures are too high. In Alpine lakes, however, these flatworms have been recorded as permanent members of the fauna of wave-washed shores.

These observations strongly suggest that temperature is a limiting factor in the distribution of *Pl. alpina* and *Po. cornuta*. The former has

PLATE XXIII



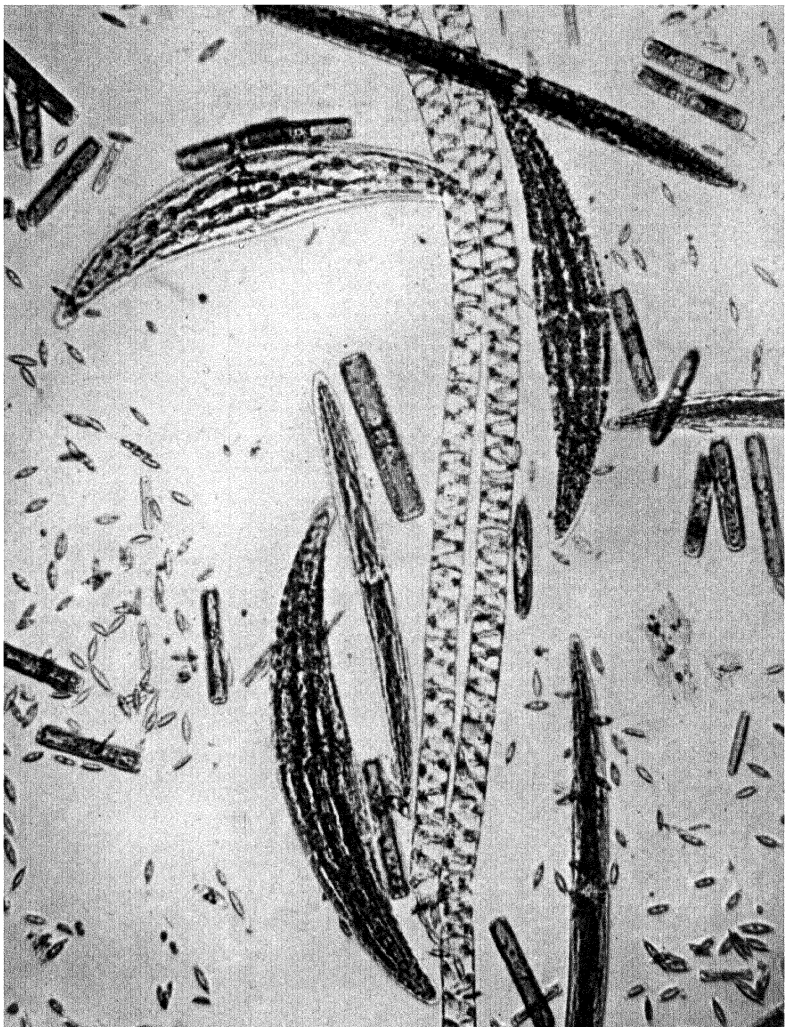


Photographs by H. M. Canter

a. A green alga, *Dictyosphaerium pulchellum* (×500). *b*. A blue-green alga, *Microcystis aeruginosa*, the cells are held together by mucilage (×400)

PLANKTONIC ALGAE

PLATE XXIV



H. M. Canter

A filamentous green alga, *Spirogyra* sp., a desmid, *Closterium* sp. (the large curved tapering cells), a diatom, *Pinnularia* sp. (the medium-sized oblong cells); a diatom, *Navicula* sp. (the small spindle-shaped cells) (×170)

ALGAE FROM THE BOTTOM OF A POND

been studied in the laboratory. The findings are that it behaves differently above and below a temperature of 12° C. When kept above this temperature its rate of movement is faster, and it behaves all the time in the same way as it behaves at lower temperatures when stimulated by something unfavourable in the environment. Rapid death does not ensue below a temperature of 27° to 28° C., but the animal will not survive more than a few weeks above 12° C. These experiments confirm what was a strong presumption from the field findings. Incidentally, 28° C. is just over 82° F., a temperature which an open-air swimming bath may reach in a hot spell and at which it is definitely " warm," but it is well below mammalian blood-heat, which is about or a little below the temperature at which many fresh-water animals die. 12° C. is just under 54° F., and at this temperature only the heartiest bathers enter the water.

It will be noted that there is a small discrepancy between the laboratory and the field findings, and *Pl. alpina* occurs in nature in warmer water than it should according to the laboratory findings. The explanation is probably that, whereas the laboratory work is based on detailed observations at frequent intervals, the field work is not. To determine exactly the limits of a species in nature it would be necessary to make regular temperature measurements both by day and by night over a long period. This has not been done, but the omission does not affect the general argument.

Pl. alpina normally reproduces at a temperature of 10° C. or less. It has been described as being " physiologically adapted " to cold water, but whether the word " adapted " is a happy choice is a matter of opinion. The result of the peculiar physiological requirements of the animal is that it is restricted to a certain type of environment, and there are those who prefer to refer to it as " physiologically restricted." It seems likely that in the Ice Age *Pl. alpina* was much more widespread, and it is often referred to as an " Ice Age Relict."

It will be convenient at this point to continue with the ecology of stream-dwelling flatworms and, for reasons which will be apparent presently, to forsake the British in favour of two Balkan species, *Planaria montenegrina* and *Pl. gonocephala*, which bear to each other a relationship similar to that of *Pl. alpina* and *Po. cornuta*. In most streams both species occur but Beauchamp and Ullyott (1932), in the course of an extensive search, came across a few streams where only one species was present. When *Pl. montenegrina* was alone, it extended from

the spring down to a point where the temperature was 16° to 17° C. When *Pl. gonocephala* occurred alone its range also went upstream to the spring, but downstream it reached a point where the temperature was 21° to 23° C. When the two occurred together *Pl. montenegrina* occupied the upper and *Pl. gonocephala* the lower reaches, and there was little overlap where they met. The temperature at this point was 13° to 14° C., so that when the two species came into competition the range of each was curtailed. This competition or mutual exclusion between two species with a similar way of life is an important factor in ecology ; it is also rather a mysterious factor. The flatworms, for example, do not possess any offensive organs and there can be no question of one species driving the other away. It appears that a slight change in the environment favours one species to the disadvantage of and very often to the complete exclusion of the other.

It will have been noted that, whenever the ecology of *Pl. alpina* and *Po. cornuta* was referred to earlier, torrential conditions were always mentioned. Cold springs where the flow is less rapid and there is some deposition of fine soil particles, are inhabited by both species and sometimes by *Po. cornuta* alone. Either rate of flow, or nature of the substratum—it is difficult to analyse their effects separately—is, therefore, a factor in the ecology of these two species in addition to temperature.

Temperature as an ecological factor rarely acts so simply as it does on flatworms. Some species may be limited in distribution because the temperature in certain years reaches a high or low value which is lethal to them at a certain stage of development ; the destruction of the forming fruit of cultivated fruit trees by a late frost may be cited as an illustration. The temperature may be at the critical point for a few hours only and the phenomenon will not be apparent from an isotherm map. Professor G. Evelyn Hutchinson has suggested that lowland species are absent from high altitudes because the average temperature during the summer is not high enough to enable them to complete their development.

Some recent work has shown that stream-dwelling nymphs of *Baëtis* and other mayfly genera die at a lower temperature and a higher oxygen concentration than the pond-dwelling nymphs of *Cloëon*. These results, though having intrinsic interest, are of little ecological value, because there has never been a detailed study of the range of habitat occupied by the living nymphs. If temperature and oxygen concentra-

View from here.

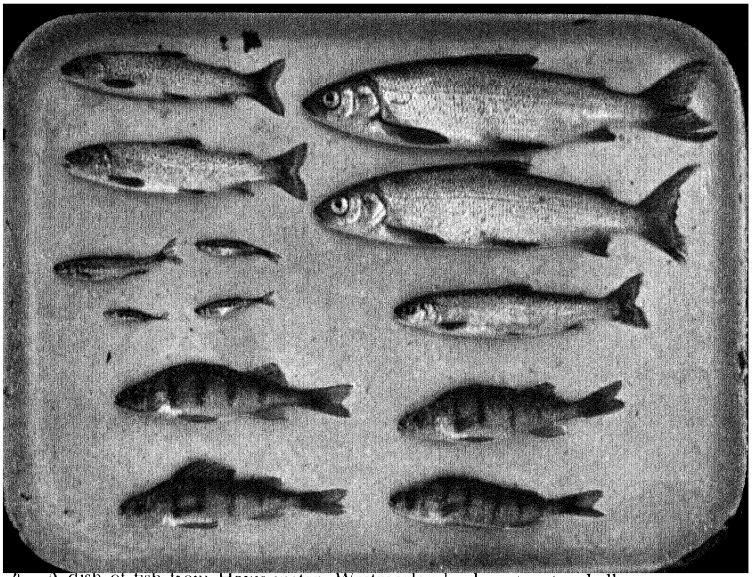
View from here.

b Damsel-fly, *Pyrrhosoma nymphula*, male May

S. Beaufoy



a. Male char from Windermere



b A dish of fish from Haweswater, Westmorland: char, trout, schelly, minnows and perch

tion are the main factors determining where *Baëtis* occurs, it should be found in cold well-oxygenated ponds, just as *Planaria alpina* extends its range to stagnant water that is cold enough ; but no such records are known to the authors, and the physiologists whose work is under discussion do not quote any.

There is one final class of organism with a restricted distribution. During the Ice Age the land, in certain places, the Scandinavian peninsula being the classic example, was weighed down by the load of ice. When the ice melted at lower levels, the sea came in and covered areas which later became dry land as the ice cap gradually disappeared and the land, relieved of the weight, rose. Sea-water was trapped in depressions and with it a sample of the marine fauna and flora. These lakes lost their salinity in the course of time as fresh-water streams, fed first by melting ice and later by rainfall, found their way to them. Most of the marine animals died but a few, possessed of greater powers of adaptability than others, survived and exist to this day. They have changed as time has gone by and are now distinct species, but they are obviously related to existing marine forms and have but slight affinity with the rest of the fresh-water fauna. Two well-known examples of these marine relicts are a small shrimp, *Mysis relicta*, and a copepod, *Limnocalanus macrurus*.

Both occur in Ennerdale Water. As far as is known they do not occur in any other Lake District lake, though only Windermere has been investigated with a thoroughness sufficient to warrant a categorical statement. It is not easy to see how this distribution came about, and it could not have been through simple submergence in the way just described. There is no evidence that the ice of the Ice Age depressed the Lake District the necessary 368 feet to bring Ennerdale Water to sea level, and, in any case, had it done so, all the other lakes would have been submerged as well. One explanation is that, at a time when Ennerdale Water was dammed up by an ice barrier and was larger than it is to-day, a fresh advance of ice pushed up part of the Irish Sea and forced it into the lake. At that time valleys to the south were free of ice, and valleys to the north were frozen solid so that they did not retain this sea-water and its fauna, if it was ever forced into them.

However, the present problem is not how *Mysis* and *Limnocalanus* originally got into Ennerdale but why, in the intervening twelve thousand years or so, they have not spread to the other lakes. Certainly

conditions in the other lakes are not identical, but it is improbable that two organisms which have managed to survive a change from sea-water to almost pure water are likely to be affected by the small differences, measurable in parts per million, which exist between the lakes to-day and which were probably smaller still in earlier times.

The most likely explanation is that these organisms have not an efficient means of dispersal. This is clearly a point which calls for close examination. Many fresh-water habitats are quite isolated, and the rest are connected only by running water, which is not a suitable habitat for many pond and lake-shore forms. Therefore, before the absence of any species from a given habitat is attributed to some unfavourable factor in the environment of that habitat, it is necessary to examine the possibility that the species is absent simply because it has failed to get there. Almost all the insects have a winged adult stage and dispersal from one habitat to another presents no difficulties, but the other groups cannot live out of water for long. Professor A. E. Boycott kept under observation for many years the snail fauna of some 170 ponds near his home, and 69 of these were what he describes as closed, that is they had no permanent surface inflow or outflow. He found that, on the average, each pond received a new species every nine years. He could only detect a new arrival when it was a species not already present in the pond, and so the rate at which snails were entering each pond from outside must have been several times greater than this. How it came about was a different problem to which Boycott was not prepared to supply the answer.

Also in his area was a reservoir which harboured certain species not found in any pond. He transferred a couple of these to a number of ponds. One soon died out, and evidently there was something in the pond environment which was unfavourable to it. The other, *Planorbis corneus*, the great ramshorn, throve in nearly every pond into which it was introduced, and Boycott concluded that its absence from ponds was due to its inability to reach them. His general conclusion was that an inefficient means of dispersal was an important ecological factor for a few species of aquatic molluscs but not for the majority.

Comparable observations for other groups are lacking, and this is a field where further exploration is much needed. But the impression is that, in general, Boycott's conclusions with snails are widely applicable. We conclude that the absence of any species from an old

well-established and apparently favourable locality is only rarely due to the fact that the species has not succeeded in reaching it.

How fresh-water organisms get from one piece of water to another is still rather mysterious. That many travel on birds' feet is indubitable, but it hardly seems likely that this means of transport is sufficient to account for all the traffic. Some have eggs or spores that can withstand drying-up.

This chapter started with a discussion on species with a restricted distribution, and digressed to consider temperature, competition, and means of dispersal as factors in ecology. Most British species, however, do not belong to a Mediterranean element which can just maintain itself in the south of the country, nor to an arctic-alpine element which is restricted to high ground in the north, nor to any special group such as the marine relicts. Most are widely distributed both on the continent and in Britain. Each one, as has already been stated, is limited to a certain range of habitat conditions and, of the various features operating to bring this about, those of a chemical nature may be taken first. A group which illustrates the sort of difference under discussion in this chapter is the mosquito genus *Aedes*. Wherever there are small hollows liable to contain water for fairly long periods, but which dry up during hot spells in summer, *Aedes* larvae are likely to be found. In woodlands the species is *Ae. cantans*, in fenland *Ae. cinereus* and *Ae. rusticus*, on heaths and moors *Ae. punctor*, and in marshes behind sea-walls and other places likely to contain brackish water the species are *Ae. detritus* and *Ae. caspius*.

Beadle (1939) has made a study of the ecology and physiology of *Aedes detritus*. He found it in natural breeding-places with salinity ranging from 10% to 122% of that of sea-water. In the laboratory the salt concentration in the body fluid of larvae was found to change with changes in the surrounding solution, but not to the same extent; the animal can exert some control, and its body fluid concentration bears to the concentration of the medium outside the same sort of relationship as the course of the back wheel of a bicycle bears to the front wheel. But the workings of the body of *Ae. detritus* are not hampered by quite wide changes in the composition of the body fluid, and this is an important difference between it and fresh-water species, which die if the salt concentration alters only slightly. Presumably it is this ability which enables *Ae. detritus* to inhabit brackish water and to live in a wide range of salinities. Other species are apparently more efficient at

maintaining a higher concentration of salts in the body fluid when in a medium with a low concentration, but they cannot survive in concentrations above a relatively low limit. When in a solution of high concentration, *Ae. detritus* apparently keeps its body fluid at a lower concentration by excreting salts.

Similarly the flatworm, *Procerodes* (*Gunda*) *ulvae*, which inhabits the inter-tidal part of stony streams, is able to live in these difficult conditions because it can tolerate changes in the composition of its body fluid. It is able to damp down the fluctuations so that they are never as great as in the surrounding water, but only when there is a good supply of calcium in the water (Pantin, 1931).

Pollution with sewage has a marked effect on the fauna, and some of the associations found in polluted rivers and ponds have been described in Chapters 7 and 14 (pp. 113 and 225). Little is known about how pollution exerts its effects. There may be a direct relation between the absence of some species and the poor oxygen concentration which pollution entails. Possibly the greater the pollution, and therefore the lower the oxygen concentration, the more important is this relationship. But how important it is in comparison with positive correlations has not been investigated.

Other differences in chemical content are much smaller than those of salinity and of pollution referred to above. The most important chemical factor in unpolluted fresh water, as far as is known at present, is the concentration of calcium. Botanists have long recognized that of the land-plants some can be classed as calciphile or lime-loving and others as calcifuge or lime-shunning. Well-known examples of the latter are bracken and bogmoss. Bracken, for example, which grows with such unwanted luxuriance on poor pastureland, is only with difficulty cultivated in the calcareous soil of the Cambridge Botanic Garden. Probably many animals can be assigned to the same two categories. Boycott recognizes a number of calciphile species of snail, and finds that the aquatic ones hardly ever occur in waters with less than twenty parts per million of calcium. A survey of the water-bug fauna of dew-ponds on the chalk-downs revealed that the three species common there were all rarities in the calcium-poor waters of the Lake District. Boycott is doubtful whether any species of mollusc can truly be called calcifuge though the pearl-mussel, *Margaritana margaritifera*, is a possible example. A number of species are found in lime-poor waters but they are not confined to such places, and Boycott believes

that their scarcity in localities richer in lime is due to the fact that they cannot compete with the calciphile species. *Corixa scotti*, which has already been discussed, is comparable.

Though a great many analyses of other chemical factors have been carried out, the number of positive correlations discovered has been few. That different species of algae flourish best in waters with different proportions of simple dissolved substances has already been mentioned, but similar relationships in the animal kingdom have rarely been demonstrated. Recently, however, Savage (1939) has kept under observation in an area near London a number of ponds to which frogs repair in the spring to breed. He finds that the ponds with more than the average amount of potassium are visited by more frogs than the rest, and the difference is statistically significant. He suggests that, owing to a different flora, the potassium-rich ponds may smell different from the others, and that the frogs may recognize this difference.

Oxygen as an ecological factor is difficult to evaluate, for it is closely bound up with flow, vegetation, and amount of organic matter. In eutrophic lakes, where the hypolimnion becomes depleted of oxygen in the summer, certain species are not found as deep as in oligotrophic lakes, and it is likely that oxygen concentration is the limiting factor. Other correlations are less clear and reference may be made to the work on *Baëtis* nymphs discussed on p. 128.

So far only inorganic substances have been considered. Organic substances possibly play a much more important part in ecology but, unfortunately, little is known about them and their role. The usual methods of analysis depend on the amount of oxygen which the organic matter will take up on combustion, or from an oxidizing substance in solution such as potassium permanganate. This gives an indication of the total amount of organic matter present but reveals nothing whatever about the different organic compounds.

A great deal of work on mosquitos indicates that the female seeking a place to lay eggs is attracted to water with a particular kind of smell, though no conclusive demonstration of this has yet been made. There are, as already mentioned, in England three species of mosquito of which the larvae are found only in rain-filled rot-holes in trees. One is rare and the other two are to be found in almost every tree-hole. The number of records of any of the three breeding in any other sort of place are extremely few, and the number of records of other species

breeding in tree-holes are even fewer. Many tree-holes are in a cavity with a small hole as the only means of access, and offer rather peculiar physical conditions; but this is not true of all, for some are in the stump of a tree which has been cut down and are no more enclosed and shaded than any other small body of water. It is unlikely, therefore, that physical conditions are of paramount importance in attracting the tree-hole-breeding species. The most plausible explanation, in the light of present knowledge, is that the mosquitos are attracted by some specific organic substance which is present in water contained in a tree cavity and not in other fresh-water localities.

In an earlier chapter (p. 105) a succession of plant species in the shallow-water region of a lake with increasing organic matter was described. In Lake District lakes different species of the water-bug family Corixidae are found on bottoms with a different percentage of organic matter (Macan, 1938). On stony, gravelly, or sandy bottoms where the percentage of organic matter does not amount to more than 10%, the minute *Micronecta poweri* occurs. Where conditions are slightly more sheltered but the bottom is no more organic, *Corixa striata* is found as well. Where there is between 10% and 40% of organic matter *M. poweri* is absent, and *C. striata* is joined by *C. fossarum* and *C. distincta*. From this point a bifurcation in the succession is apparent. Where there is silting and *Phragmites* persists, ultimately to give rise to *Salix-Phragmites* swamp, *C. fossarum* becomes the common species and eventually, when swamp conditions are reached, is replaced by *C. sahlbergi*. Where there is little or no silting and *Phragmites* is replaced by sedge (*Carex*) and then bogmoss (*Sphagnum*), *C. distincta* becomes the common species and is then replaced by *C. scotti*, which in its turn gives way to *C. castanea*.

Figs. 16 and 17 present some of the evidence on which these statements are based. Fig. 16 summarizes the results of extensive observations in Windermere, and shows how the composition of the population changes as the percentage of organic matter in the soil increases; Fig. 17 is based on a smaller series of observations in a Lake District tarn. No analyses of the mud were made, but the nature of the vegetation gives an indication of the nature of the soil. In Windermere, where most of the bottom in shallow water is stony, gravelly, or sandy, and soils with a high percentage of organic matter are confined to a few places, *C. striata*, the species typical of an inorganic substratum, predominates and is found at nearly every station. In

contrast, in the tarn, where most of the soil is peaty and organic, *C. scotti* is the species found in almost every catch. In Windermere the succession nowhere reaches a stage where *C. castanea* comes in;

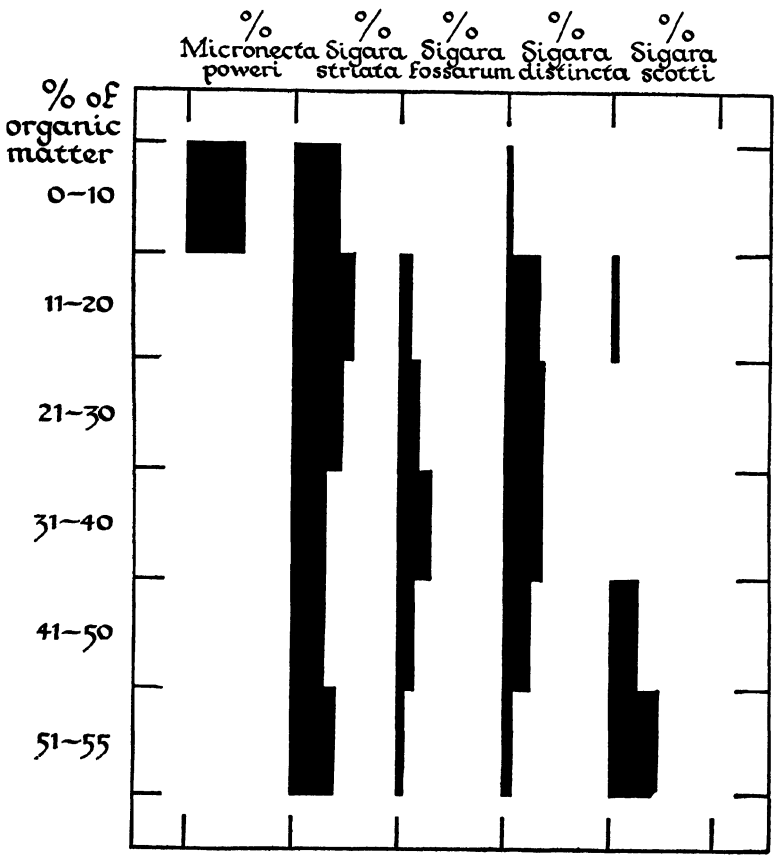


FIG. 16
Succession of Corixid species with increasing percentage of organic matter in the soil of Windermere.

nor does the tarn span the whole series, though it is the first and not the last member which it lacks. *C. sahlbergi* occurs in such places as the fen at the head of Esthwaite, already described, and in the similar

conditions where the outflow from Blelham Lake flows into Windermere.

These bugs do not feed by sucking plant or animal juices after the manner of nearly all the other members of the order, but sweep up small particles from the bottom, rather like a vacuum cleaner. Presumably the occurrence of each species is related to the nature of the bottom and not to the vegetation directly, and the plant succession is parallel with and not antecedent to the bug succession. Little is

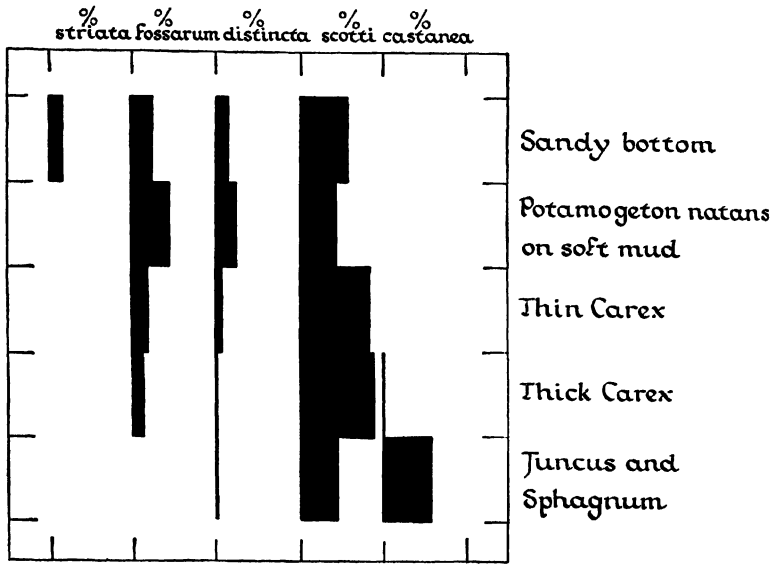


FIG. 17
Succession of Corixid species in Wise Een Tarn

known about the nature of the relationship. Popham (1943) has recently shown that in several species the intensity of pigmentation may vary within rather wide limits and is influenced by the background on which the young develop. In nature specimens are only rarely found on a bottom with which they do not harmonize in colour intensity, and, if they are placed on such a bottom in captivity, they appear ill at ease and may attempt to fly away. Furthermore, if fish be present, they devour corixids which do not match the background in greater

numbers than those which do. These observations, however, do not provide a complete explanation of corixid distribution, because there may be two bottoms of the same colour intensity but different nature, e.g. silted or unsilted, and they will be inhabited by different species of water-bugs.

It would, to quote the words of Professor Boycott, " be unconventional beyond the bounds of propriety to make no mention of hydrogen-ion concentration." It is commonly denoted by the symbol pH. At pH 7 a substance is neutral. Below pH 7 hydrogen ions are in excess of hydroxyl ions and conditions are acid, and above pH 7 the reverse obtains and conditions are alkaline. pH at one time enjoyed a great vogue among ecologists, partly because it is very easy to measure and a reading can be obtained in the field by mixing a drop of " indicator " with a little of the water to be tested and matching the resulting colour with a set of standard tubes. Its popularity was enhanced by a certain worker who discovered a tree-hole with a pH of 4·5, a degree of acidity which the general run of fresh-water habitats rarely exceed. As a result of some not very critical experiments he reached the conclusion that the tree-hole-inhabiting species of mosquito were unable to survive except in an acid medium. Shortly after the publication of these results, two widely read text-books were written, and both referred to them as an example of pH as an ecological factor. About this time Professor D. Keilin started observations on a tree-hole near his laboratory in Cambridge. This had a pH of 9·5, a value on the alkaline side which few ordinary fresh-water habitats exceed. Over a period of ten years Keilin (1927) found that all three species of tree-hole-breeding mosquito flourished in it. But there was no timely text-book to bring this piece of work to general notice.

An alkaline pH usually indicates a fairly high concentration of calcium, but the alkalinity may be due to other substances such as magnesium. An acid pH indicates a low concentration of these substances. But, in water where there is very little in solution, pH may vary considerably according to whether the plants are producing oxygen, which they do in daylight, or carbon dioxide, which they do at low light intensities. pH, therefore, gives only a rough indication of conditions obtaining in a body of water and its importance in ecology is not as great as was formerly thought.

A female about to lay eggs may react to some simple physical

feature of the environment. *Anopheles culicifacies*, a carrier of malaria in west and south India, illustrates this ; the example is so striking that it is worth describing here, although the species does not live in Britain. Workers had known for a long time that this mosquito breeds in ricefields when the rice is small, but disappears when the rice plants reach a height of about a foot. Detailed chemical and other investigations failed to reveal any change which would explain why. Eventually two workers managed to observe the female laying her eggs, a difficult feat since mosquitos oviposit at night ; they found that this species, unlike all the others investigated, which alight on the water to lay their eggs, flew a tortuous course over the breeding-place and dropped her eggs from the air. Any obstruction rising out of the water, such as rice plants, makes this flight impossible and so prevents egg-laying. The observers were able to bring the appearance of eggs in an experimental pond to an end by inserting all over it glass rods which projected about a foot above the water surface.

A less striking, though instructive, example may be drawn from mosquitos at home. Two workers found that six ponds which they were investigating could be divided into two groups, according to the mosquito fauna. Detailed chemical analyses and an exhaustive study of the algae were made, and the data compiled are most valuable, because small ponds have been neglected by fresh-water biologists. But the workers did not find what they were looking for—some chemical or botanical factor which would correlate with the ecology of the mosquitos. Quite incidentally, in one of their papers, they mention that the ponds of one group were perennial, and those of the other group dried up during the summer, but they attributed no particular significance to this phenomenon. It was actually the clue they were seeking, for the permanent ponds were inhabited by species which lay their eggs on standing water, and the temporary ponds by species which oviposit on damp ground.

Of the British water-boatmen, *Notonecta maculata* glues its eggs to the surface of some solid object such as a log, a stone, or a concrete wall, and the other species insert theirs in plant tissues. Probably this is why *N. maculata* abounds in concrete tanks and similar places and is often the only species present, but is less numerous in weedy ponds where the other species predominate.

Captain Diver, whose survey of South Haven Peninsula between Bournemouth and Studland in Dorset is one of the important modern

contributions to ecology, has observed that adults of different species of dragon-flies and hover-flies, all of which are aquatic in their immature stages, haunt different types of landscape. One will hawk up and down woodland glades, another in more open conditions where however there are occasional islands of trees or shrubs, and a third over an even sward of vegetation. If suitable conditions are not present, adults will not be present, and the result may be that larvae are absent from quite suitable habitats. This is a good example showing the importance of observing exactly what animals do in their wild state, a branch of study rather fallen into disfavour among professional scientists, and among naturalists as well, since the days of Fabre, Réaumur, and Swammerdam, though the ornithologists should be exempted from this generalization. When it revives, interesting advances in ecology are likely.

CHAPTER 9

FOOD CHAINS AND PRODUCTIVITY

PREVIOUS chapters have been concerned with the different kinds of animals in a habitat ; this one is concerned with the total number or, where possible, the total weight, regardless of the species present.

First it is necessary to describe the food-chains in rather more detail than has been done in previous pages. Of the surface-dwellers, both the bugs and the beetles live almost entirely on dead or disabled land animals which fall on to the surface of the water. The whirligig-beetles, gyrating upon the surface of the water, are apparently seeking food. If some land creature fall upon the surface of the water and lie there struggling, a quiescent group of whirligigs will suddenly start to move, and soon one of them will find it. The successful individual will continue to whirl around while devouring the morsel as quickly as possible. One is tempted to suppose that it does this in order that the others shall not suspect that it has found the object which has excited them all. The surface-dwellers are very rarely found in the stomachs of fish and there is nothing in the water which preys on them to any extent. In Windermere in August trout are feeding largely on land animals which have come to grief on the surface, so that they are to some extent in competition with the surface-dwellers. These also enter into the general scheme when they die and sink to the bottom of the water but, as the surface is so small compared with the volume of even quite a small pond, their contribution is of little significance.

In the open water the primary producers are the algae of the phytoplankton. They can utilize the energy emanating from the sun to build up substances of the sugar and starch type from carbon dioxide and water. Given phosphorus, nitrogen, and some other

substances, they can also build up proteins. The animals cannot make use of solar energy in this way and are dependent on plants for the material out of which they build their bodies, reproduce, and obtain the energy used up by the activities of life.

It is likely that the larger algae are not eaten extensively by animals, but the smaller ones are devoured by most of the planktonic crustaceans and by rotifers. These creatures probably also feed on particulate matter, some, or occasionally much, of which is derived from debris washed into the lake. Possibly they also feed on organic matter in solution. That this plentiful source of food is exploited by the zooplankton was first postulated by a marine biologist, Putter. It was shown, however, that his theory was erected on an inaccurate basis of fact and the whole idea came into considerable disrepute. The question is still unsettled. But Juday (undated) has shown that the amount of organic matter dissolved in a soft-water lake was a little greater than that in suspension and in the bodies of planktonic organisms put together, and in two hard-water lakes it was several times the amount. There is an a priori likelihood that this rich source of food is utilized.

A few of the planktonic Crustacea and the phantom larva, *Chaoborus* (Plate XIVc, p. 83), are carnivorous and live on other members of the plankton community.

In Windermere char feed on the zooplankton and on little else all through their lives, though at spawning time they have the habit of eating each other's eggs. In some lakes trout of all ages also make plankton their staple diet, though this is exceptional. Very young perch feed on the plankton until they reach a length of about six inches. Minnows also exploit this source of food, but, as they do not move far away from the edge of the lake, the inroads which they make upon it cannot be very great.

There is a cycle within this cycle in the open water but at present little is known about it. When planktonic organisms die they undergo at least some decay in the water, and give rise to both particulate and dissolved organic matter. It is probable that bacteria are the most important agents in this process, though the breakdown of the hard parts of Crustacea is brought about mainly by fungi; but the exploration of this field has only just started. Bacteria are a source of food for some of the Protozoa, and both they and the Protozoa are eaten by the Crustacea.

Much of the dead plankton falls to the bottom, where part is decomposed by bacterial action and part is devoured by the animals which dwell there. The bivalve molluscs have rows of minute lashing threadlike processes known as cilia on their gills, which are very large. These cilia keep a current of water passing over the gills, and fine particles in suspension are trapped and conveyed to the mouth in a stream of mucus. The worms probably feed like their more familiar terrestrial relatives by ingesting mud and digesting out of it anything which is digestible. No general statement can be made about the Chironomid larvae, for there are so many different kinds, but one feeding technique has been observed both in species which make tunnels in plants and in species which live in their own tubes. The larva spins a net over the exit to the tube or tunnel. It then undulates its body and causes a current of water to flow through the net. Particles in suspension are strained out, and periodically the larva turns round and devours net and all. It respins its trap and the process starts again.

The bottom fauna as a whole feeds mainly on detritus but some of the forms are carnivorous and feed on other members of the community. The larva of *Sialis*, the alder-fly, is one example, and others are to be found among the worms and the Chironomids.

Some coarse fish grub readily on the bottom but in Windermere the bottom fauna is not, apparently, preyed on extensively by fish. Eel stomachs contain a fair proportion of *Pisidium*, and perch stomachs frequently contain larvae of *Sialis* and nymphs of *Ephemera*, the may-fly, both of which are probably obtained mainly in shallow water.

The food-chain in the region of attached plants is more complex and much less is known about it. Here also the planktonic algae play a part as primary producers, but most important are the rooted plants and the algae which grow both on them and on the rocks and stones. Some of the caddis larvae eat the leaves of pond-weeds and so do some of the snails, but on the whole the algal film seems to provide most of the food for the herbivorous animals dwelling in this habitat. Many of the snails, mayflies, and stoneflies scrape the algal felt off stones and other substrata, and minnows also subsist partly on an algal diet.

Carnivores abound in this part of the aquatic world and have various means whereby they secure their prey. The water-beetles of the family Dytiscidae, and the water-boatmen *Notonecta* and *Naucoris*

(Plate XIX, p. 112), are active and powerful swimmers which can, if needs be, overtake their prey by superior speed. The dragon-fly nymphs (Plate XVI, p. 95) and the water-scorpions (Plate XIX, p. 112), on the other hand, lie concealed and wait until some suitable piece of food swims unsuspectingly within range. The lowest part of an insect's feeding appendages, the labium, is usually a flat, relatively immovable plate well provided with sensory hairs but otherwise not modified to take any active part in the capture or mastication of food. In the dragon-fly nymph the labium is hinged and provided with two movable teeth, and can be projected some distance in front of the insect's head to seize any passing prey with the two teeth. If the intended victim is just out of reach of the fully extended labium, the dragon-fly nymph can make a short but rapid dart after it by ejecting water from a special contractile chamber in the hind part of the gut. The forelegs of a water-scorpion have an outer segment which fits into a groove in the inner segment like the blade of a pocket-knife folding into the handle, and with these limbs they can seize and hold in a powerful embrace any animal which comes within reach. Like nearly all bugs they have sucking mouthparts, and once the prey is secured by the forelegs it is impaled on the mouthparts and sucked dry.

The tiny fresh-water polyp, *Hydra*, hangs motionless from the leaf of a plant or other point of vantage, with long tentacles trailing in the water. Any small organism which blunders against these tentacles is harpooned by minute pointed and poisoned threads, which are shot out from special cells in the tentacles. Once secured and paralysed it is conveyed to the mouth by contractions of the tentacles and pushed into the inside of the body to be digested.

The leeches are also carnivorous. Most feed on small animals, molluscs being a favourite article of prey ; a few attack fish, and one is said to obtain blood from water-birds by entering the mouth or nostrils and fixing itself to the back of the throat. The medicinal leech, the only one which will attack man, is now very rare in the British Isles.

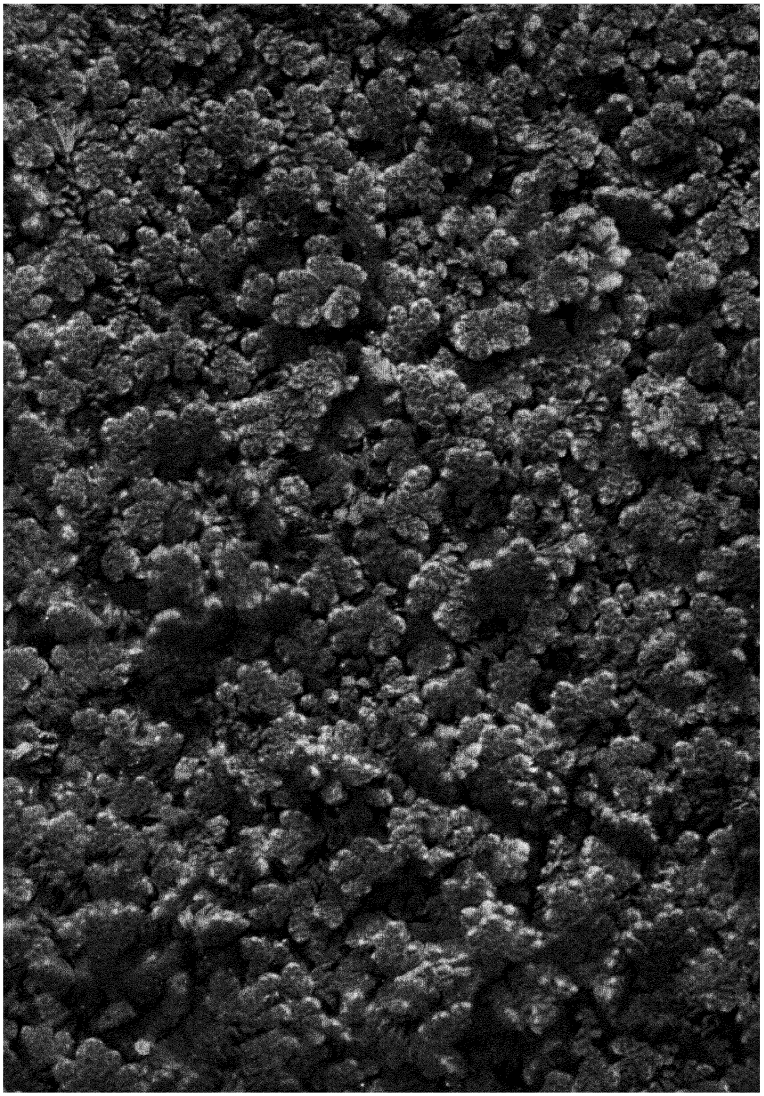
Another group of animals subsists by scavenging. The flatworms may be compared to the carrion-feeders on land, for they devour the carcases of any terrestrial or aquatic animals which fall to the bottom of the water. The fresh-water shrimp *Gammarus*, and the water hog-louse *Asellus*, also partake of this kind of diet, though it is believed that they are more catholic in taste and devour both plant and animal

remains. Organic matter which has been reduced to a fine state of division is eaten by the Corixidae or lesser water-boatmen ; they sweep up particles off the bottom with mouthparts which are highly modified for the purpose and not like the piercing and sucking mouthparts found in the rest of the order. Particulate matter is the food of three other kinds of animal, all of which secure it in different ways. Sponges maintain a current of water through their bodies by means of flagella ; *Simulium* larvae attach themselves in a fast current and strain the water with rake-like mouthparts ; and various caddis larvae also living in a current build a special net to filter the water. The detritus feeders may be subsisting to a considerable extent on the remains of terrestrial plants and animals, and are then part of a food-chain which is not aquatic in origin.

All the organisms living in the shallow water are preyed on by fish, and probably all British fish, except the char, rely mainly on this source of food for at least part of their lives. In Windermere perch take to this diet at a length of about six inches and forsake it when they have reached a length of about eight inches, after which they feed on smaller fish. Trout diet changes in the same way but not until a much greater length has been attained. Even the pike, when very young, eats large insects such as dragon-fly nymphs before it adopts an exclusively fish diet. Towards the end of the summer trout feed to a considerable extent on terrestrial insects which have alighted on the water surface, so this is another point at which the aquatic food-chain is augmented by material which did not originate in the water.

The last aquatic link in the food-chain is provided by predaceous fish, especially the pike. In Windermere the pike feeds mainly on perch in summer and on char in winter, these two species being in the shallow water for spawning purposes at these different seasons. Man, several kinds of bird, and otters are terrestrial animals at the end of the food-chain; and parasites also have a place, about which very little is known but which may be important.

It must be pointed out, before we leave the subject, that the details of the food-chains have not been worked out. The keeper of an aquarium is fully aware that any of the carnivores will attack whatever it can overpower, and if he mixes his animals indiscriminately he may witness the most ferocious struggles. But what is the staple diet of any species under natural conditions remains to be discovered. Obviously a creature such as a dragon-fly nymph, when it first emerges



John Markham

The water "fern," *Azolla*, carpeting the water surface Norfolk. December



John Markham

The shining pondweed, *Potamogeton lucens*, in a stream near Glastonbury, Somerset June

from the egg, cannot tackle anything much larger than a water-flea, but by the time it has reached its full size it is one of the most formidable of all the smaller aquatic animals. From the practical point of view it is important that more should be known about this subject. Many people imagine that "Nature" has things neatly arranged so that each type of animal exists in the right quantity to exploit available resources to the full. In fact the equilibrium is probably always unstable and the balance between predator and prey constantly fluctuating. It is an established general principle that the later links in a food-chain tend to be less restricted in diet than the earlier, so that, if there is a scarcity of one food species, the predators turn their attention to some other and a fair balance is maintained.

In a pond the whole chain is more circumscribed and less elastic, and there is not so much scope for compensation of this sort. Indeed the smaller the water body the greater is the fluctuation of the predator-prey relationship. Instances are periodically reported in the newspapers of ponds where a solitary pike, after having apparently eaten everything eatable, has become an item of news by attacking in desperation the nose of a cow desiring to drink, or a swan, or even the feet of a paddling urchin. Another extreme example, but one which is apparently of regular occurrence, is described by Pennington (1941), who studied the sequence of events in tubs filled with rain-water. Algae were the first colonists and then came rotifers which fed on the algae. They became very numerous and reduced the algal population to a level where it no longer produced enough oxygen for the teeming animal population. All the oxygen in solution was used up and all the organisms died. Then the cycle started all over again.

Obviously any scarcity due to over-cropping or other cause low down in the food-chain will exert an effect all the way up forming what in current English is known as a bottleneck. But how far any case of low production is due to a shortage of the fundamental raw materials and how far to bottlenecks between the raw material and the finished product is a line of investigation which still awaits attention.

Trout certainly and other fish probably feed fairly indiscriminately on whatever comes their way. They may for a time prey exclusively on one species, as every fly-fisherman knows, but such a habit does not persist for long. But there are certain groups which are taken less readily than others. The Corixidae (lesser water-boatmen) are a

group which, although frequently present in great numbers in fish-ponds, are seldom eaten by fish, and the surface-dwelling bugs also are found but rarely among the stomach contents of fish. The reason is not known. Other groups are not preyed on extensively because they live under stones or in other places where they are not readily accessible.

A practical point, which the American workers have stressed, is that, if good fish-growth is to be obtained, the fish must be able to graduate to food of ever increasing size as they themselves grow.

One final consideration of a general nature is the amount of potential food lost at each stage of the food-chain. For fresh water there is the detailed work of Dr. M. E. Brown (1946), who fed trout on butcher's meat and made a careful study of the amount eaten and the resultant growth under various circumstances. She found that it took about 6 lbs. of meat to produce 1 lb. of trout. This problem has been intensively investigated for domestic animals by agricultural research institutions, and it is found that 7 lbs. of food to produce 1 lb. of animal is an average all-round figure.

The amount of living matter produced in different natural waters may now be examined. The algae of the phytoplankton are the primary producers in the open water, and, as has been described, there are a great many different species of all shapes and sizes, some with vacuoles of oil or gas, some with skeletons of lime or silica, and some without either. A quantitative study is, therefore, not easy. The first problem is how to catch the organisms. Much of the recorded data is based on material collected with a fine-mesh net, but many species are so small that they will pass through any net which has holes of sufficient size to filter water reasonably rapidly (see Chapter 3, p. 38). A complete list of what is present can be obtained only by enclosing a volume of water in a suitable receptacle and then allowing the algae to settle; some of the species are disintegrated by centrifuging. This means that the population of only a very small fraction of the whole water-volume comes under examination.

The determination of the relative numbers of each species present is not as straightforward as might be thought. *Asterionella*, the chief diatom in Windermere, is illustrated on Plate XX, facing p. 113. One specimen consists of several cells which, though joined together, are individuals biologically. At some times of year there are more cells to a specimen than at others. The question is, therefore, should

each specimen be logged as a unit, or should each cell of each specimen be counted.

Another problem is how much organic matter does each species contain. On account of the vacuoles and skeletons possessed by some species, it bears little relation to size. Each species can of course be kept in pure culture till it has multiplied sufficiently to produce a sample for analysis, but the work involved by such an undertaking would be immense.

The greatest and most important difficulty is to assess the rate of reproduction in nature. A crop of turnips can be weighed when it is harvested, and the exact amount produced per unit area is evident. But an algal crop is quite different, because the individuals are reproducing and dying all the time, and there is no simple means of discovering the extent to which these two processes have been going on in the interval between two samplings.

The individuality of a zooplankton organism is not in question, but the other problems are applicable to animals just as much as they are to plants ; and there is a further difficulty that animals can move and avoid a net. Some move faster than others and so the proportion of species in the catch will not be the same as in the water. Prof. P. Ullyott, working at Wray Castle some years ago, found that more animals were caught by a black net than by the more conventional white one, and this result was obtained, rather unexpectedly, even in the dark. Plankton may also be collected by a pump and this has certain advantages ; but there will be a zone where the current produced by the suction is of such a strength that some species can escape and others, less powerful swimmers or with less marked response to current, will not, and so again a differential catch is obtained. The theoretical ideal is a very large cylindrical trap somewhat on the lines of the closing water-bottle illustrated on Plate II, facing p. 37, but made of bolting silk on a frame. There are, however, practical difficulties in the operation of such a device.

The result is that there is no exact information about how much plankton is produced in any lake during the course of a year. The most complete investigation is that made by Birge and Juday (1922) in Lake Mendota, Wisconsin, U.S.A. These workers tentatively express the opinion that the plankton population reproduces itself between once a week and once a fortnight. On this basis the annual production in Lake Mendota lies between 11½ and 23 tons per acre.

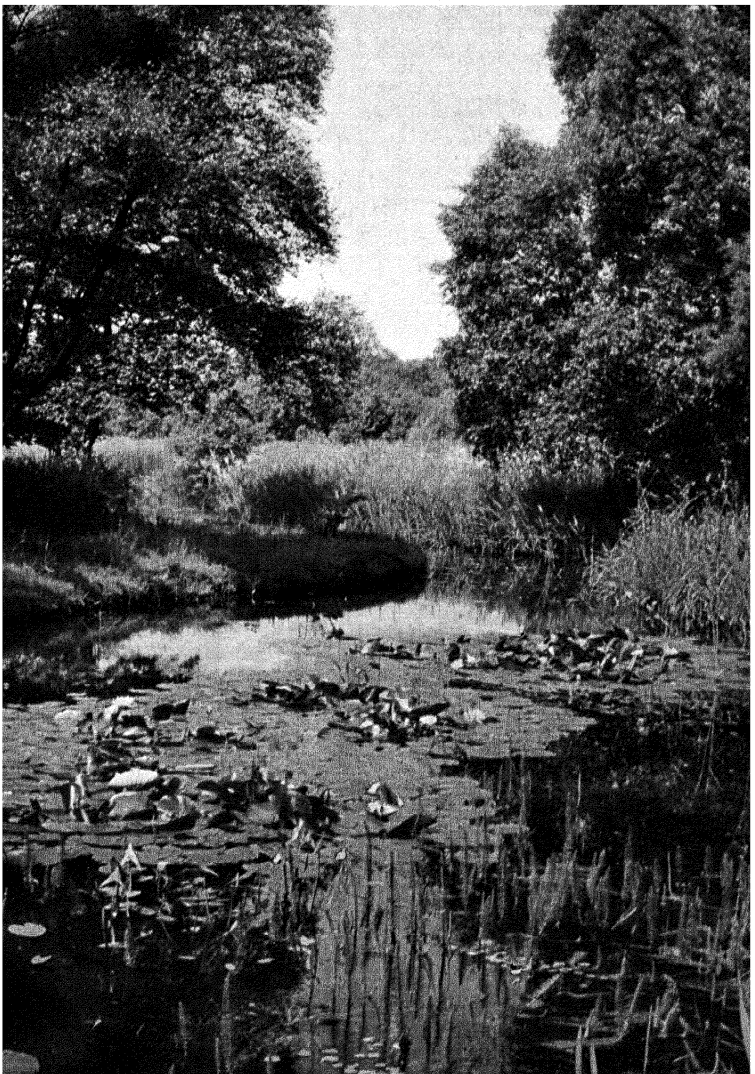
This is a fairly wide margin of error but it is the opinion of two of the most eminent workers on the subject and, for the present, the best available.

Observations in Lake Mendota and several other Wisconsin lakes have been made over a long period of years. Samples were taken with a net and the small organisms which passed through a net were obtained by centrifuging. The proportions varied widely at different times of year but, on the average, the weight of organic matter in the centrifuge plankton or nannoplankton was about ten times the amount in the net plankton. Plants contributed 93% and animals 7% of the total. The standing crop was calculated on the assumption that distribution was uniform throughout the lake.

Bearing in mind that the figures for plankton production are but rough approximations, we may compare the amount produced in lakes of different types. Lake Mendota itself may be taken as a typical eutrophic or rich lake with a fairly high concentration of calcium in the water. The ratio of its plankton production to that of two soft-water lakes with smaller drainage areas is approximately 100 : 33. Compared with another American lake, Cedar Bog Lake, which provides a good example of dystrophic or peaty conditions, the ratio is 100 : 8·6. Lake Mendota is rather more productive than the Fure Lake in Denmark, one of the eutrophic Baltic lakes, the ratio being 100 : 77.

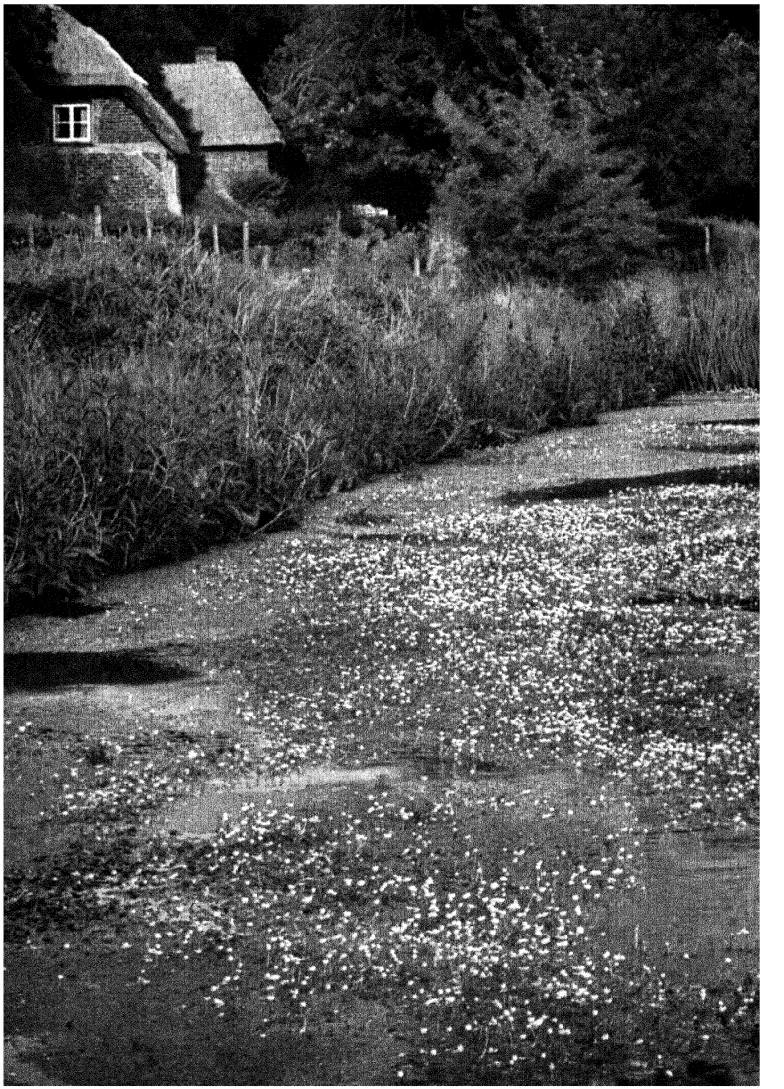
A series of net plankton catches made each month from February to December in 1936 is the only information available for Windermere. It is possible to compare these figures with the net plankton catches in Lake Mendota. The smallest standing crop in lbs. per acre of dry organic matter, which Birge and Juday reckon to be about one-tenth of the live weight, occurs in March in both lakes; the figure is 16 in Mendota and 2 in Windermere, giving a ratio of 100 : 12. The highest is 90 lbs. per acre in Mendota in December and January and 32 in Windermere in June, giving a ratio of 100 : 36. If the average for 11 months for each lake be compared, the ratio is 100 : 25, according to which Windermere is less productive than the two soft-water lakes investigated by Birge and Juday. As Windermere is enriched by quite a large amount of sewage effluent this ratio is unexpectedly low. But there are several possible sources of error; the two most important are, first, that the Windermere samples are based on a single year's observations only and it is known that the

PLATE 33



John Markham

Water-lilies, marestail, frogbit and arrowhead in a backwater, Calthorpe Broad, Norfolk July



Robert Welwyn

Stream choked with *Ranunculus fluitans* and other vegetation River Dever, Hampshire May

total amount fluctuates from year to year, and second that the comparison is based on net plankton, while all the others are based on total plankton. It is not known whether the ratio of total to net plankton is similar in Mendota and Windermere, or even of the same order of magnitude.

To summarize, the annual crop of plankton produced in Lake Mendota, a typical hard-water, eutrophic lake, is twelve times as big as that in Cedar Bog Lake, a typical dystrophic body of water; perhaps four times as big as that in Windermere, a soft-water lake enriched by sewage; three times as big as that of two soft-water lakes lying near it in Wisconsin; and one-third as big again as that of a eutrophic Baltic lake. More productive and less productive lakes than the two extremes quoted are known.

It is easier to estimate the production of the burrowing animals which dwell in the mud. They are confined to the surface layers; they cannot avoid the grab; they are fairly evenly distributed; and the determination of the number of generations is not as difficult as in the case of plankton organisms. Many have but one generation a year or less than this, probably none has more than a few, and, since the adults are not aquatic, it should be possible to work out exactly how many individuals there are at one place, and how many generations per year the different species present pass through. The work would be tedious, since so many of the Chironomids cannot be named as larvae and must be reared to the adult stage before the species can be identified, and in fact it appears never to have been done. Birge and Juday are content to assume that species which spend more than one year in the aquatic stage cancel out those which have several generations in the year, and that a reasonably accurate estimate of the total annual production may be obtained from an average of the standing crop at different times of year. This is a general practice. The published figures show great variation in the number of animals per square metre of the bottom in different lakes, and the amount of bottom fauna frequently does not correspond with the amount of plankton.

It will be convenient to start with the greatest depths of the various lakes, the region where the fauna, though possibly rich in individuals, is relatively poor in species, and comprises (except for insignificant numbers of representatives of other groups) only Chironomid larvae, worms (Oligochaetes), pea-mussels (*Pisidium*), and phantom larvae

(*Chaoborus*). The depths of Lake Mendota, 20-23·5 metres (65-77 feet), have an average of 15,265 animals to the square metre, but 10,830 of these are phantom larvae, which occupy a somewhat indefinite position between the burrowing and the planktonic animals. The live weight of this fauna is 69·68 grammes, which, converted from the international metric to the British system, is equal to 627 lbs. per acre. In Fure Lake the population is 2,280 individuals per square metre so that the ratio between it and Mendota, taking the latter as 100, as before, is 100 : 14 ; but, if the phantom larvae, which do not occur in Fure Lake, are omitted, the ratio is 100 : 51, which approaches more nearly to the 100 : 77 plankton ratio in the two lakes.

Of the Baltic lakes, Esrom has been studied more intensively than any of the others. It is of about the same depth as Mendota, and the population at 20 metres is 4,180 individuals to the square metre ; the weight is 36·3 grammes, which is 327 lbs. per acre. Phantom larvae are abundant in both lakes, Chironomid larvae are more numerous than Oligochaetes in Esrom Lake, but it is the other way round in Lake Mendota. Comparing the two without reservations, Mendota has four times as many bottom animals as Esrom, but they weigh only twice as much.

The Danish workers have sufficient observations from other lakes to make comparison with Esrom possible, and Berg (1938) has collected all the results together. Three have a bottom fauna only about one-third of that of Esrom. All receive some sewage pollution, and Berg is of the opinion that the sparse fauna is connected with this, an unexpected finding since sewage, if not in excess, is usually associated with an increased fauna. It appears unlikely that the sewage affects the fauna by causing oxygen deficiency, as it does in rivers, since in any case oxygen deficiency is a characteristic feature of the deeper parts of eutrophic lakes. In Mendota, for example, there is a period of about two and a half months from mid-July till the beginning of October when there is no detectable oxygen in solution in water brought up from a depth of 20 metres. The nature of the relation between pollution and a poorer fauna in the Danish lakes remains obscure.

Berg quotes the figures obtained in a number of lakes in other countries, and of these two may be taken from among those classed as eutrophic. Lake Simcoe in Canada is 45 metres (148 feet) deep.

The weight of the fauna between 14 and 45 metres is 6·2 grammes per square metre (55 lbs. per acre) and the number of individuals is of the order of 800. Lake Yxta in Sweden is shallower, having a greatest depth of only 6 metres (20 feet), but the fauna is much sparser, and between 5 and 6 metres the weight per square metre is but 1·5 grammes (13½ lbs. per acre). Taking Esrom as 100, the weights of the fauna in these three lakes stand in the ratio of 100 : 17 : 4. If Mendota were taken as 100, these figures would have to be halved, so there is a great range of variation among lakes classed as eutrophic. On the other hand, Paul Lake in British Columbia is described as oligotrophic but it has a bottom fauna which weighs twice as much as that of Lake Simcoe.

As examples of oligotrophic and dystrophic lakes a series in the south of Sweden may be taken. The highest number of bottom animals per square metre is 245 and the lowest 45, and so a comparison based on the number of animals, and taking Esrom Lake as 100, gives a ratio of 100 : 5 : 1. This is not very different from the ratios between lakes classed as eutrophic.

These figures have been selected because they illustrate the general absence of relation between the amount of bottom fauna and the productivity in other parts of the lake, and the fact that at the present time we are not able to explain why some lakes have a greater bottom fauna than others. It appears likely that the productivity of the bottom fauna is controlled, to some extent at least, by factors peculiar to the mud. It is known that a mud made up largely of undecomposed plant fragments, that is a bottom of what may loosely be called peat, is not highly productive, nor usually is a sandy bottom. These represent extreme types and not much is known about the intermediates, particularly their chemical and physical properties. Studies of this kind will, perhaps, provide the clue to the great differences in the amount of bottom fauna found in different lakes. Moreover, it is desirable that the results should be based more on accurate knowledge and less on assumptions about the number of generations per year of the various species.

So far the fauna at the greatest depths has been discussed. Usually it is at a minimum in this region and increases with decreasing depth. This is true of Esrom Lake. Above the pure mud, which is confined to the deepest parts of the lake, shells of dead molluscs contribute a considerable proportion of the bottom sediments, and in this zone live

molluscs also preponderate. The greatest weight of animal matter, including the shells of the molluscs, was found between 8 and 9 metres and amounted to 11,480 grammes per square metre, which is just over 100,000 lbs. or about 45 tons per acre ; but this does not represent a year's production, as the molluscs, which are the main constituent, live longer than one year. The greatest number of animals was found at a depth of 2 metres. Here there were 10,810 animals to the square metre but the total weight was much less than at greater depths. The enormous preponderance of molluscs is illustrated by the fact that at a depth of 8-9 metres the total weight of animals without the molluscs is only 18 grammes per square metre. Esrom Lake cannot be considered typical as it is inhabited by the Zebra Mussel, *Dreissensia polymorpha*, which has only recently invaded fresh water and is probably still extending its range. It has not been in Esrom Lake for long. It is this bivalve which contributes most of the enormous mass of animal matter at depths between about 6 and 12 metres. Its arrival is clearly an event of major importance in lake biology and more detailed determinations than exist at present of the precise conditions under which it flourishes, of its position in the food-chain, and of the status it will ultimately maintain, will be awaited with interest. This last point is important because new arrivals often flourish exceedingly at first and then sink back to a less outstanding place in the biological scheme.

Windermere has a remarkably sparse fauna of burrowers, and the population is of the same order as that of the poorest lakes considered in the preceding pages. Humphries (1936) records the following numbers of animals per square metre, 230 at a depth of 6 metres ; 100 at 9 metres ; and 30 at 12 metres. At greater depths there is probably not much further diminution in the numbers, but not many collections have been made.

The population of the zone of attached vegetation is less easy to assess because the substratum is much more diverse, and it is difficult to find a sampling area which does not include several different " micro-habitats," each with a different population density. In Windermere, Moon (1934) has published some observations, and, though his figures are based on single samples, they give a rough guide to the density of population along the lake shore. On the bare rock face he found 91 animals per square foot (983 per square metre), 80 of these being fresh-water limpets ; this population is probably higher

than the average. On the exposed shore with stones and boulders he found populations ranging from 10 to 119 per square foot (108 to 1,285 per square metre) ; and in bare sand the population, though restricted in kind largely to Chironomid larvae and pea-mussels (*Pisidium*), was larger, from 73 to 315 individuals per square foot (788 to 3,402 per square metre). In a sandy bay (Moon, 1936) with *Phragmites* and *Littorella* he found that the densest population occurred at a depth of $2\frac{1}{2}$ feet, where there were 660 animals to the square metre.

Where pond-weeds grow thickly the population is much denser. There are no data for Windermere, but the point is well brought out in the classic study of running-water populations by Percival and Whitehead (1929), who worked on streams in the West Riding of Yorkshire. In thick moss growing on stones and boulders they record 431,941 animals per square metre and, at a station with *Potamogeton perfoliatus* they took 243,972 animals. Where there was no thick cover of vegetation the totals were much smaller : 4,600 on " cemented stones," that is a relatively stable bottom of fairly small stones, and 3,316 on a typical unstable bottom. Seventy-five per cent of the fauna in the moss was Chironomidae ; in the last two types of habitat larger animals such as Ephemeroptera and Trichoptera were the important elements. The difference in total weight would, therefore, be less but it would still be considerable.

Further information about the density of river faunas is available from the surveys of the Ministry of Agriculture and Fisheries, though the figures which they give usually make no distinction between burrowing animals and those dwelling on weeds and stones. Pentelow, Butcher and Grindley (1938) give a table comparing two other rivers with the Bristol Avon, and in a modified form it is reproduced as Table 5 on page 154.

These results from rivers are even more bewilderingly diverse than those from lake bottoms. In the first place the figures obtained by Percival and Whitehead do not seem to be of the same order as those of Pentelow and his colleagues, and at first glance it almost seems that an extra nought has been acquired somehow, though a second glance shows this to be out of the question. Both teams used the same sort of apparatus and sieves with the same size of mesh, and there is no obvious explanation of the differences between their respective results.

TABLE 5

Highest and lowest number of animals per square metre in three rivers

River	*Scouring effect of floods*	*Calcium*	*Nature of the station*	*No. animals per sq. m.*	*Remarks*
Tees	Great	Moderate	Stones and boulders	106	
			Ditto 300 yds. below sewage outfall	847	
Lark	Slight	High	Muddy bed	508	
			Stony bed	3,031	
Bristol Avon	Slight	High	Sand and gravel with *Ranunculus fluitans* 2½ miles above source of pollution	1935 484 1936 1,964	Lowest '35 Lowest '36
			Gravel and stones with some emergent vegetation 300 yds. below source of pollution	1935 5,788 1936 19,940	Highest '35
			Submerged plants on silt bottom ¾ mile below source of pollution	1935 2,076 1936 24,864	Highest '36

The Tees has a sparser population than the other two rivers. It drains less fertile land, but the main reason is probably the fierce scouring by floods, which affects the animals both directly and also indirectly by preventing the establishment of weed-beds. The figures indicate that sewage pollution leads to a denser fauna, though it is perhaps scarcely necessary to say that this is true only if pollution is

not excessive. Otherwise the data do not permit any generalizations. It will be noticed that the same stations in the Avon had populations which in 1936 were anything from four to twelve times as big as in 1935. Pollution came to an end after the 1935 and before the 1936 collecting season, and this presumably must be related in some way to the change. But the first of the stations quoted was 2½ miles above the source of pollution and the nature of the relationship remains obscure. Perhaps the main conclusion to be drawn from a comparative study of river faunas is that a great deal more work must be done before a coherent picture embracing all the results can be drawn.

There is no exact information about the number of animals inhabiting different species of plant, but it may fairly be assumed that the population will depend roughly on the surface area presented. A water-lily or floating-leaved pond-weed with a long stalk surmounted by a single large flat leaf at the surface will offer a smaller area than, for example, the Canadian pond-weed with numerous leaves at all levels. The faunal density in the zone of attached vegetation bears, therefore, no direct relation to the productivity of the open water of a lake.

The weight of fish present in any body of water, except in special fishponds, is even less easy to ascertain. The animals are not evenly distributed and they take evasive action when efforts are made to catch them. The American workers have obtained some figures by poisoning the whole of a pond or small lake and so getting hold of the entire fish population. Then they have restocked the water and the effect has usually been beneficial, as it has been possible to stock with the fish which the angler prizes most, or with pan (i.e. species which man catches and eats) and predator fish in a proportion which experience has shown will lead to a good yield of the former. But this technique does not seem to have been tried outside America. Fish work has usually been done by institutions with a purely practical programme and, therefore, not in the same lakes as the work on other animals. There are few fish productivity figures to compare with the ratios already cited, and it seems best to defer the whole question to Chapter 13, in which practical fish production is described.

The total productivity of a lake thus depends on many factors. The amount of plankton depends on the amount of energy provided by the sun, and is limited by the quantity of certain inorganic salts

present and also by the depth to which the light penetrates. This is reduced by extraneous matter in suspension and also by a vigorous growth of phytoplankton. In two lakes which are probably somewhere near the extremes, the amount of plankton produced in a year was in the ratio 100 : 8·6.

A greater variation in the population of the bottom muds is found, the amount produced being over 100 times more in some lakes than in others. The density of the bottom fauna does not seem to be related closely to the amount of production in the surface waters and is probably controlled to some extent, perhaps a large extent, by physical and chemical processes in the mud which at present are little understood.

Production of attached vegetation is to some extent dependent on the amount of nutrient salts available, but the governing factor is the amount of lake bottom of suitable depth. The fauna of this zone is even more dependent on the character of the substratum. The production of fish depends on the quantity of animal food available.

For four of the Wisconsin lakes, two soft-water and two hard-water, Juday (undated) has calculated the ratios in the summer standing crops of the various types of organism and finds the following ranges : zooplankton : phytoplankton 1 : 14 to 1 : 16 ; total animals : total plants 1 : 6 to 1 : 12 ; fish : other animals 1 : 4·7 to 1 : 9·6. A large amount of variation is to be expected, but on the whole these figures confirm that a ratio of about 1 : 7 expresses the relationship between successive stages of the food-chain in fresh waters. Juday (1940) calculates that barely 1% of the solar energy falling on the lake is made use of, but shows that this utilization compares favourably with that of various land crops.

These are some of the findings of academic limnology. It is interesting to examine in the light of them some of the activities of man in his efforts to achieve the production of more fish. He can interfere with the food-chain at various points. At the base he can add nutrient substances to the water ; this, the artificial manuring of ponds, is discussed in Chapter 13. At the other end he can alter the ratio of fish-eating to other fish, and also reduce the number of less desirable kinds which exploit the same food-supply as those which are considered more desirable ; an essay along these lines is described in Chapter 12. Finally he may alter the substratum in such a way that it will provide a foothold for more of the animals on which fish feed,



John Markham

Clearing weeds from a ditch near Glastonbury, Somerset April



S. C. Porter

Moorhen on nest Suffolk July

and a discussion of this topic occupies the rest of the present chapter.

Greatest production of the animals on which fish feed is attained when the substratum supports a growth of rooted plants or attached mosses. These are likely to be absent where the bottom is unstable, that is places in streams and rivers where there are banks of mud, or small round stones. Frequently a groyne will protect a mud-bank for long enough to enable plants to gain a foothold, and once this has happened the mud-bank may be fixed permanently because weed-beds have a good stabilizing effect. A groyne is popular in trout streams for, by contracting the width of the channel, it causes an increase in the speed of the current, and the result of this may be that one side of the river is washed clear of mud, and a gravel bottom is uncovered and kept clear. If gravel stretches for the trout to spawn in are scarce, this is a valuable result. Shifting stones in a stream present a more difficult problem. If a pool is dammed up, some silt may settle and plants may establish themselves, but frequently such streams are liable to violent floods, which may sweep away the dam, as well as any weed-beds which have gained a foothold. Where natural cover cannot be induced to grow, recourse must be had to artificial cover made from bundles of brushwood or bracken weighted and thrown into the water, and similar devices.

Vegetation, like many other good things, is required in moderation, and excessive growth will seriously reduce the living space available to fish. It also interferes with fishing. On south-country chalk rivers the problem is quite different, and preventing the growth of too much vegetation by constant cutting or hoeing is one of the main pre-occupations of those concerned with managing the waters.

The over-fishing problem is familiar to all fishermen; each fish must be given a chance to breed before it is killed. The same applies to lower levels of the food-chain, and there is always a danger, in the restricted environment of a lake or river, that some animal on which the fish feed readily may be kept at an undesirably low level by the activity of its predators. It is sometimes practicable to screen off a shallow bay or a ditch leading into a stream in such a way that the food animal, a snail for example, can enter or leave the reserve without hindrance, whereas the predator is excluded completely. Within these reserves a good stock of food organisms will maintain itself and, when the population becomes large for the space available, individuals will tend to move out into the main stream or the lake, where they

may serve their purpose, anthropocentrically speaking, of providing food for fish.

Another popular device is the flyboard, of which the purpose is to increase the number of nymphs of the Ephemeropteran genus *Baëtis* in streams and rivers. These insects crawl below the surface of the water to lay their eggs, and usually attach them to the underside of a stone or some object in contact with the bottom. Caddis larvae then come and eat large numbers of them. The flyboard is just a piece of wood floating at the surface of the water. *Baëtis* finds that it offers a suitable surface for oviposition and the board soon becomes covered with eggs. But the caddis larvae will not climb along the wire by which the flyboard is moored and consequently the number of eggs left unmolested to hatch is much greater than usual.

No detailed study of the biological significance of any of these practices has yet been made, but there is no reason to doubt that they do achieve what is claimed of them. On the other hand, the biologist frequently looks with some scepticism on attempts to augment fish food by introducing organisms not already present. A well-established river, lake or pond is likely to contain all the species for which it provides suitable conditions. But, of course, stocking with suitable organisms is a good step to take in a stream recovering after a cause of serious pollution has been removed, or in a pond which has been drained.

CHAPTER 10

LIFE AROUND THE WATER

A RIGID distinction between water and dry land is one of the main aims of man, and his efforts in pursuit of this objective produce one of the major differences between country which he has colonized and country which he has left untouched. Many plant associations which once covered great areas of Britain are now represented by fragments, and often the animals which dwell in them have been even more affected; for an animal is influenced by the average conditions of a wide area, whereas the presence or absence of a particular plant species may depend on the conditions obtaining within a quite limited compass. Before these communities are examined some of the terms commonly applied to them may be noted, for Tansley (1939) has suggested certain precise definitions based on accurate botanical surveys. The four terms are swamp, marsh, fen, and bog. Swamp is wetter than the other three, and at no time of year can a man traverse a swamp without getting his feet wet. It is the final stage of development of an aquatic habitat. It was doubtless widespread in the fen district at one time but elsewhere was more limited than the other types of community. The typical vegetation of swamps is emergent and consists of reeds, sedges, reedmace and other plants, according to conditions, some of which have been described on p. 103 in connection with the development of reed-beds in sheltered bays in Windermere.

In winter or at any time of year after heavy rain, marsh, fen, and bog may be well inundated, but the normal summer water level is only just above the ground level. The soil is always waterlogged, but in dry spells a man may pick his way across these types without getting his feet wet. Marsh has a mineral substratum. A glacial lake, particularly one on a flat plain, may be surrounded by extensive areas of

marsh growing on the boulder clay. In earlier times vast tracts of land on either side of the lowland courses of rivers were covered by marsh, growing on a subsoil of gravel, sand, or silt deposited by the river in flood (cf. Fig. 5, p. 46). Alderwood is the typical plant community of marsh conditions in Britain.

Fen and bog both occur on a substratum which is mainly organic, that is derived from the accumulation of plant remains, and the difference between them is that bog is markedly deficient in lime and other bases, and fen is not. In Britain the classic type of fenland occupies a great stretch of country in North Cambridgeshire, South Lincolnshire, and parts of the adjacent counties. All the water which flows through it comes from the chalklands or limestone and is rich in bases, but there is little oxygen in the waterlogged soil. Decomposition is therefore very slow, and the accumulation of plant remains leads to the formation of peat. Nearly the whole of the area is now kept free of water by means of pumps so that it may be cultivated ; in a few small reserves only may the natural vegetation be studied, and even then allowances must be made before the flora of the pre-drainage era is deduced from the present artificially natural state of affairs.

Wicken, which for long has been National Trust property, is the best-known fen, thanks to the researches of Dr. H. Godwin and other workers from the Cambridge Botany School. *Phragmites communis*, the common or Norfolk reed, is the dominant species of the reedswamp, and persists for a long time after swamp conditions have been superseded by fen. The first dominant fen species is the fen sedge, *Cladium mariscus*, which forms a dense mat excluding all but a small number of other species. The soil level is built up rather quickly and, when it reaches a point where it is above the average winter water-level, colonization by bushes begins. The alder buckthorn, *Frangula alnus*, is the most abundant species of bush, but there are three others which are fairly plentiful. For some unknown reason alder is scarce in Wicken, though it is a dominant species in the fens which develop around the broads in Norfolk.

Cladium and other fen plants maintain themselves between the bushes for a long time but eventually are forced out as the bushes grow up and the canopy closes. Their place is ultimately taken by species which are able to live in deep shade.

The bush stage is known as carr and is believed to lead on to oak-

PLATE XXV



A. R. Thompson

Otter



PLATE XXVI

A R Thompson

Water-vole

wood ; but this, though highly probable, is not an observation of fact.

The succession over a great part of Wicken Fen has been deflected by man, who cuts *Phragmites* for thatching, *Cladium* for thatching or kindling, and *Molinia coerulea* (purple moor-grass or flying bent) for " litter," that is bedding for cattle. If the *Cladium* is cut every four years the establishment of bushes is prevented, and the *Cladium* persists beyond a stage at which it would otherwise have disappeared. But its growth is not as vigorous as when it is left undisturbed and its dominance is less complete ; *Molinia* becomes an important member of the community, which the fenman refers to as " mixed sedge." *Phragmites* also persists and there are other characteristic species.

If the cutting is annual, *Cladium* does not survive, and *Molinia* comes to dominate the vegetation which, in the fenman's parlance, is now known as " litter." *Phragmites* is also a member of this community, in which *Carex panicea* (carnation grass) and *Juncus subnodulosus* (obtuse rush) are subdominant.

Wicken Fen is divided into strips each under different ownership, and different people have cropped their plots according to different rotas. The fen, as a result, presents a mosaic of plant communities, and Godwin and his co-workers were able to show that the nature of each one is related to the treatment it receives.

Unspoiled fenland is found round the Norfolk Broads, and on a small scale this part of the country to-day is probably what great areas of fenland were like 400 years ago. The plant succession is, in general, similar to that just described though it tends to be rather more variable. One notable difference, the dominance of alder in the carr, has already been alluded to. Well-developed fenland also surrounds Lough Neagh in Ireland, where the general picture is similar, though there appears to be a rather more clearly defined zonation at different water-levels. But fen vegetation is not confined to regions with a calcareous water. Pearsall has described a typical fen community at the head of Esthwaite Water, one of the Lake District lakes, and it appears that in this case the copious supply of fine silt is the factor responsible.

Finally there is the formation which in Ireland is known as a bog and in Scotland as a moss. Tansley decided that the two are synonymous, but in his usage he inclines towards bog. The present authors, without wishing to offend national susceptibilities, also favour the word bog. They can then refer to the characteristic plant, *Sphagnum*,

by its common English name, bogmoss ; otherwise they would have to call it mossmoss.

Sphagnum is almost invariably present where bog conditions prevail and is often dominant ; but there are a number of other species which occupy an important place in the community according to small variations in the conditions. Familiar names are cottongrass, beak-sedge, bog-rush, crowberry and bilberry. Less abundant but probably equally familiar species are sundew, butterwort and bog asphodel.

Bog conditions will be the ultimate phase of any piece of water which is deficient in bases. Any mountain tarn will eventually pass through this stage ; a good example in the Lake District is Blindtarn Moss above Grasmere. Fen conditions in the Lake District depend on a good supply of silt and not on a base in solution and therefore, as the fen is built up, the edges will gradually be cut off from a supply of silt, and fen plants will be replaced by bog species. In Esthwaite north fen to-day there is a thick growth of *Sphagnum* at the edges and it is gradually encroaching on to the zone where, a decade or so ago, sallows and other bushes were common. Any waterlogged depression in base-poor areas (i.e. hard rocks in the north and west, and sandy heath in the south) will tend to develop bog vegetation. Tansley recognizes three types of bog—valley bog, raised bog, and blanket bog. Everything so far considered is valley bog. It depends for its existence on impeded drainage, and it never loses contact with the surface water. Although austere, it is not quite so austere a habitat as the other two, for the most barren soil yields some dissolved salts.

In the fens of East Anglia patches of *Sphagnum* may occasionally be found on top of tufts of sedge or in other elevated situations. Calcium is unfavourable to *Sphagnum* which, in consequence, is found in such regions only where it is out of contact with the ground water. In East Anglia development goes no further than this, and *Sphagnum* is visited as a botanical curiosity. But in similar situations in Ireland development does proceed, and it is probably the greater rainfall and higher humidity which makes the growth of *Sphagnum* possible. Starting from some raised tussock it spreads outward and upwards until eventually it may smother a region of calcareous fenland ; many of the bogs of central Ireland probably had such an origin. The product of this process is known as a raised bog, for it grows up into a rounded hump, which may be of considerable dimensions. The characteristic

feature is that it is watered only by rain, mist and dew. It is, therefore, an extremely rigorous habitat and certain species, notably some of the reeds and sedges, which occur in valley bog, are not found on raised bog. There is a constant building up and breaking down accompanied by a succession of plant species and the sequences have been studied in great detail. A neat round hump develops, and the top may become so dry that heather grows upon it. Then, for some reason, the bog becomes unstable, erosion starts at the top, and pools are formed. These pools extend under the influence of the wind, and eventually eat their way to a point where they run down the hill, leaving miniature valleys behind them. They carry down much peaty matter, which spills over and smothers the vegetation at the edge of the bog, thereby widening the base on which it can develop. Then the bare scars left by these pools are colonized by plants, and a phase of regeneration sets in. Building up and erosion alternate in this way, while all the time the bog is growing bigger and bigger.

Raised bog may start on a valley bog if climatic conditions are suitable, and it seems probable that origin from such a site is easier than origin from a calcareous base. The climate of Ireland, Scotland, Wales, and North England is suitable for the formation of raised bogs. In the central limestone plain of Ireland, where they are known as red bogs, good examples may be seen, but in the other countries good types are hard to find as most of them have been drained by man.

In a moderately humid climate raised bogs develop only in damp places such as valley bog or fen ; but in the west of Ireland and the west of Scotland the humidity of the air remains at such a high level throughout the year that bog develops almost everywhere where the ground is fairly level. This type of bog, Tansley's third category, is known as blanket bog. It is found also at high altitudes on Dartmoor and the Pennines, where the increased rainfall and lower temperature of the greater height probably compensate for the lower average humidity. Blanket bog has been less affected by man than any of the other types of vegetation considered in this chapter.

The above account of the plants of swamps, marshes, fens, and bogs, sketchy though it is, shows a series of relationships between the plant and its environment. These relationships are apt to be more definite with plants than with animals living around the water. Indeed when it comes to the birds, mammals, reptiles, and amphibians, with which the rest of this chapter is concerned, it is often difficult to

decide which kinds qualify for inclusion. Among the birds, for example, one would not usually think of the swallows as dependent on water; but consider the following observations which show how two broods of swallows could fairly be considered in the productivity balance sheet of a tarn in the Lake District.

Plate XI, facing p. 80, shows Three Dubs Tarn, a typical artificial fish-pond of a type which might be found anywhere in the rocky parts of Britain. A floating cage (Plate IIIb, p. 44) covering one-third of a square metre of the tarn surface and moored out in the middle, caught in the season of 1947, 2,996 Chironomids and other insects which had emerged from larvae dwelling in the bottom mud. In the shallower water, where vegetation was thicker, there were fewer Chironomids but more larger creatures such as dragonflies and caddisflies; the total catch was 1,993 individuals. The mean of these two figures may fairly be taken as a basis from which to calculate the total number of insects emerging from the tarn during the season of 1947. The surface area is 16,188 square metres and so the final answer is 121,167,180 or 121 million to approximate to the nearest million. A pair of swallows nest in the boathouse of Three Dubs Tarn every year, and in 1947 they raised two broods. The parent birds may be seen hawking continually over the tarn and they doubtless feed extensively, perhaps entirely, on insects which have spent all their growing life in the water. In fact, in this instance, swallows are a highly important part of the animal association dependent on the water.

There are other species of insect-eating birds which may, in particular circumstances, be closely connected with the productivity and the food-chains of fresh water, but in this chapter we have included only those which feed extensively on the products of fresh water and are to be found on water for the whole year or the greater part of it. Visitors on migration do not qualify, and the ducks and geese are treated sketchily because they have been covered by Mr. Vesey-Fitzgerald in volume two of the NEW NATURALIST series.

The other vertebrate animals (other than fish) associated closely with fresh water comprise three mammals and eight amphibians. There is no reptile in Britain which can be included as aquatic or semi-aquatic, although the grass-snake, *Natrix natrix*, is often seen near water or even in water swimming with considerable dash. This is a modest list, which has remained modest in spite of the many doubtless well-meaning but usually ill-advised attempts to enlarge it. At the



PLATE 37

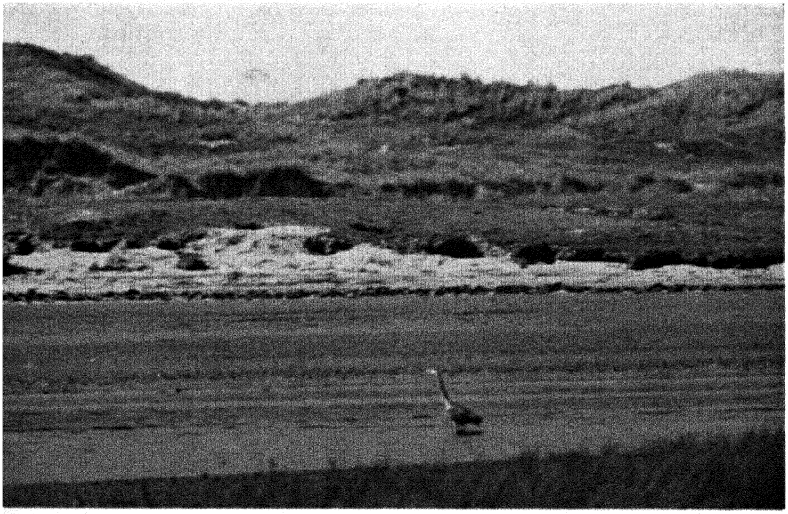
Eric Hosking

Black-headed gull at nest Yorkshire June



Eric Hosking

a. Kingfisher on perch. Yorkshire. May



John Barlee

b. Heron feeding. Ireland. August

present moment there is a fourth aquatic mammal, the coypu or nutria, at large in this country, and the memory of a fifth, the musk-rat, is far from dim. On the debit side is the beaver, *Castor fiber*, which was exterminated from Britain some time about the twelfth century. It was once common and its skeleton is found quite frequently in fen-land peat and other deposits. But it was a large animal, like many other semi-aquatic mammals it has thick soft fur which was highly prized by man, and it dwells in colonies and so was more conspicuous than solitary species. These three factors doubtless contributed to its extinction from Britain as man gradually cleared and drained the lower courses of the rivers where it lived.

The three native aquatic mammals are the otter (*Lutra lutra*); the water-vole (*Arvicola amphibius*) and the water-shrew (*Neomys fodiens*). The otter (Plate XXV, p. 160), the fox (*Vulpes vulpes*) and the badger (*Meles meles*) are the only moderate-sized Carnivora which have managed to avoid complete or almost complete extinction in Britain. All three sleep underground and hunt by night, and this, coupled with a keen wariness, is probably the reason for their success. But the fox and the otter are also pursued for sport and by virtue of this enjoy some immunity from other methods of destruction. The otter is widely distributed in Britain. It haunts the larger lakes and lower reaches of rivers, lying secure by day in a burrow, technically a holt, which is usually in the bank of a river, but may be at some distance from the water. In north Scotland and in Cornwall otters dwell in caves along the shore and hunt in the sea.

The main diet is fish, which the otter pursues with agility and skill, but its tastes, like those of most carnivores, are catholic, and it will feed on other water animals such as crayfish and frogs, and is stated to be a great enemy of moorhen chicks. It may range inland and go after rabbits and sometimes it raids poultry yards. Many fishermen regard it as an arch-enemy but Vesey-Fitzgerald (1946) states that, since it feeds mainly on eels and coarse fish which compete with game fish for food, in a salmon river it does more good than harm. But in a pond or stream devoted exclusively to trout it can do great damage, and, if in a frolicsome mood or giving its young some tuition, it may destroy a large proportion of the population in one night, killing far more than it can eat. But no lover of beauty could wish the otter to follow the beaver to extinction from the British Isles.

A dog otter, which is larger than its mate, may attain a weight of

nearly two stone, though this is exceptional, and there is considerable variation in weight. There is only one litter in the year, and the cubs, which may number five though fewer is usual, are born any time from spring to high summer.

The water-vole (Plate XXVI, p. 161) is a rodent. It is sometimes erroneously referred to as the water-rat but, like the other two British voles, it has a shorter and blunter muzzle and a shorter tail than the rats. Further, its ears are almost concealed in the fur of the body and do not stand out like those of rats. It is common and widely distributed in England, Scotland and Wales, though unknown in Ireland, and is to be found in the slower reaches of streams and rivers ; it inhabits places where there is plenty of vegetation and soft earth banks into which it may burrow. Its tunnelling habits make it unpopular in artificial ponds with earth dams, and in places where canals and drainage ditches are banked up above the level of the land which they traverse.

The water-vole is a vegetarian, and may frequently be seen sitting up on a patch of vegetation in midstream nibbling a young shoot which it holds in its fore paws. If scared, it drops into the water and disappears, for it is a good diver and swimmer. It is not encouraged in places where water-cress is grown, and it may also damage osier beds, but otherwise it is harmless, though it has been known to wander inland and attack root crops when hard pressed. Unfortunately it is sometimes mistaken for the brown rat and persecuted in consequence. Brown rats may dwell in a stream bank in burrows very like those of a water-vole colony but their feeding habits are quite different.

The water-vole is the largest of the British voles. It appears to be less prolific than the others, and is said to produce only one litter in the year. The young number six or seven.

The shrews may be distinguished at once from the voles, rats and mice, by the long tapering snout. If the mouth be opened, a more fundamental difference is seen. The voles and their allies have large characteristic chisel-like teeth at the front of the mouth, and there is a gap between them and the grinding teeth farther back. The shrews have a mouthful of teeth rather like our own, though there are more of them. The incisors are quite small and the canines or eye-teeth are large ; then, without any gap, follow the premolars and molars, each with several sharp cusps. The shrews belong to the order Insectivora, and the others to the order Rodentia.

The water-shrew is the largest of the three British species and it has stiff hairs fringing the tail and feet. The hairs on the body give it a characteristic broad rectangular appearance under water. The back is black or blue-black, sometimes with a brownish tinge, and the belly ranges in shade from dirty white to pure white ; some specimens have white ear-tufts. It is not as common as the water-vole and it is absent from Ireland. Like the vole it lives in burrows in the bank and sallies forth for food into the water, in which medium it is a capable performer. But, unlike the vole, it is a predator and seeks out caddis larvae, snails, and other invertebrate animals on the bottom. It may occasionally attack the spawn and fry of salmon and trout ; there are probably few predators of which this cannot be said. Weasels are stated to hunt it assiduously and it frequently falls a victim to the pike.

The female water-shrew constructs a nest at the end of a long burrow and there, in May, she brings forth six to eight young. There may be two more families in the season.

The musk-rat *Ondatra zibethica* is a rodent rather larger than the water-vole, and its natural homeland is Canada. It has inhabited parts of eastern Europe for many years, having been introduced originally on account of its fur, and has recently become established as a wild animal in several parts of western Europe. It has proved a doubtful asset in some places at least, as it creates an extensive series of burrows and, if the site is a canal bank or the earth dam of a pond, its tunnels may undermine the structure sufficiently to cause collapse.

The proposal to introduce the animal into Britain after the 1914-18 war was vigorously opposed in certain quarters but efforts to induce the Government to forbid its importation were not successful, and musk-rat farms were started all over the British Isles. Inevitably some specimens escaped and, by 1933, the creature was well established in the wild state at a number of places. The thickest populations were in Shropshire and Perthshire. The Ministry of Agriculture and Fisheries instituted a vigorous campaign against it, and sought the collaboration of the Bureau of Animal Population of Oxford in order to obtain the necessary knowledge about its biology and natural history. The trapping was successful and within a few years the musk-rat was believed to be extinct in Britain.

As already stated, the musk-rat is a great burrower. Newcomers make fresh holes of their own and will not enlarge any pre-existing

water-vole burrow, nor, usually, utilize those made by other musk-rats. The terminus of one burrow was found to be 30 feet from the river's edge. The entrances are frequently several feet beneath the water surface, but, where the water level is liable to fluctuate, there may be a series of adits and exits at different levels. In marshes and places where all the land may be submerged, the musk-rat builds "houses" of vegetation. Occasionally the young are born in these but the more usual birthplace is underground. The food is almost entirely vegetable, and it seems that the animal has a habit of cutting a food-plant into suitable lengths and then bearing these off to eat in the security of a burrow. Frequently some of the lengths get left behind and it is these floating on the water surface which often betray the presence of the musk-rat. Some animal matter is taken. As any vegetarian knows, it is difficult to feed on plants without taking in some of the animals which are attached to them, and the lower animals which subsist on a vegetable diet must consume much animal matter incidentally. But traces of swan-mussels have been found in the stomachs of musk-rats, and so large an organism, and a mud-dweller at that, must have been taken deliberately.

The first litter makes its appearance in April and is followed by a second and sometimes by a third. The average number of young is seven. The young do not attain sexual maturity in the year of birth, and the musk-rat does not reproduce as rapidly as was once feared. A tendency to wander becomes manifest towards the end of the year, and, in the following spring, when the breeding season starts, there is a second period of restlessness, though this one, unlike the other, seems to affect only the males.

The coypu, *Myocastor coypus* (Plate XXVII, p. 176), or nutria, to give it its commercial name, is also a rodent, though of much greater size than any so far mentioned; a stone is no more than an average weight for a full-grown specimen. Like the musk-rat it is a foreigner (though it comes from South and not North America), and it has fur which is valued highly, so that the idea of keeping it in farms in England seemed profitable. The first specimens came in by air in 1929, and within a few years there were some fifty farms in the country, most in the south and south-east. All of them, however, appear to have closed when the war started in 1939. It is scarcely necessary to state that specimens escaped. In Norfolk the big reedswamps provided a good habitat, and the animals became well established.

The coypu feeds on aquatic vegetation and is particularly fond of reeds. As it also destroys these plants by trampling them down, it has reduced the reedy areas quite appreciably in some places where it is numerous. It uses reeds to make a large nest, rather like a swan's nest to look at, and in it the young are born, usually five at a time. But they do not remain long in this exposed situation and within 24 hours they have taken to the water. The mother has a peculiar feature in that the teats are situated on her back so that the young can feed while she is swimming. After a short period the young are eating vegetation like their parents. They may have become parents themselves in eight months, but usually the period is nearer a year. Gestation lasts about five months, and breeding apparently takes place all the year round.

The coypu does burrow but its retreats are seldom more than a few feet long. They are often open at both ends, and the mouth is usually at water level. The young do not dig much and frequently seek refuge in the burrows of some other animal. The modern moralist who deplores idleness must find pleasing the not uncommon sequel, for the burrow may prove to belong to a rat, who extends no hospitality to the refugee but treats him as an intruder and as a welcome addition to the larder. The burrowing activities are not, therefore, very serious though they might become so if the population were very dense. The coypu first earned a reputation as a pest in the winter of 1942-43 when it started raiding cabbage patches. Later, damage to sugar-beet plantations was recorded, and the Norfolk War Agricultural Executive Committee instituted a trapping campaign. They too sought the collaboration of the Bureau of Animal Population in order that scientific observations might be made.

The British Amphibia include three newts, three frogs, and two toads; two of the frogs are introduced aliens. All three species of newt are fairly widespread, though the great warty newt, or great-crested newt (*Triturus cristatus* or *palustris*) is most abundant in the south of England, and the palmate newt (*T. helveticus*) is most abundant in higher latitudes and also at higher altitudes. In many parts of the country the common newt, or smooth newt (*T. vulgaris*), is not the commonest species of the three.

During most of the year newts live under stones, in walls, and in other damp places, and they lie hidden all day so that they are rarely seen, except by those deliberately seeking them. They come out at

night to feed on various small invertebrate animals. In April they travel to some pond, and there, for a month or so, they live an aquatic existence quite different from their previous terrestrial way of life. The male develops a crest down his back and a characteristic and striking pigmentation so that he becomes an ornate and handsome animal. The female is occupied with the production of eggs and each one is laid singly and attached to some object, often the leaf of a plant, which is rolled round the egg and glued to form a protective case. By June the male has begun to lose his crest and his gay colouring, and gradually the adults disappear from fresh water. The young emerge from the egg as tadpoles and lead an aquatic life for four or five months. Sometimes winter overtakes them while they are still immature, and then they do not become adult until the following season. The fully-formed newt leaves the water and does not return to it until three or four years later.

No more harmless animal than the newt can be imagined but it is still regarded with fear and horror by many people. The Reverend J. G. Wood, writing nearly a century ago, has some almost unbelievable tales about local superstitions. On one occasion he captured some specimens and transferred them to a cattle trough as a convenient reservoir whence they might be taken at his convenience for detailed observation in the aquarium in his study. But the farmer, when he discovered it, came greatly agitated to the parson and demanded the immediate destruction of the newts which, he asserted, had caused the death of a calf. In vain did Wood point out that the calf in question had never been near the trough, that the newt was a harmless creature possessing no organs of offence, and that, since every horsepond on the farm contained newts, not one beast should be alive if the farmer's reasoning were right.

The common frog, *Rana temporaria* (Plate 27b, p. 122), is a widespread and common animal to be found almost anywhere where suitable conditions obtain. It belongs to an order which has only partially mastered the art of existence on dry land and it does not possess an impermeable skin. It must, therefore, always dwell in a damp atmosphere, or it runs the risk of drying up. It is a predaceous animal feeding on a variety of invertebrates, slugs and worms being favourite items in the diet. The capture of these needs no special technique but the frog can also capture flies and other insects which could escape from such a slow-moving animal did it not possess a

special device for securing them. The free end of the tongue points down the throat and not towards the outer world like the human organ. It is bilobed at the tip and covered with a sticky saliva. It is extensible and can be projected with great speed to seize some agile creature which is resting at what appears to be a safe distance.

Frogs spend the winter in a torpor in the mud at the bottom of some pond. They are one of the first animals to become active in the spring, and mating and egg-laying take place soon after the end of the hibernation period. At this point earlier writers on natural history were wont to insert a lyrical passage about the frog as a harbinger of spring and then pass on. To-day, thanks to the researches of Savage (1934 and 1935), much more is known about the factors which influence the behaviour of frogs when they first emerge from hibernation. The exact time of emergence is difficult to establish but it is probably several weeks before spawning. During that period frogs travel to the ponds where they spawn. The number of frogs arriving at some ponds is greater than at others, and frequently frogs will leave a hibernating-pond which looks to the human eye a perfectly satisfactory place for egg-laying and travel some distance to a spawning-pond. Arrived there, they seek out a few restricted areas where the eggs will be laid. There is a clearly marked pre-spawning period during which frogs seek out the oviposition places; having found them they hang about and, although the males may sometimes mount the females, there is no croaking and no spawning. Then one night the males become vociferous and the females start to lay eggs, and the sudden onset suggests that there is some trigger stimulus which is not apparent to the human observer. The date is not the same each year but in some ponds spawning is rather regularly earlier or later than in neighbouring ponds.

Mr. and Mrs. Savage made detailed observations one year in one particular pond; they chose a spawning-pond which was not as popular as many of the others, so that the number of animals which they had to handle was not too great. The spawning-season lasted twelve days, from 22nd March to 2nd April. Each night the observers captured for quick observation all the frogs in the pond. Any new-comers were marked with a label tied round their middles before return to the water, and the label number of any which had been marked on a previous night was noted. At the beginning there were many males present, and they remained in the pond for several days

at least, some being successful in securing more than one mate. As the days wore on, some of the males departed and a few late-comers arrived. Every night a few females came to the pond; they were seized by a mate, they laid their eggs, and then they departed; no female was ever found twice. It was presumed from this that the behaviour in an aquarium, where a male may remain clinging to a female for several days on end, is abnormal; it was demonstrated that, if such a pair be transferred to water taken from a spawning-pond, oviposition takes place within a short space of time.

The female frog has horny granules on the skin and the human observers found that they could easily distinguish a female frog in the dark by touch. A female, who, having laid her eggs, is bound for the bank, will croak at any male who tries to seize her, whereas, before the eggs have been shed, the female never uses her voice. Her thin condition also serves, it is thought, to indicate to the male that he has not found a suitable mate.

These are the observed facts and they present several interesting problems. First there is the question of what determines the spawning time, and also the spawning order of a series of ponds. Savage obtained the co-operation of observers all over the country and was able to gather a great deal of data. It became apparent quite soon that the climatic conditions on the night when spawn is first laid are unimportant. It took place on warm nights, on cold nights, even including nights with frost, on wet nights, and on dry nights. The only correlation which came out of the figures was that the observers tended to put off till to-morrow their visit to the ponds if the day was wet. But climate over a longer period is important. Early oviposition was invariably associated with a wet February; if February was dry, then frog spawn appeared on a later date than the average. In February wet conditions are usually associated with mild weather and if it is dry the temperature is low; accordingly it is difficult to separate the effects of temperature and rainfall. But spawning is frequently earlier at higher altitudes and there appears to be a correlation between this and higher rainfall.

Those ponds which are the most popular as spawning-places have a concentration of potassium higher than the average. It is probable that neither rainfall nor potassium react directly on the frog; Savage suggests that it may be through the intermediation of algae. Much rain early in the year will wash nutrient salts into the pond and may



S. C. Porter

Little grebe on nest. Essex June



Ian Thomson

Pair of reed-warblers at nest. Norfolk. June

cause an earlier development of phytoplankton. That certain species of algae have a characteristic smell is well known to waterworks engineers, and perhaps frogs choose a spawning-pond by its smell. There is probably no direct connection between any one species of alga and the nutrition of the tadpole; but possibly a certain alga is associated in the frog's nervous system with suitable conditions for egg-laying and the subsequent development of the young. Furthermore, Savage puts out the suggestion that the exact spawning-locality in a pond is chosen on account of some algal feature, and that the stimulus which starts spawning is some vegetational change. All this correlation with plants is hypothesis at present; but it is in accord with the facts, and will provide a starting-point for investigation when a team of the right combination tackles the problem.

Frogs' eggs hatch about a week after they have been laid, the exact length of the incubation period depending on the temperature. At first the tadpoles remain congregated together but eventually they disperse to seek their food, which is mainly filamentous algae. The tadpoles are preyed on by almost every predator, and one may imagine their soft bodies make tasty and nutritious eating. One of the authors has seen eight *Hydroporus* beetles set upon a tadpole several times larger even than all the attackers put together, and eventually by combined efforts, like a pack of wolves, overpower and devour it.

After an aquatic life of nearly three months the tadpole undergoes a remarkable metamorphosis, changing from a swimming aquatic herbivore to a hopping terrestrial carnivore; but the details are too well known to require repetition.

The edible frog, *Rana esculenta*, is not indigenous to Britain but has been introduced many times and is now established in some parts of the fens, and around London, though it has never spread very far from the original point of release, and has died out in several places where it was once known.

The marsh frog, *Rana ridibunda*, resembles the edible frog but is larger. Mr. E. P. Smith, who thought at the time that it was the edible frog, was the first person to set it free in this country, and he has given an account of its early years at large in the *Journal of Animal Ecology* for 1939. In 1935 some specimens which he had obtained the previous winter bred in an ornamental pond in his garden in East Kent, though the breeding was not very successful, since most of the tadpoles fell a prey to fish. In June two individuals migrated to a mere about

half a mile away and in October the rest followed them. Wandering in these two months, but particularly in October, appears to be characteristic of the species.

In 1936 the frogs bred in the mere and produced a great many young, their success being probably due to the fact that all the predator fish had perished in a drought two years previously. There were a few records of specimens at various points round about, and there were a few complaints about the noise of the frogs croaking at night.

In 1937 a peak was reached. The frogs spread over an area which was roughly a square having sides about 28 miles long. Most of the area was old marshland intersected by dykes and drains, but the frogs appeared in one lake on the uplands 14 miles distant from the mere and unconnected with the marsh area. The noise set up by the frogs at night was so great that nobody living in the vicinity could sleep. It is said that one of the tyrannies which drove the French peasants to rise up and start the French Revolution was that they had to spend the night flogging the water to keep the frogs quiet whenever aristocracy saw fit to sleep in the country. The frogs of East Kent also raised strong feelings, and a parish meeting of protest sent complaints to the Ministry of Health and to the local M.P. But both the Ministry and Parliament behaved much as did the House of Peers when Wellington thrashed Bonaparte. The daily papers, needless to say, made the most of the phenomenon. The result was unexpected. A brisk demand for frogs came from other parts of the country. The reason is not stated, except that one place ordered about 200 to cope with a plague of mosquitos; a surprising purchase, for it is unlikely that frogs of any kind have any effect on populations of mosquitos.

In 1938 it appeared that the zenith was passed. The frogs were still numerous but something had checked the wholesale increase of the year before; it scarcely seemed likely that the activities of the salesmen were on a large enough scale to be the cause. But most unaccountable of all was the fact that the frogs were silent. The whole story remains a mystery. Twelve specimens were introduced originally; after three years it appeared as if they might flourish like the rabbit in Australia, and their vocal efforts constituted a major nuisance. Then quite suddenly their numbers began to dwindle and their song ceased. That was the situation as it appeared to Smith at the time. Actually the check was probably not as great as he supposed, for, in 1949 in a personal communication which he was kind enough to make,

he writes that the frogs are more abundant than ever, though not as noisy as formerly.

The common toad, *Bufo bufo*, is encouraged by most people to-day because in a garden it devours slugs and other animals in disfavour with the cultivator. Like the frog it must find some damp retreat into which to withdraw when the sun is up, for it cannot control the loss of moisture from its surface, though it does not lose water as rapidly as the frog. But the idea that it is a beneficial creature is of recent growth, and the wildest beliefs about its venomous nature are even now hardly dead in the more backward parts of the country. The Reverend J. G. Wood describes a scene which one cannot picture without a smile. He was walking with some French friends in France. One of them spotted a toad beside the pathway and, recoiling in horror, he raised his stick to strike the animal dead. But before the blow could descend the Englishman had rushed in and seized the uplifted arm. Then Wood bent down to pick up the toad, and now it was his turn to be seized and forcibly restrained; nothing could convince the Frenchmen that painful death would not follow the touching of a toad. Finally it was agreed to sprinkle some tobacco on the toad's back, for the Frenchmen were convinced that this would kill the animal, and Wood knew quite well that it would not. And so the party proceeded, a compromise having been reached and international unity restored.

The toad usually spawns a fortnight or more later than the frog, frequently choosing large bodies of water. Pairs are found in Windermere and certain of the perch traps, about which there is more in Chapter 12, catch numbers of them every year, even at a depth of 20 feet. The process of egg-laying takes much longer than in the frog, and during the course of it the eggs, which are attached together in a long string, become wound round plants and other obstructions in the water. When all the eggs have been laid, the female repeats certain movements which she made at the beginning of spawning but no eggs come forth, and at this the male releases her. Any male which may seize her subsequently is dismissed in the same way.

The natterjack toad, *Bufo calamita*, which is smaller and has a light stripe down its back, is restricted to a few parts of the country, though where it does occur it may be numerous. The neighbourhood of ponds in the slacks between sand-dunes is a favourite haunt.

The water-beasts, being so few in number, have been considered

one by one roughly according to the order in which they come in the zoological scheme of classification. The water-birds are more numerous, and many of them can be related more definitely to the environment. Therefore it is preferable to take them according to their habitats, starting, as before, with Ennerdale Lake and passing through a series to rich lowland localities.

The most primitive, Ennerdale, is an inhospitable lake for birds and, though many species may be seen upon it when migration, hard weather, or rough seas bring them from their usual feeding-grounds and resting-places, there are but two which make a regular living from it. One is the dipper, a species more typical of streams, and the other is the cormorant, of which one or two can usually be seen sitting in security on the small pile of stones which constitutes an island in the middle of the lake. This bird does not breed inland in the Lake District, though there are records of it doing so elsewhere, but repairs to the sea coast where it nests in colonies on cliffs. A few birds haunt the lakes all through the year, and numbers inland increase during the winter. It is almost exclusively a fish-eater, and in Ennerdale presumably preys on trout and char, because there are no other fish for it to eat. It is one of the few birds capable of catching fish in the deep and coverless conditions of Ennerdale, for it can swim under water with the aid of its legs and wings with remarkable agility. A trout weighing 2 lb. has been taken from the maw of a cormorant and it is regarded as a most undesirable bird by most fishermen.

On Windermere, however, the cormorant is probably beneficial, for it is one of the factors operating to keep the excessive population of perch in check, its diet consisting largely of this fish. Mr. P. H. T. Hartley has studied its behaviour and has collected together the results of other ornithologists. The cormorant, it seems, feeds three times a day at very much the hours when man is wont to take his breakfast, lunch and tea. When not feeding, the birds sit on small rocky islands out in the lake, and so it is easy, if tedious, to make out how often and when they feed. The average weight of fish per meal is probably about half a pound and, as there are about twenty birds hunting the lake, upwards of five tons of fish are consumed by them during the course of a year. To the local inhabitants the cormorant is a fish-eater and therefore a villain, and they shoot him when they can; which is not very often, for he keeps the lake swept with a wary eye from his post of vantage, and seems to know more about the range

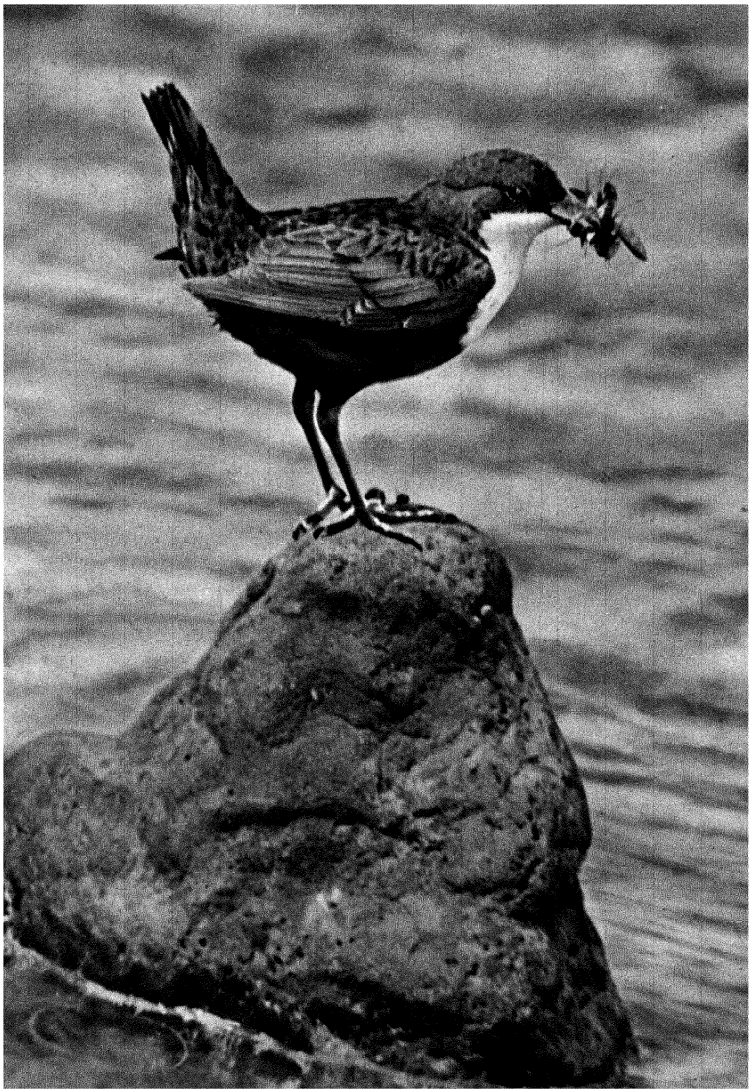


PLATE XXVII

Coypus

Eric Hosking

PLATE XXVIII



Dipper

Fred Jefferson

and accuracy of shotguns and rifles than many of the people behind them.

Windermere is not a favourable place for a permanent bird population for two reasons. First there is no extensive development of reed-beds, and secondly throughout the summer there are a great many humans in pleasure boats. The most conspicuous bird is the mute swan, though one may doubt from its behaviour whether it is really to be classed as a wild species. According to the text-books the swan feeds almost entirely on vegetable matter, but on Windermere for several months of the year its diet includes—or did include in more opulent times—a wide range of animal, vegetable and mineral matter, for the swans feed readily on whatever they can beg from those enjoying a picnic beside the water or dwelling in a houseboat or cruiser. It is also alleged that swans consume a lot of the char spawn, which is deposited in shallow water in winter-time.

The nest is usually in a reed-bed, though sometimes one of the islets is chosen. No secrecy surrounds the nesting of the swan ; well-trampled reeds, a vast mound of dead reed-stems making up the nest, and the colour of the bird itself advertise what is afoot for all to see. Fortunately for the swans most of the human population believe that one blow from a swan's wing will break a man's leg, and that any intruder is likely to be flung back into the water thus disabled and left to drown. An untimely rise in the lake level is more likely than the human robber to bring the reproductive efforts to naught.

A few ducks and other birds may breed on Windermere in the reed-beds or in the woods near the water's edge, but their nest-making is unobtrusive, and, by the time the lake is well thronged with holiday-makers, the parents and the young have departed to some less frequented stretch of water. The ornithologist will follow them perhaps to Esthwaite Water or Blelham Tarn which, besides being less haunted by man, have also more extensive reed-beds.

Several pairs of great crested grebes (Plate XXX, p. 181) nest on Esthwaite, and the species is also to be seen on Blelham. In April it selects some suitable site well hidden in the reeds and constructs a nest of reed-straw, partly floating and partly supported by the reeds. Three to five eggs are laid in May, and there is usually but a single brood in the season. The grebes are expert swimmers and divers, and capture small fish and also invertebrate animals.

The little grebe or dabchick is also a characteristic species of reed-

fringed lakes though it tends to move to smaller bodies of water to breed. The nest is a heap of vegetation (Plate 39, p. 172), and, like its larger relative, the bird has the habit of covering the eggs whenever it leaves them. The young take to the water at once and soon become expert divers, disappearing below the surface not only in search of food but also when danger threatens. In the earliest days a parent may seek safety below the surface with a young one clinging to its back. The point of reappearance may be a considerable distance from the point of disappearance ; as much as 40 yards has been recorded. The little grebe feeds on small fish such as sticklebacks and on invertebrates ; it may itself fall a victim to a pike.

A third species associated with this type of lake is the coot (Plate XXIX, p. 180), a bird which is gregarious and often to be seen in large numbers, particularly in winter when it tends to gather in the lowlands on the largest stretches of water. It nests in reeds or on land at the water's edge, and lays six to nine eggs, sometimes as early as March. It is also a diver but, unlike the two preceding birds, it is mainly a vegetarian ; but any animal feeding on pond-weeds cannot avoid consuming large quantities of animals as well.

On a calcareous eutrophic lake, as compared with an oligotrophic one, there is no sharp difference in the bird fauna as there is in the invertebrate fauna, but a lowland lake with a basin so shallow that weeds can grow everywhere and with thick reed-beds all round the edge will support a much greater population of birds than a deep oligotrophic lake in a mountain district. The optimum habitat was probably the open mere, which was a feature of the fenlands before they were drained. Now these have gone and the effect has been great, for aquatic birds are adapted rather than adaptable, and, unlike many woodland species, they have not been able to colonize new types of country when their typical haunts have been destroyed.

But it is on the truly fen species that man's activities have fallen hardest. Cranes, spoonbills and Savi's warblers breed no more in the British fens, and several other species are, or have been, on the verge of extinction. But, during the last 40 years, the setting aside of reserves and special measures to protect rare species during the nesting-season have achieved good results. The ruff bred regularly till 1871, but since then there have been only a few records of nests and the status of the species is doubtful. The breeding status of the marsh-harrier is still dangerously weak, though that of Montagu's harrier is

better, and improving. The black-tailed godwit, almost extinct in 1829, has possibly re-established itself as a regular breeder, and the bittern and avocet certainly have. The bearded tit concludes the list of species which have probably been saved from extinction.

Rivers and lakes cannot be separated clearly according to their bird fauna, but most naturalists will tend to associate certain species with either the one or the other, and it is convenient to keep them apart as has been done hitherto. But it must be emphasized that we are not seeking to make a distinction between river birds and lake birds.

Mountain streams and rapid reaches of the foothills are haunted by the dipper or water-ouzel (Plate XXVIII, p. 197), but where the flow is sluggish this species disappears. Accordingly it is familiar in the north and west of England and in Scotland and Wales, but a rarity in south and east England. It is a distinctive bird with its wren-like shape, its white breast, its habits of perching on a stone in midstream and making curtseying movements, and of flying straight up the river close to the water surface uttering a high-pitched whistle as it goes. It ranges almost to the top of the Pennines and nests up to 1,700 feet, but in winter it withdraws to lower altitudes and frequently establishes a beat along some suitable stretch of lake shore. Breeding starts early in the year, in March or the beginning of April. The nest is built, if possible, on some vertical face either on a bank or a slab of rock or beneath a bridge. The bird has been known to make use of holes and there are records of nests located behind waterfalls. The nest is usually a carefully built domed structure like that of a wren, but larger. The eggs number four or five and there are two and occasionally three broods in the year. The food is mainly aquatic invertebrates, which it pursues under water, either swimming by means of its wings, or, more usually, walking along the bottom. It overcomes its natural buoyancy by spreading its wings at the appropriate angle so that the current presses its body downwards. Flying insects are sometimes taken in the air.

Farther down a stream, where the water flows less turbulently, there will be a reach which is the territory of the kingfisher (Plate 38a, p. 165), another bird found usually beside running water and rather exceptionally around ponds and lakes. The nest is at the end of a tunnel in some soft earthy bank and consists mainly of regurgitated fish-bones. There are about seven eggs and they are laid towards the end of April, with sometimes a second brood in the course of the

summer. The bird is a fisher which secures its prey by diving. It commonly has a perch commanding a view of some suitable stretch of river, from which it dives obliquely into the water when a minnow or stickleback or the young of some larger fish comes into view. Sometimes it dives from a hover. Insects and other invertebrates are also eaten.

Another bird of the lowland river is the heron, though it is to be found anywhere where there are suitable hunting-grounds. It is a gregarious nester though many of the colonies contain only three or four nests. They are usually in the tops of tall trees, and the business of nesting starts early in the year, sometimes before March. The heron is a fisher and predator, but its method is unlike that of either of the two preceding species and indeed unlike that of any other bird so far mentioned. It selects some suitable shallow and there it stands motionless, or stalks forward slowly and deliberately, until some creature comes within reach of its long sharp bill (Plate 38b, p. 165). Frogs, water-voles, birds, especially young chicks, crayfish and other invertebrates all fall a prey to the heron, but it is primarily a fish-eater. As such it is persecuted by the human fisherman, sometimes unjustly, for it takes many eels and other fish which compete for food with species more prized by the angler, but sometimes with reason, when it is found haunting some stream or pond where there is nothing but game fish. However, we refer our readers on to p. 201, where the question of fish stocks is discussed.

As the river becomes slower and broader and more fringed with reeds along the margin, the number of bird species increases. Dabchicks, coots, mallard, teal and other ducks, swans, and other birds of the large lake may be encountered.

On stagnant water decreasing size goes together with a decreasing number of species until there is but one left, the moor-hen or, more appropriately, the water-hen. A pair may be found on quite small ponds, even on those of less than one acre in extent, if there be some cover provided by reeds or overhanging bushes. The nest is made in reeds (Plate 36, p. 157) or in overhanging vegetation, though sometimes it is in a pollard willow or other tree by the water's edge. Five to ten eggs are laid in April, and there may be three broods in the year. The bird can dive and it feeds on aquatic plants, but it also forages on land and consumes grain, fruit or even grass. Otters are said to eat many moor-hens.



Eric Hosking

Coot

PLATE XXIX



PLATE XXX

Great-crested grebe

Eric Hosking

Mallard (Plate XXXI, p. 188) and teal and, more rarely, some of the other ducks nest on overgrown ponds, but they are but temporary visitors leaving soon after the young can fly. In the winter they congregate on larger sheets of water, sometimes at great distances from the breeding-place. The mallard appears to be a genuine omnivore among birds. It feeds on aquatic weeds and will also seek food in the cornfields or pick berries from the hedgerows; but it is known to eat frogs and frog-spawn and other animals which could not possibly be taken incidentally with vegetable food.

A big pond which has reached the swamp stage is often chosen by black-headed gulls (Plate 37, p. 164) for a nesting-place. Their gulleries may be found in a variety of different situations, on sand dunes, around a group of small ponds, even in trees, but the favourite place is some pond or lake where there is a floating mat of vegetation. Such a situation offers some protection from the depredations of man, who cannot force a boat through the floating plant mat and dare not walk upon it; and some protection is needed, for the screaming of the great concourse of birds proclaims the whereabouts of their breeding-place for miles. The nests are piles of vegetation, and the eggs usually number three; they are laid in late April or early May and a second brood is sometimes reared. The food is varied but chiefly insects. They consume wireworms as the plough exposes them and they also take craneflies; there are records of their congregating to batten on plagues of bracken-clocks and antler-moth caterpillars, so they are to be numbered with the beneficial species. But the fisherman looks askance at their habit of hawking over the water and snapping up mayflies and other emerging insects.

CHAPTER II

ANIMAL TRAVELS

MOST authors use the word migration for almost any travelling from one place to another, either of single animals or of flocks of animals. Here the term is used in the restricted sense proposed by Heape (1931) to include only those travels which involve a return journey. A further item in Heape's definition is that the two places of sojourn should be separated by an area in which the animals are never found except when passing through it or over it on migration. The annual journeys of the swallows and the cuckoos provide one of the most familiar examples of migration. The phenomenon is not necessarily connected with reproduction, as it is in these two instances.

Among animals which live in fresh water two fishes, the eel and the salmon, perform migrations which are among the most remarkable feats achieved by any organism. Aristotle knew that at certain times of the year eels go down to the sea, that they have no obvious sexual organs, and that the small elvers which ascend rivers are the young of the eel. The sex organ of the female eel was first described in 1777, that of the male about a hundred years later, and, apart from this, it is true to say that there was no advance on what was known to Aristotle till nearly the beginning of the present century. It might almost be said that there was retreat rather than advance, for some of the theories propounded in the interim were very far from the truth and did not always take into account such facts as were known. It gradually came to be accepted, however, that eels bred somewhere near the mouths of rivers, either in the estuary or in the sea, a fallacy which has only quite recently been exposed.

In 1856 a flat transparent fish living a planktonic existence was found near the Straits of Messina. It was not obviously related to any

known fish and the genus *Leptocephalus* was created to receive it. Forty years later two Italian workers showed that this creature was in fact a young eel. *Leptocephalus* is, therefore, invalid as a name, but it is convenient to use it as a description and to refer to the leptocephalus larva or leptocephalus stage in the eel's life-history.

In 1904 a Danish worker, Johannes Schmidt, investigating the life-histories of various fish of commercial importance in the research ship *Thor*, caught a leptocephalus in deep water off the Faeroe Islands. It was a significant event, for it suggested that the commonly accepted view of a shallow-water breeding-place for eels might be wrong. Schmidt undertook to find out where the eel did breed, and committed himself thereby to a quest which was not crowned with success till 1920, sixteen years later.

In 1905 and 1906 the *Thor* sailed to more southerly collecting-stations in the Atlantic, and many leptocephalus larvae were collected. In 1907 there was no voyage and Schmidt turned his attention to the adult eel. He found that its range extended from the north of Norway to the Azores and Egypt (see Fig. 18), and that there was not more than one species, contrary to the views of several previous workers who had recognized a varying number of different species. This lent some support to an idea, which Schmidt was formulating, that all the eels from Europe and the Mediterranean might have a common breeding-place.

Attention was then turned to the Mediterranean and, after many stations had been worked and many specimens examined, Schmidt was able to show that the farther from the Straits of Gibraltar the bigger were the leptocephalus larvae. This led him to suggest that the Mediterranean eels bred at some place outside the Mediterranean and that the leptocephali returned to that sea from the Atlantic through the Straits of Gibraltar. The Italians had hitherto held almost a monopoly of research on the eel, and they viewed with disfavour the incursion of a foreigner into their field. They deprecated forcefully the suggestion that "their" eel should breed anywhere but in "their" sea, and one may surmise that scientific judgment was swamped in the stress of personal and national feelings.

Meanwhile the Norwegian vessel, *Michael Sars*, had collected off the Azores specimens of leptocephali smaller than any which had previously been brought in. It was evident to Schmidt that the solution of his problem demanded a research vessel with a cruising range

greater than that of *Thor*, and for this he was constrained to wait. He did not waste time, however, and he set about securing the co-operation of a number of Merchant Service captains, who undertook to make collections for him while at sea on their lawful business.

The result was that Schmidt had at his disposal data from all over the Atlantic and, when in 1913 he set out in a schooner, he was able to go straight to the place where he believed that his quest would end. His findings confirmed his expectations, but he was not quite satisfied that his evidence was as conclusive as it should be, and he was condemned to a further period of waiting, for the schooner was wrecked and then war came to put an end to Atlantic exploration.

At length, in 1920, he was able to set out in the research vessel *Dana*, provided by the brewers of Carlsberg beer. He was able to fill in the details left undisclosed by previous voyages, and he felt justified in committing his findings to print. The English reader will find an account in *Nature* for 1923 and 1924. The most comprehensive treatment of what is known about eels to-day has been published in France by Bertin (1942).

Schmidt did not actually see eels laying eggs, and his deductions about the place of oviposition were based on the distribution of larvae of different sizes. Fig. 18 shows one of the ways in which he summarized his findings. Each line encloses an area outside which eel larvae below a certain size were only very rarely found, and the figures inserted on the lines show the size in millimetres. Larvae less than 10 mm. long have, except in rare instances, been found only in a restricted area of the Atlantic. This area, Schmidt concluded, is where the eggs are laid. The smallest larvae of all are found at a depth of about 400 metres, and so it is probably at about this depth that oviposition takes place. It is near the limit to which any light penetrates, and the particular area is characterized by a rather sharply marked temperature-gradient, and at 400 metres (1,300 feet) is enclosed by the 15° C. isotherm. The ocean floor is 4,500 metres (nearly 15,000 feet) below the surface in this part of the Atlantic.

It is thought that oil globules in the eggs counterbalance them so that they neither rise to the surface nor sink to the bottom.

Egg-laying takes place from March to July, and the newly hatched young swim up to the surface layers of the sea. In the summer in the western Atlantic they abound, but they are gradually swept away to the eastward by the current which flows perpetually towards the shores

of Europe. By the following summer they are in mid-Atlantic, and by the summer after that, in which they enter their third year, they are approaching the edge of the European continental shelf. In the winter a change or metamorphosis takes place and the flat transparent leptocephalus turns into an eel-like elver.

Elvers may reach the extreme south-west of Ireland as early as November, though the main invasion does not take place till January. The west coast of England is reached a month later. The coasts exposed to the Atlantic receive the greatest number of elvers, but

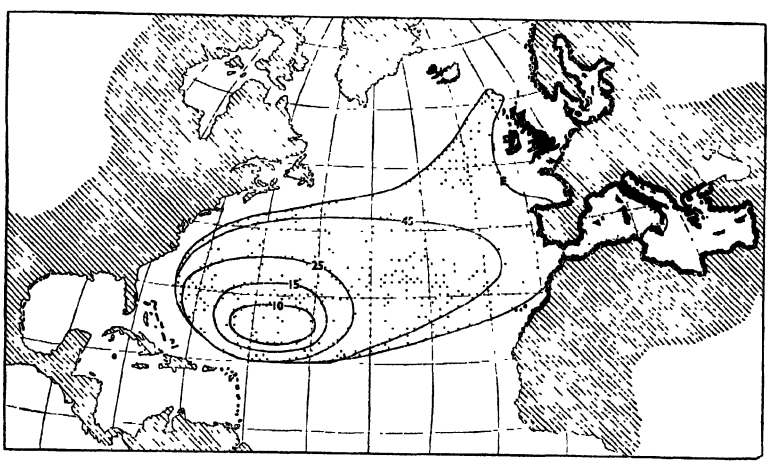


FIG. 18

Life history of the eel. Each line encloses the area beyond which leptocephalus larvae of the size shown do not occur; the figures show length in millimetres. Coasts invaded by elvers are shown black. (After Schmidt, 1922)

some drift on, and there is no coast which may not be invaded by at least a few. The remotest corners of the Baltic are reached, though the numbers attaining this destination are small; before the war a German firm operated a station on the Severn to catch elvers, which were then transported to stock north-European rivers.

The elvers which journey on to the farthest destinations celebrate their third birthday on the way, and continue to grow all the time. In the most northerly area of the Baltic, specimens less than 200 mm. long are never seen.

It will be noted from Fig. 18 that those larvae which are carried into higher latitudes metamorphose while still far out to sea and leptocephali do not reach the shores of north-European countries, but those that pass into the Mediterranean may travel as far as Italy before all have metamorphosed. The Mediterranean was the place where the original *Leptocephalus* was taken.

Under the influence of fresh water elvers travel actively. Some turn aside into coastal lagoons and marshes near the estuary, while others run far up the rivers and finally reach the remotest ponds, sometimes after an overland journey made possible by heavy rain. Those which travel far nearly all turn out to be females, and those which find a harbouring place without a long journey nearly all turn out to be males. It is possible that the sex of the eel is not determined genetically, as is that of most animals, but may be influenced, in part at least, by the environment.

The leptocephalus, in its $2\frac{1}{2}$ years of life, feeds on other animals in the plankton, but it makes remarkably poor growth and attains a length of no more than 75 mm., which is about three inches. It fasts for a while during the period of change into the elver stage, some of the tissues are resorbed, and weight is lost; Schmidt estimates that about 1,500 elvers go to 1 lb.

The main feeding and growing period in the life of the eel is spent in fresh water, and during this time it is known as a yellow eel. In due course, after a shorter or longer period according to the temperature, the food supply, and other environmental factors, the eel undergoes further changes. As far as is known, these are related to size, and in Windermere the period is from 9 to 19 years for females and 7 to 12 years for males, which do not grow as large as the females. The changes involve the pigmentation of the skin, the "yellow" eel becoming a "silver" eel, and enlargement of the eyes and nostrils.

On some dark and stormy autumn night, with the streams and rivers running high, the silver eels leave the pond or lake where they have dwelt so long and set off on the return journey across the Atlantic. In many other animals the onset of migration is closely correlated either with the development or with the degeneration of the sexual organs, but it seems that the stimulus which sets off the eel must come from some other source, for the sexual organs do not start to develop until it is well on its way.

Not a great deal is known about the eel after it has left fresh water.

It starts its sea journey with a body richly stored with food material and, in fact, the flesh of the silver eel comes second only to that of the salmon in food value. Possibly this store is sufficient for the whole of the journey across the Atlantic and no food is taken in the sea, a view supported by the observation that there is considerable degeneration of the alimentary canal. Finally, six months or so after setting out, the eels reach the area in the south-west corner of the Atlantic where the eggs are laid. Nothing is known about the process of oviposition nor of what happens to the parent eels once this has been accomplished. Nobody has ever taken a full-grown eel returning to fresh water and, though the possibility that existence continues in the sea cannot be ruled out, the degeneration of the alimentary tract provides strong support for the belief that the eels die when reproduction has been achieved.

It is an extraordinary life-history and one which confers no benefit upon the species as far as can be made out, and so its significance has been widely discussed. Perhaps the most plausible explanation is that which relates it to Wegener's idea of continental drift. According to this hypothesis, the Atlantic was once a comparatively narrow channel separating the Old World from the New, and the eel, journeying to the sea to breed, had no great distance to go. Gradually America and Europe drifted apart, and presumably the piece of sea with the conditions which the eels chose for oviposition travelled with America and receded from Europe, as the gap between the continents widened. The breeding journey of the eel became longer and longer until to-day it covers some 3,000 miles. Supporters of this hypothesis point to the prolonged larval life, unknown in any other fish, and to the fact that during this stage growth is extremely slow. What was once a comparatively short and rapid stage has been progressively drawn out as the distance to be covered has steadily waxed greater and greater.

There is much that is remarkable and unexplained in the life-history of the eel, but perhaps nothing more so than how it finds its way across miles and miles of featureless sea to one particular patch of the Atlantic.

No less remarkable and even less known is the life-history of the salmon, which is the exact antithesis of the eel, since its main feeding and growing period is spent in the sea and its youth in fresh water. No mystery shrouds the whereabouts of salmon eggs; they are to be found in rivers and large streams where the bottom is of coarse

gravel or moderately small stones. They take a long time to hatch, the actual rate of development depending on the water temperature, and they may lie for several months. The young salmon, which are known as parr, are usually active by April or May and feed voraciously on whatever animals they are able to obtain. Growth depends on various factors, notably the supply of food and also the temperature; in winter the parr are inactive and do not grow at all, the critical temperature being, apparently, about 7° C.

As with the eel so with the salmon, size appears to be the chief factor determining the age at which migration to the sea takes place; and there is a further resemblance in that both fish undergo a change in colour before leaving fresh water. The parr loses its characteristic thumb-like black marks down each side and its red spots, and becomes a silver-coloured smolt.

Under exceptionally favourable conditions the change and the departure for the sea take place after one year in fresh water, but smolts are usually two years old and often three or even more. The smolts move downstream, feeding as they go, and eventually in May or early June they reach the head-waters of the estuary, where they congregate. Then one day they all disappear into the unknown. That is not a figure of speech; nobody knows whither they do go. A certain number of salmon have been caught by trawlers in the sea but the number is insignificant when compared with the number of trawlers and the number of salmon. The fish are somewhere where they are not caught by the ordinary commercial methods of capturing sea-fish. Something about them may, however, be learnt from an examination of their scales. The scales increase in size as the whole animal increases in size, and the continual addition of material to the periphery leads to the appearance of a series of concentric rings. When growth is slow, these rings are close together, and when it is rapid they are wide apart. The salmon, returning from the sea, has alternating bands of close-set rings and widely separated rings, and from this it is deduced that the fish has been in places where, presumably because of the cold, growth in winter is much slower than growth in summer. This being so, the age of the fish can be read quite easily from the scales, and since, furthermore, there is a fairly good correlation between the size of the scale and the size of the fish, it is possible to tell how big the fish was at any given time in the past.

The factors which stimulate the salmon to return to fresh water

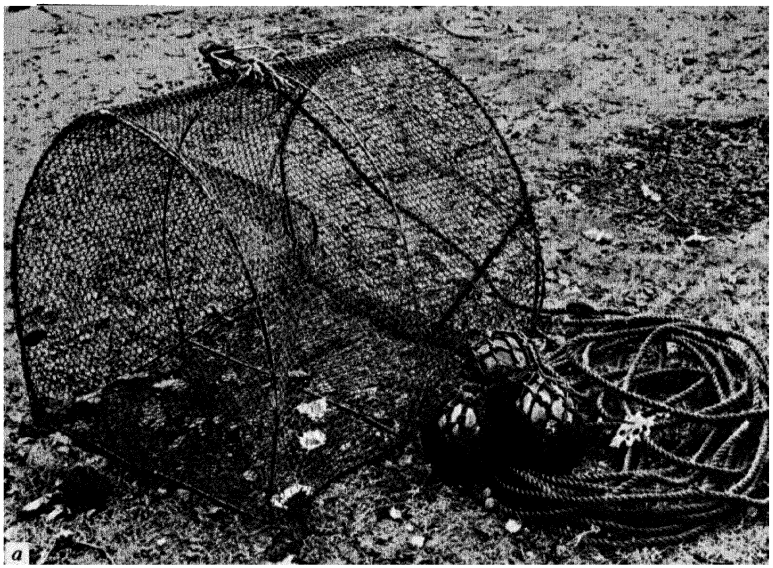


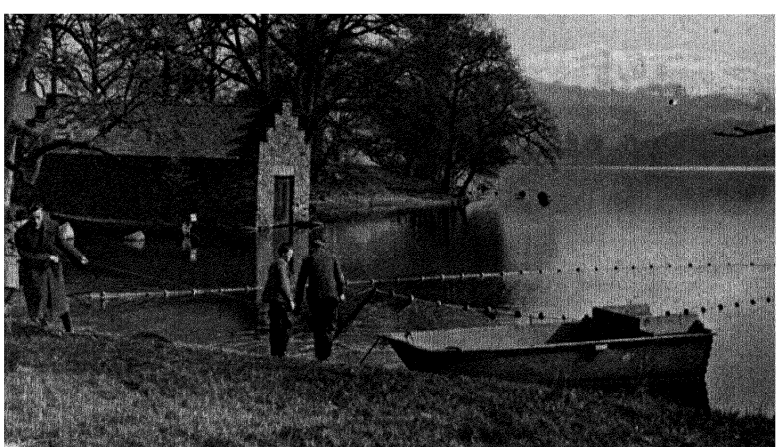
PLATE XXXI

John Armitage

Mallard

PLATE XXXII





Photographs by E. D Le Cren

a Perch trap
b. Hauling in a seine

are quite unknown, though the problem is one of both commercial and intrinsic interest, as the time of return is so variable. Some salmon, known as grilse, are back in coastal waters a year after leaving them ; others may spend two, three, four or five years in the sea. Nor is there any greater degree of regularity in the time at which the fish return from their feeding-grounds. Some, known as spring fish, for it is in the early months of the year that they appear off the coast, have evidently, from the scales, come away before the period of rapid summer growth has started. Others, known as summer fish, arrive later, and their scales show that they have been growing rapidly immediately prior to their arrival in coastal waters. It would seem that, unlike the spring fish, they have lingered to feed before the urge to migrate has sent them seeking fresh water, and some linger longer than others.

A grilse may weigh as little as 2 lb. or as much as 14 lb., though the average weight is between 4 and 6 lb. Of the other fish it is roughly true to say that they increase by an average of 10 lb. for every year spent in the sea. Ten pounds in a year is very good growth judged by fresh-water standards. These figures refer mainly to Scottish fish and come from Menzies (1925), which reference may be consulted for further information about the salmon.

Arrived in coastal waters, the salmon tend to hang about in shoals until such time as there is a good flow in the rivers. They then enter fresh water and begin a leisurely journey upstream. Serious travelling does not take place until the water is fairly warm, that is April at the earliest in Scotland, and no attempt is made to negotiate obstacles as long as the temperature is low.

The most remarkable thing about this period in the life-history is that it is a time of fasting, and the fast may be of very long duration. A few fish will perhaps enter rivers in February ; they will not spawn before October and probably later, and there is no doubt that some fish spend as long as ten months in fresh water. The late-comers, which do not arrive until summer is well on the wane, and often do not travel as far inland as spring fish, will have a much shorter fast, but a period of several months without anything to eat is, on the average, a regular feature in the life of the salmon. It is a phenomenon which the biologist finds difficult to explain, especially in view of the angler's experience that, during their fast, salmon will on occasion take bait, fly, or lure.

Spawning may begin as early as mid-October and finish as late as January, though most of it is accomplished in November and December. The female fish selects a piece of river with a bed of stones and gravel and there, with a few flicks of her tail, she shifts some of the bottom and lets her eggs fall among it. The final result, known as a redd, is a small mound with the eggs in it and a hollow from which the mound has come. The male is in attendance throughout, and leaves his mate's side only to chase away possible rivals.

The effort exhausts the male to such an extent that he seldom survives long enough to get back to the sea. The female lives on more often, though she may have lost between one-quarter and one-third of her weight as a result of spawning. Known as a kelt, she returns to the sea and may come back to fresh water to spawn again. The whole process leaves a characteristic scar on the scales, making it possible to tell if a fish has spawned before. It is found that the percentage of females spawning a second time rarely exceeds five, but there are a few records of fish which have come back three and even four times. Menzies records the capture of a fish which had gone down to the sea originally as a two-year-old smolt and had returned to spawn for five consecutive years. He records that the oldest salmon ever caught had lived thirteen years and spawned four times.

Occasionally, as has been demonstrated on the River Dee, male parr may become sexually mature without ever going down to the sea, and such fish, though no more than a few inches long, may even mate successfully with a full-grown adult female.

That life-histories of equal complexity and interest cannot be related for the invertebrate inhabitants of fresh water is probably because the details have not been unravelled rather than because they do not occur. It is significant that among insect groups we must turn to mosquitos, studied so thoroughly because of their relation to disease, to find a clear-cut example of migration. *Anopheles sacharovi* in Palestine leaves the neighbourhood of its breeding-places in the autumn and flies for distances of up to 20 miles to find a place to hibernate. It spends the winter in a torpid condition in some dark damp stable or cavern and then in the following spring it flies back to the breeding-place to lay its eggs. The female has been impregnated the previous year, and all the males die at the end of each season when the weather gets cold. Incidentally, one result of this migration is that villages which enjoy immunity all through the main transmission season are smitten

with malaria just as it is coming to a close. Individuals of *Anopheles hyrcanus* in Bengal and Burma fly from the marshes where they breed during the winter and seek out the rice-fields as these are filled up during the monsoon. When the rains come to an end and the rice-fields begin to dry up, there is a regular flight of *A. hyrcanus* back to the marshes. But the exact nature of this mass movement is not known. One strange feature, which we learn from Major R. Senior-White, is that few mosquitos feed while on passage.

A journey connected with reproduction is made by certain stream-living flatworms. We propose to refer to it as migration though strictly it does not conform with Heape's definition, because there is no territory where the animals are never found except on migration. *Planaria alpina*, which has been mentioned several times already in other connections, first attracted the attention of Beauchamp and Ullyott because there was marked disagreement among previous workers who had observed it. Some held that it moved downstream with the current and others maintained that its normal reaction was to go against the current.

Beauchamp (1933, 1937) made a series of observations and experiments both in the field and in the laboratory. After a long period of trial and error he was able to provide the animals in captivity with conditions under which they would thrive. The main initial difficulties were due to substances dissolved out of the pipes of the water supply and from the paint which had been used inside the trough where the observations were made. This trough was several feet long and held about half an inch of water which could be kept running. An ingenious supply system was devised so that the direction of the current could be reversed at intervals. A flatworm was placed in this trough and the water supply was adjusted so that, whenever the flatworm was getting near to one end, the current was reversed and accordingly kept constant in relation to the direction of movement of the animal.

In cold springs sexually mature specimens may be found at any time of year, but generally sexual development is a winter phenomenon associated with a temperature of less than 10° C. When an individual is sexually mature, it tends to move against the current, and in his trough Beauchamp was able to keep specimens progressing steadily against the current for prodigious distances. In nature one of two things happens. The individual, toiling up the stream, may exhaust its food reserves and be unable to find sufficient forage to maintain

them. When this occurs it begins to reabsorb the material which had originally been destined as a provision for the embryo. With the onset of this process the reaction of the flatworm to the current changes and thenceforth it goes downstream.

In the lower reaches it is likely to encounter a better food supply and to be able to obtain the wherewithal to mature its eggs once more. It then starts upstream again. This sequence of events may take place several times, but eventually, unless the animal is unusually unfortunate, the second of the two alternatives mentioned above comes to pass: the planarian reaches the spring-head and there it lays the cocoon containing its eggs. This done it goes downstream either until it reaches the point where the temperature is too high (see p. 126) or it has fed well enough to become sexually mature once more.

Emigration is another term used in a restricted sense by Heape. He applies it to certain mass movements of which the best known are those of the lemming and the locust. The distinguishing feature of emigration is that there is no return. It is associated with a big increase in population, which is certainly sometimes due to an abnormally high rate of reproduction. Then suddenly the greater part of the population sets off and embarks on a journey which almost always ends in disaster; apparently these mass emigrations hardly ever result in any increase in the range of the species. The whole phenomenon clearly merits a distinct name, but here we shall refer to it as "mass emigration," leaving the term "emigration" for use in a looser and wider sense.

Mass flights are sometimes undertaken by various insects which spend part or all of their lives in fresh water, but it is difficult to know whether they should be regarded as true mass emigrations or whether they are no more than the random wanderings which every species makes within its range. Mass flights are not uncommon among certain dragon-flies. *Libellula quadrimaculata*, a common British species, is a noted wanderer, and what may be mass emigrations of large swarms are not infrequently recorded. The species is circumboreal in distribution, occurring in both the Old World and the New. The southern limit of its range extends to Sicily and the Caucasus in Europe, and to Kashmir in Asia. The native British population is probably augmented frequently by immigration from the continent of Europe.

Swarms of another dragon-fly, *Sympetrum fonscolombii*, which has an unusual range extending from S. Africa to N. Europe and China, rather rarely invade Britain. Frequently they consist of males only, but on some occasions females have been observed as well. The result has been the establishment of a colony which occasionally has perpetuated itself for three or four years, but which has always died out in the end. Evidently conditions in the British Isles are not suitable for this species, and, as far as is known, it has never become established as a regular inhabitant. Its continued occurrence on the British list is due to immigration. *Sympetrum flaveolum* is taken rather more frequently than *S. fonscolombii* but it likewise maintains itself in Britain only by immigrating from continental Europe.

Records of immigrations and other mass flights refer to dragon-flies far more often than to other groups. It is pertinent to ask whether this is because dragon-flies are more powerful fliers than other insects or because they are a more thoroughly studied group and are more conspicuous on the wing. The question cannot be answered but it is germane to point out that another well-studied group, the butterflies and moths, cannot by any means be described as having great powers of flight, and yet exhibits some remarkable examples both of migrations and mass emigrations.

It is likely that among other, more obscure aquatic groups there are comparable travels, though up to now the subject has been little studied. Balfour-Browne has made some observations on the beetles invading open tubs full of water, and another group about which something is known are the water-bugs. Walton (1943) describes a long series of observations on the water-bug fauna of North Somerset, and they include some records of population changes in a single pond. On each visit Walton continued collecting till it became difficult to secure any more specimens, and then he counted and identified his catch and returned it to the pond. It is a rough and ready method of obtaining an idea of the total number of bugs present but it is sufficiently accurate for the purpose required, and a really feasible alternative technique is difficult to think of. The population began to increase in September and by early October it was about four times what it had been. Metamorphosis of nymphs into adults could not account for the rise, and it was presumably due to immigration. By mid-November the population was back at its original level. Walton suggests that in the autumn, when all the nymphs have completed

their development, there must be considerable overcrowding in any pond where the year's breeding has been successful. The reaction to this is emigration and the emigrants arrive in other ponds such as the one which he had under observation. Many moved on and the composition of the population showed that different species departed at different times, one sex sometimes leaving before the other.

One may surmise, though it is no more than this, that there is much flying about of this sort but that it has been overlooked because a water-bug on the wing is not large and conspicuous, and therefore does not attract the attention even of the entomologist. It would seem that they drop into places in a haphazard way, for Walton records *Notonecta* landing on the shiny black top of a car. Another observer was taking advantage of a fine afternoon to tar the roof of an out-house when he was surprised, and perhaps vexed, to find large Corixids landing on the tar and getting stuck in it ; however he was sufficiently enlightened to call in a local entomologist, and the occurrence was put on record. It would appear, therefore, that water to an air-borne water-bug is no more than a shiny surface. But each species is confined to a narrow and well-defined range of conditions, some account of which is given on p. 134. It must, therefore, be assumed that, when a water-boatman arrives in a place where conditions are not suitable, it moves on again rather soon and ultimately finds a suitable place to live in by a process of trial and error.

If all the flying about which has been postulated really does take place, there is probably considerable mortality while it is going on. Walton was once watching water-bugs flying away from the muddy shallows of a river in the bright sunshine of an autumn afternoon, when a bat appeared and started to hawk up and down catching them. Then a sparrow-hawk swooped down and seized the bat—a most unusual food-chain, as Walton observes.

Mention of bright still autumn afternoons is found frequently in the few records which have been made. One of the present authors, walking on the Cumberland fells on a sunny windless afternoon in October, saw Corixids flying into small peat pools nearly 2,500 feet above sea-level. Twenty-three were caught in the space of three-quarters of an hour, and the interesting feature about the catch was that it consisted largely of a species very rare in the Lake District. If, as seems probable, the specimens had come from somewhere outside,

they must have flown six miles at the very minimum. On another occasion when climatic conditions were similar, though the season was spring, Corixids were seen leaving a pond in considerable numbers (Macan, 1939). In travels of the type just discussed the animals take to the wing of their own volition and set out in a direction which they themselves can choose; though nothing is known about the factors by which they do orientate themselves.

Finally there is a class of travel to which Heape has given the name dispersal. The traveller is a passive participant, transported by the wind or by some other agent such as a larger animal. Obviously fresh-water animals which do not have a winged adult stage cannot get from pond to pond, if there is no water connection, except by this means. Such meagre information as does exist has been discussed already in connection with the ecology of snails, on p. 130, and the remarks offered here refer only to the wind dispersal of animals which can fly. Once again a really striking instance is to be found only in the mosquito family and outside the British Isles. When the men of the Eighth Army were encamped in the desert before the battle of Alamain, mosquitos appeared among them, apparently as a result of a strong south-easterly wind, and there was even a small amount of malaria transmitted. The surrounding land was familiar to the Army and to the Royal Air Force and was known to be desert without water or at least without suitable breeding-places for the species in question. The mosquitos must have been transported by the wind for at least 30 miles.

Stuart (1941) has recently published some interesting information on the Chironomids breeding in rock pools at a place on the Clyde. The rocks shelve very gently down to the sea, and there is a gradation from pools which contain brackish water to pools which contain fresh water. A species which breeds in the pools nearest the sea can fly, but mating and egg-laying take place very soon after the adult has emerged —usually before either sex has used its wings. Species from the fresh-water pools do not mate so soon and take to the wing before mating. Stuart suggests that, though promiscuous dispersal of the latter by the wind will cause the death of many individuals before they have reproduced, the chances that some will reach a suitable breeding-place are sufficiently high to be of benefit to the race. But the brackish-water breeder will stand a very small chance of finding a suitable place for egg-laying if it is blown away from the immediate vicinity

of the sea, and its peculiar mating habits appear to be adapted to guard against such an eventuality.

Moon has described how, when the level of Windermere rises, those members of the fauna which are readily motile quickly move on to the newly inundated land. A big flood will cover grassland, and some animals, such as *Gammarus*, may be found among the grass stems. But the flat *Ecdyonurus*, adapted to spend its life clinging to stones, will not travel any farther when it comes to the edge of the stony region. A fair amount of colonization takes place within a matter of hours but it seems that the phenomenon is no more than the result of the random movements which the population is constantly making.

Berg records a general migration of the fauna into deeper water in the autumn and into shallower water in the spring. Some of the mayflies and stoneflies seek out the edge of the water immediately before emergence. Other animals seek deeper water in winter because the vegetation in the shallows dies down, and they can find the cover which they require only in the quieter regions at greater depths. But there is also a migration by animals not affected in either of these ways. The greatest number of zebra-mussels, for example, is found in deeper water in winter than in summer. There has been much discussion about reaction to temperature and to oxygen concentration but, since no clear-cut correlation has been demonstrated, there seems nothing to be gained from setting out the arguments here. This is an example of migration not directly concerned with breeding.

We must leave this aspect of fresh-water natural history as we have left others—a series of isolated observations many of which are far from complete. Fish, which are large and visible to the human eye at a distance, and which moreover have a practical importance as a source of food, have been well studied for many years. The smaller animals, the invertebrates, which can scarcely be seen and certainly not identified except at close range, and which are mostly without obvious practical importance, have been little studied. Such information about them as there is shows that the subject is well worth study; but at the present stage no general conclusions or wide inferences can be drawn.

CHAPTER 12

STOCK AND CROP

A PRELIMINARY to the main substance of this chapter is the topic of the relationship between the size of a fish and the attainment of maturity, for this relationship is quite unlike that found elsewhere in the animal kingdom. Most animals have a definite size when full-grown, and variation on either side of the mean is slight. A somewhat stunted specimen may be produced by insufficient food, but, in general, if the food supply is not sufficient to enable the animal to attain the size usual for the species, it is not sufficient to support life at all. Sexual maturity is usually attained some time before full size.

But sexually mature fish of one species may be anywhere in a very wide range of sizes. For example, trout in a Highland lochan or Lake District tarn may never grow larger than ½ lb., and at half this size they may breed and behave in every way as normal fish. But in a good chalk stream in the south of England many of the specimens will weigh 2-3 lb., and in some of the larger lakes trout weighing 10 lb. are not uncommon. Few other fresh-water fish grow as big as this, but all show a considerable range in size.

The reason why some populations of fish are made up largely or entirely of small specimens is a matter of the greatest concern to the fisherman, and we believe that some examination of the subject will prove of interest also to naturalists who are not anglers. A great deal of work has been done in America, and in the application of science to sporting fisheries the U.S.A. has a long lead over the rest of the world, but, because the Americans deal with different kinds of fish, their work is of theoretical rather than direct practical interest to us. Since this chapter has a practical bias, a start with European work is more logical, and the investigations of Professor Gunnar Alm in

Sweden may be noticed first. Alm is director of the State Institute of Fresh-water Fishery Research, and his paper (1946) describes the results of many years' observations on populations of perch.

He quotes the results of the measurement of individuals in big samples of fish from thirteen different lakes. In the lake in which the fish were biggest on the average, the average length was 25·8 cms. for male and 30·9 cms. for female fish ; in the lake with the smallest fish the average length for males and females was 9·9 cms. and 11·6 cms. respectively. Thus the average length in the lake with the biggest fish was nearly three times that in the lake with the smallest fish. Frequently the lengths in a large sample varied rather little on either side of the mean : in other words in any one lake all the fish tended to be large or small or medium-sized and not of many different sizes. The average size in one lake varied somewhat from year to year. The larger fish usually had a greater weight relative to length and so were better fish in every way. In general there was a relation between the average size of fish and the size of the water-body, the small fish coming from the small places.

How the rate of growth and the age of a salmon may be read from its scales has been described on p. 188. Alm found that the perch scale was less satisfactory than the salmon scale, and he was not prepared to deduce from the size of the rings the length of the fish at earlier ages. But he confirmed by extensive observations on marked fish that they indicated the age clearly, except in a few specimens of great age. The age-size investigations showed that perch in all the lakes grew at approximately the same rate for the first two years of life. After that growth might slow down almost to a standstill, or, at the other extreme, continue at the same rate. Those fish which continued to grow tended to live longer than those which did not.

Sexual maturity was found to depend on size. The male might be mature at one year old, but this was exceptional, and most mature males were two years old at least. The female was never mature at the age of one year, rarely at two and usually not till four. Alm found that samples taken outside the breeding-season contained roughly equal numbers of the sexes, but, as might be expected from their earlier maturity, males frequently preponderated greatly in a sample of spawning fish.

Alm postulates and proceeds to examine three possible causes of poor growth : heredity, direct action of the environment, and indirect

action of the environment through the food supply. Typical stunted populations were transferred to waters where growth was normally good; the transferred fish proceeded to grow well also. Alm is not prepared completely to rule out heredity, for quick-growing and slow-growing strains undoubtedly exist, but his results showed that, in general, stunted populations are not made up of fish that are constitutionally incapable of growing larger.

Investigations on the environment were carried out in a series of ponds, or tarns as Alm calls them, using the Norse word which will be familiar to north-country readers, and in a lake. This lake had been renowned for its big perch in the early years of the century, when anglers flocked to fish in it. After the 1914-18 war fishing was prohibited, and it was not resumed until the early thirties. The lake was then found to contain no big perch but a great abundance of little ones. A research team was sent to investigate, and they decided to try the effect of reducing the population. In 1937 they removed about 25,000 fish by means of traps and nets, and in subsequent years they not only continued to use these measures against the adults but attacked the population in its earliest stages. Branches were placed in the water, the female fish chose these as spawning-places, and then the removal of the branches in due course led to the destruction of a great deal of spawn. The result of this drastic reduction in the total number of fish was highly satisfactory. In 1937 most of the fish were between 14 and 16 cms. long, and the biggest taken was only 20 cms. long. Even in 1938 some effect was apparent, the most frequent length being between 17 and 18 cms. Steady improvement was maintained, and in 1945 the modal length was 21 cms., that is half as big again as it had been when the observations started, and greater than that of the longest fish taken in the first year. The conclusion is that the population had become too great after the ban had been imposed on fishing, the total food available when shared among all the fish enabled them to grow to a small size only, and a typical stunted population was the result. When the numbers were severely reduced, there was more food per head and each fish was able to attain a greater size.

The ponds, which were poor peaty tarns of the dystrophic type, contained small fish. Intensive fishing was tried, but it did not produce an increase in the average size as in the lake just mentioned. It seemed that they were incapable of supporting a population of good fish and Alm suggests three reasons: first, perch feed on zooplankton when

they are small but graduate to larger animals as they grow bigger. Dystrophic waters frequently have a rich zooplankton feeding on the organic matter washed in from the surrounding land, but a small population of larger invertebrates. There is therefore plenty of food for the smallest perch and many survive, but little for them when they reach the stage of requiring larger animals to eat. Secondly, the tarns are thermally stratified in summer, the hypolimnion becomes depleted of oxygen, and this restricts the volume of water in which the fish can forage. Thirdly, the tarns remain rather cold all through the season and this retards growth. Here too the conclusion is that the main reason for the stunted population is the insufficient food supply.

There is a school of thought which maintains that environmental factors other than temperature may affect fish growth directly. For example, big trout are rarely found in areas deficient in lime, and the view is that growth is adversely affected by an acid reaction or some other factor associated with lime deficiency. But the rival school, which associates the better growth with a better food supply in calcareous waters, seems at present to have on its side the balance of such scientific evidence as there is.

If it is accepted that a stunted fish population is usually due to an insufficient food supply, there are certain implications which are not generally accepted by those who practise fishery management. The first is that, since any one body of water can obviously support a certain weight of fish and no more, the weight of each fish will depend on the total number of fish present. For example, if a pond can support 100 lb. of fish, it may contain 400 fish weighing $\frac{1}{4}$ lb. each, 100 fish weighing 1 lb. each, or 25 4-pounders. This theoretical consideration is borne out by some figures quoted by Swingle and Smith, the American investigators whose work on adding artificial manures to fishponds is discussed in the next chapter. Three similar ponds were dressed with fertilizer, and the authors claim that the applications were made in such a way as to keep the food production relatively constant. The ponds were stocked with bluegill fingerlings of uniform size, receiving 6,400, 3,200 and 1,300 respectively. At the end of the season the ponds were drained and the surviving fish counted and weighed. The average weight in the first pond was 0·8 oz., in the second 1·5, and in the third 3·8 oz., and when these figures were multiplied by the number of survivors it was found that the total weight of fish in the three ponds was 320, 300 and 306 lb.

The logical deduction from this is that a fishery may sometimes benefit from a reduction of the fish population, a view which conflicts with the widely held idea that the cure for all fishing ills is to stock the water. This disagreement between common practice and research finding has caused certain scientific men to fly to an extreme and condemn *in toto* the fish hatchery and the policy of stocking. Thus Thompson (1941) writes: "In the light of our present information it is not impertinent to inquire which helps fishing more, fish-eating birds or fish hatcheries. . . . Fish culturists seem to believe that some magic attaches to the hatchery pond and that it is the cure-all for every fishing ill. The value of the hatchery was not seriously questioned until recent years, when the results of marking experiments and of population and growth investigations began to show that it has a negligible effect on fish yield, at least in waters comparable to those of Illinois. The Illinois Department of Conservation recognizes this and has not expanded its hatcheries in recent years, nor does it plan to do so. So firmly entrenched is the old idea, however, that it will probably require years of educational effort and demonstration to convince people that it is wrong."

There can be little doubt that a great deal of hatchery work is wasted effort, if it is not positively harmful, but the pendulum has swung too far, and it is unreasonable not to allow that the practice may sometimes have its merits.

In 1938 the Fresh-water Biological Association undertook to investigate the biology of coarse fish at the request of the National Federation of Anglers, who provided the funds. Mr. P. H. T. Hartley (1947) was appointed to undertake the work. His investigations, as was inevitable in the time at his disposal, did not probe as deeply into the subject as some of the others mentioned in this chapter, but they merit notice because of the balanced approach and neat formulation of the problems. He writes in his introduction that, at the start of the discussions with the National Federation of Anglers, it was assumed that "deficiencies of numbers and poor qualities of stocks were alike to be made good by the straightforward policy of restocking. . . . As discussions proceeded it became obvious that in making this assumption of the universal adequacy of the policy of restocking, a very great deal was taken as proven which was in fact open to question. It was seen that the fundamental problem was not the principles and practice of rearing coarse fish."

These initial obstacles having been negotiated, Hartley set out to discover three things about each specimen of as many of the British species as were available within reach of his station in East Anglia : first what it had been eating, second how big it was, and third how old it was (from its scales). With plenty of information from many localities, and with the information culled from the continental literature, it was possible to base on the last two items conclusions about how big each species should be at a certain age, if it were not to be classed as a stunted specimen. The object was to provide a reliable yardstick by which anglers and angling bodies could judge the fish of their waters before embarking on any policy of improvement.

For further guidance fish were divided into five classes : 1, large and young ; 2, large and old ; 3, average ; 4, small and young ; 5, small and old. If the fish be found to belong to any of the first three of these categories, it may well be decided that no steps are necessary, though if fish be large, it is possible that the water might carry more fish, and stocking would improve the sport for anglers. If the fish be small and all or nearly all are young, the population is being cropped too severely either by the anglers or by some other predator. Only after further investigation can it be decided whether the best policy is to impose restrictions on the angler's bag, or to start a campaign against pike or otters or whatever else is believed to be the culprit. If the fish be small and old, and Hartley fears that in all too many British waters fish do belong to this category, then the stock must be reduced. Existing limits on total catch or minimum size may be lifted, but trapping or netting will probably be necessary too. There is also the suggestion that predators might be introduced, but this is another controversial issue and we shall return to it later.

Hartley has produced simple criteria for the use of practical men who have only their leisure hours and their own resources for their fishery and its improvement. All that is required is, first, sufficient perseverance on the part of a few individuals to learn the technique of reading scales and then to apply it to a fair sample of fish, and, secondly, sufficient co-operation from all members to ensure that a representative portion of the season's catch is made available for weighing and scale-reading.

A good example of a scientific investigation obviously involving a great deal of work, is that of K. R. Allen (1945) on a river in New

Zealand. He points out that the facts about population which should be known as a basis for fishery management are :

1. The total number of fish at any one time.
2. The number in each age-group.
3. The average weight in each age-group.

The first of these categories, the total population, constantly arises as a problem in fishery work and usually proves the most difficult to solve. Allen caught many fish by netting, marked a proportion of them, and returned them to the river. Then, knowing the total number of marked fish, he calculated that this stood to the whole population as the proportion of marked fish to total in subsequent nettings. Clearly large numbers of fish must be examined if an answer worth anything is to be obtained, but Allen's work fulfilled this condition and, as he found incidentally from his marking experiments that the fish tended to stay in one part of the river, he concluded that his calculations were reasonably accurate. The total weight of fish is referred to as the stock.

4. The production, that is the total weight of fish grown in a given period. Total number of fish multiplied by average weight gives the total weight for an age-group, and the increase in the interval between two samplings is the production.
5. The crop, a term which Allen uses for the weight of fish removed by anglers.
6. The weight of fish destroyed in other ways.

Americans refer to the total weight of fish in a pond or lake (Allen's stock) as the carrying capacity, and they frequently measure it by the marking technique already described. But they have also obtained exact data by poisoning an entire body of water and collecting all the fish as they float to the surface. Powdered derris (5% rotenone) is applied at the rate of about 15 lb. to the acre, and a few sticks of dynamite are often thrown in to ensure thorough mixing. The effect wears off quite soon and the locality is restocked ; it is claimed that by restocking with certain species in a certain proportion the sporting properties are improved.

Thompson (1941) of the Illinois Natural History Survey gives data about the rate at which a pond may be fished. In Louisiana,

latitude 30° N., a weight of fish equivalent to the carrying capacity may be removed during the course of a year without fear of overfishing. But farther north, where fish growth is slower on account of lower temperature, the proportion is lower. In Illinois, latitude 40° N., 50%, and in Wisconsin, latitude 46° N., no more than 20% of the carrying capacity should be removed in a year. It is to be presumed that these figures are no more than rough approximations, but they illustrate an attitude and an approach which is worthy of notice.

But to pass from some of the more ambitious to some of the more humdrum aspects of American fish conservation, we find that a great deal of importance is attached to "catch per unit effort." Many of the fishing clubs are well organized and disciplined, and a careful record is kept of the number of hours which each member spends fishing, and the number and weight of the fish which he catches. As a check, fish are netted and the average weight of fish per haul recorded. If the amount of fish caught in the average hour on a line, or per average haul of the net, declines, overfishing is diagnosed. But, if people catch a lot of little fish, it is concluded that they are not fishing enough.

Overfishing may be counteracted by stocking, and by measures against predators; underfishing by trapping, netting, and introducing predators. This last, already mentioned as a controversial topic, is not so regarded by the Americans. Their literature contains precise instructions about the proportion of predators to pan fish (in Britain we should call them table fish) which should be introduced into a pond or lake which has been poisoned or emptied. For European waters opinion is much less definite, though Alm (1946) records improvement in the average size of perch after the introduction of pike into some lakes in Sweden.

The practical application of trapping and netting may be illustrated by an account of some work in Windermere. To make its purpose clear a recapitulation of the relationships of the common fish will be useful (Frost, 1946). Plankton is taken by char and by small perch, but, as the former feed out in the open in deep water and the latter in shallow water, the competition between them is probably slight. The invertebrate fauna of the stones and weeds in shallow water is preyed on by moderate-sized perch and moderate-sized trout, which means most of the population of both species, and also by the eel, though this fish probably feeds more in deeper water. Small and

moderate-sized fish are eaten by large perch, large trout, and pike, and of these the last is the most important ; it feeds mainly on perch in summer and char in winter. Taking the perch as the central point, it competes for food to some extent but probably not seriously with the char ; it competes with the trout ; but it is a food for the pike and, if it were not abundant, greater numbers of more highly prized species might be devoured.

During the 'thirties, Windermere was thronged with innumerable perch of very small size ; a few fishermen who knew exactly where to go could be seen returning triumphantly with 2- or 3-pounders, but for the majority half a dozen to the pound was a catch of big fish. There was reason to believe that this excess of perch had developed during the last few decades parallel with other changes in the lake which, as described earlier, had been proceeding relatively rapidly. And it seemed likely that with this rise the more highly valued trout and char had declined. Fishermen with a lifetime's experience of the lake spoke of bigger and better catches in their youth, and there was no reason to doubt their statements, although figures to substantiate them did not exist.

The work in other countries pointed to the conclusion that nothing but benefit would come of a drastic reduction in the number of perch. The survivors should be able to grow to a larger size, and there should be bigger trout ; the absolute numbers of this fish would not be affected, for that depends on events in the inflowing becks, where the early stages are spent, but with fewer fish to prey on the available food supply the average size should increase. Char also might show an improvement. But how were the perch to be caught ? There were no fishing restrictions to be relaxed ; perch were pulled out in thousands by holidaymakers every year but the number was probably but a fraction of the total population. Windermere was much too big to poison, even had such a step been feasible for other reasons. Nor could predators such as pike and cormorants be encouraged, for the local fishermen would have asked pertinently how it was known that their depredations would affect perch more than the other fish. It is one thing to introduce predators into an American lake which is being stocked after draining or poisoning and where a fresh start is possible if it turns out that a mistake has been made, but another to meddle with the balance of nature in a place where the slate cannot be wiped clean if the interference does not work out according to plan.

The staff of the Fresh-water Biological Association had been wont to catch perch for their own purposes with a seine, a long net which is laid round a selected area and then towed in to the shore by parties at either end of it (Plate XXXIIb). Their experience was that, though large numbers of perch could be caught in this way, it was not a practicable method of making serious inroads on the population.

Then war gave fresh impetus to what had previously been little more than idle speculation, and the necessity for maximum production of food in Britain provided a second motive. The perch in Windermere might be turned to good account as a contribution to the nation's larder, and after the war, when once more fresh-water fishing had only recreative value, sport should be improved.

But the cat was still unbelled. Then Worthington recollected the primitive traps of reeds and *Papyrus* stems with which he had seen the natives of Africa catching fish in Victoria Nyanza and the other great lakes. He copied the idea in fencing wire and wire-netting, and produced a cylindrical affair with a re-entrant funnel similar to that of the lobster-pot (Plate XXXIIa, p. 189). These traps caught nothing in the winter, which was not unexpected, for perch are in deep water during the cold part of the year, but with the coming of spring they gave results which surpassed the most optimistic hopes. As the fish came up into shallow water in April on their way to spawn, they flocked into these traps in large numbers, till sometimes it seemed there could scarcely have been room for another fish. Why they should do this was a puzzle to the investigators at first. It was thought that curiosity might impel the fish to examine the bright objects, for the traps of new galvanized wire-netting were conspicuous. But then traps painted different colours, some black, some white, and some red, were set in the lake. To the general surprise the black traps consistently caught more than any of the others. Later it was noticed that the traps were festooned with spawn, and it seems probable that the female fish chooses objects of this type on the bottom of the lake as a place to lay her eggs. It will be remembered that the Swedes knew they could reduce a perch population by putting branches in the water and removing them when they had been covered with spawn.

The traps are lowered to the bottom of the lake, each attached to a glass ball or a cork float. A series at different depths indicate at what depth the greatest catch is to be made, and in the rest of the lake all the traps can be set at this depth. As the fish advance

into shallower water, the traps are brought up nearer the shore. For some six weeks, from late April to early June, trapping proceeds hectically, then spawning is over, the fish disperse in the shallow water, and the numbers which enter traps is so small that fishing is not worthwhile. In the early years traps were emptied thrice a week during the season, but latterly once a week was found sufficient.

Sometimes a pike enters one of the traps and, although the entrance is only three inches wide, specimens of up to 4 lb. in weight have managed to squeeze through. The perch population inside is quickly reduced by such an intruder and no more will enter as long as it is there.

1940 was a year of trial and experiment. Results were satisfactory and it became evident that here was a method whereby large numbers of perch could be removed from the lake. Two problems remained: first, what was to be done with the fish, and, second, where was the labour to come from. Clearly the fish had no value on the fishmonger's slab, for many weighed no more than 1 oz. A lake perch is not by any means to be despised as a table fish, but it requires skinning and it has a great many bones. The housewife could not be expected to skin enough one-ounce perch to make even a war-time meal, and few people have sufficient time or patience to pick the flesh from so tiny a skeleton. The solution came when it was discovered that the perch could be tinned. Violent disturbance in a rotary mixer was found to rub off nearly all the scales, and cooking under high pressure softened the bones as it does those of sardines or salmon. Moreover, the perch-trapping season in the spring fell conveniently at a time when sea-fish, such as sardines and sprats, were not available for canning, so Mr. Banks, head of a fish-canning firm in Leeds, promised to take all the perch which could be supplied to him. He canned them in oil or war-time tomato juice and put them on the market as "Perchines."

The Association's staff could provide some of the necessary labour but a great deal more had to be found somewhere. The co-operation of local residents interested in the lake and its fishery was sought, and there was a generous response, almost every one who owned a rowing-boat, and many who did not, volunteering to give assistance. The lake was divided into areas, each based on some convenient landing-place, and within each area traps were allocated to people who lived or kept a boat conveniently near, usually 20-30 to each man. On the appointed day, in the evening, for many of the helpers had businesses

to run or jobs to work at during the daytime, the lifting of the traps would begin. Each man emptied the traps of his beat into a box, made a record of the total weight, and then took the catch to the landing-point, leaving the traps in position once more. Then, late at night, a lorry collected the catch from each landing-place and took it away to Leeds.

In 1941 trapping started in earnest, though only in the north basin of Windermere. The season lasted ten weeks, and the catch was 25½ tons of perch, 2½ cwt. of eels, and 2 cwt. of pike. In 1942 both basins of the lake were fished, and the total catch increased somewhat, amounting to 30½ tons of perch, 5 cwt. of eels and 2½ cwt. of pike. Thenceforward both basins of the lake were fished but the catch began to decline, being 13½ tons of perch in 1943 and 6 tons in 1944. Since then it has been relatively constant at about 5 tons per year.

It is interesting that the catches stand in just the same relation if they are expressed as the average weight of fish per trap in the six best weeks of the season. The figures for the north basin during the first four years are 21·1, 11·3, 6·0 and 2·9 lb. per trap, and thereafter the amount remains roughly the same. These figures show a drop to about half the previous catch each year up to 1944, just as those for total catch did. The south basin figures are similar, but the average is a little higher each year, which is interesting since other studies have indicated that the south basin of Windermere, which receives the sewage from Bowness and Windermere town and the drainage from the fairly thickly populated Esthwaite valley, is more productive than the north.

Obviously this drop in catch was related to a reduction in the total population ; but just how is not known, for there has been no information about the total population of perch in the lake. Total catch, and catch per trap, after dropping steadily became constant at about one-sixth or one-seventh of the original total. Possibly this is a measure of the reduction of the whole population, but until certain aspects of perch behaviour have been investigated further, a conclusion would be premature. When the population of a certain area is thinned by netting or trapping, infiltration from adjoining areas probably brings about uniform fish density in a fairly short time. But this may not continue indefinitely and there may be a density at which there is little tendency to invade adjoining areas, whether these be sparsely inhabited or not. The traps evidently attract fish, but from how far

they attract them or to what extent the principle just enunciated may operate is not known. Other objects may be more attractive than the traps, but whether this be so, what the objects are if it is, and how frequently they occur on the bottom of the lake are all unanswered questions. These are some of the unknown factors which make a simple relationship between catch and total population unlikely. But research continues and an answer to the problem is being sought assiduously.

The average size of Windermere perch is little bigger than it was before 1941, an unexpected result which is under investigation at the moment. Scientific data for the trout and char have not been obtainable, since it is not possible to organize a proper creel census on a lake fished by so many short-term visitors, and the capture for examination of large numbers of these two game-fish would not be permitted by the fishery board. The remaining possibility was to send a circular to all fishermen with long experience of Windermere asking their opinion on whether or not the fishery had improved. The majority stated that both char- and trout-fishing were better than they had been before the perch-trapping started, the fish being bigger and more numerous.

The reduction of the perch population led to the danger that the pike might take heavier toll of trout and char, and accordingly in 1944 a campaign against this species was inaugurated. Again there was the problem of how to catch large numbers and again the answer came out of Africa. The African carp or ngege (*Tilapia esculenta*) is caught in special nets which are made in this country but never used here. They are made of a fine flax twine (35/3 ply) with a large mesh, 2½ inches knot to knot. Each net is a sheet about 50 yards long and 10 feet deep, and it is fitted with corks along the top and lead along the bottom. It is stretched across some suitable stretch of lake, and the fish entangle themselves, usually behind the gills, if they chance to strike it.

Some of these nets were procured and tried in Windermere, suitable lengths being stretched from the shore into deep water, athwart the track of any fish cruising parallel with the shore. Results were satisfactory, for most trout and all char passed through the meshes, and pike ranging from 2½ to 31 lb. and monster trout weighing up to about 10 lb. were caught. The capture of these large trout was an advantage, for they also are fish-eaters, and they are too large to be attracted by anything which the fisherman offers them. Fly-caught

trout from Windermere are usually under 1 lb., and the angler who captures with a spinner a fish weighing over 5 lb. may expect to see his photograph—with the fish—in *The Westmorland Gazette.*

Nearly 3 tons of pike were removed from the lake in the first season, the winter of 1944-45. The next two both yielded catches about half that of the preceding season, just as the perch-trapping had done. In the fourth season, 1947-48, the catch was of the same order as that of the preceding season and in this too there was a resemblance to the perch-trapping. The "catch per unit effort" had dropped considerably and the total population of pike has evidently been drastically reduced. But the exact extent of the reduction is not known because there is no information about the total population.

It is unlikely that man can do anything to reverse evolution and change Windermere back into a typical char-trout lake, and, if it were possible, an argument against the step would be that it would make the lake less productive. If man wishes to maintain in the lake a good stock of char and trout, there is little doubt that he will have to take active steps to keep one side of the balance of nature continually weighted. This large-scale ecological experiment on the fish of Windermere, which is described and discussed more fully by Worthington (1950), has shown how the weight can be applied, but it remains to be discovered how much weight is required to keep the balance constant at any given point.

CHAPTER 13

FISHPONDS AND MANURING

THIS chapter, like the last, opens with some remarks about fish growth. The growth of fish will not be good unless they are getting enough to eat, but, when the food supply is sufficient, other factors which affect growth come into play. The maximum rate of growth is different in different kinds of fish; thus, according to the German fish cultivators, a carp will increase its weight by about 12 oz. during its second growing-season, whereas a trout will not put on quite as much as half that amount. The growth-rate may vary within one species and as an example—an extreme example, it must be pointed out—some results obtained by Mr. Langman, keeper at Wray Mires fish hatchery, near Wray Castle, may be quoted. A sample of ordinary rainbow trout measured, on the average, 3·6 inches at the end of their second year; the *shasta* race of the rainbow trout, under identical conditions, averaged 5·6 inches.

Temperature is another factor which influences fish growth. The European carp farmer reckons to produce rather less than 1 lb. of carp, per individual fish, in a year, but in the higher temperatures of Palestine and India production at the rate of 1 lb. per month has been claimed. Thompson (1941) gives an interesting table showing how productivity in America increases with decreasing latitude.

One final preliminary point is the place in the food-chain of the fish which is to be cultivated. Each link yields only about a seventh of the amount of living matter produced by the link before it. If, therefore, a piece of water contains a plant-eating species, it will produce seven times more fish than if stocked with a carnivorous species. The weight of fish-eating fish, such as the pike, will be seven

times smaller again. The figure seven is an approximation which has been discussed in Chapter 9 (p. 146). Thompson (1941), working in Illinois, found that a pond containing only non-fish-eating species would produce five times as much as one inhabited by piscivorous fish.

These three theoretical considerations will serve to introduce the study of productivity as it presents itself to the practical fish-farmer. Most of the research was done in Germany between the two wars, though latterly the main advances have come from America. A comprehensive summary of the published work was made by Dr. C. H. Mortimer on the outbreak of war in 1939, and the results edited by two colleagues after his departure for war service (Macan, Mortimer and Worthington, 1942). In Britain it is now a matter of centuries since fresh-water fish have been cultivated for any but sporting purposes, and the stew-pond of the monastery and the manor has long since fallen into disuse. Presumably the rise of the sea-fishing industry and the improvement of communications between fishing-ports and inland markets have combined to bring this about.

The yield of a fish-farm can be measured exactly, and possible sources of error, which cause so much concern to the hydrobiologist investigating a natural lake, do not arise. A known weight of fish is put into a pond which has previously been empty; at the end of the season the pond is drained again, and the amount of fish flesh produced during the year can be ascertained precisely.

Of the theoretical points outlined above, temperature is a factor beyond human control. Artificial heating of a pond is not commercially practicable, and the cultivator must normally depend on the heat provided by the sun at the place where he happens to live. It is interesting to note, however, that ponds kept at a temperature higher than normal for North Europe by the discharge from factories of water used to cool condensers provide a favourable habitat for the snail, *Physa acuta*, a species otherwise almost confined to the Mediterranean region and probably originally found only there. The presence of the snail is evidence that the water contains nothing toxic to animal life and so should be suitable for fish cultivation; there would seem to be scope for enterprise on the part of some firm with a pond of this sort.

The ideal fish for pond culture feeds entirely on vegetable matter. Such fish occur in the African lakes, but not in European waters.

Many of the coarse fish do feed to some extent on vegetable matter but they grow well only when a good proportion of animal food is available. From the point of view of the food-chain, therefore, there is not much to choose between our various fresh-water fish, though theoretical considerations would rule out the pike. Actually, most of the European work has been done with three fish, the carp because of its rapid growth, the trout because of its high value as a table fish, and the tench because of its hardiness and ability to do well under conditions which prove unfavourable for the other two.

Schäperclaus (1933), in the standard German text-book on the culture of fish in ponds, gives some figures about the production of fish which may be expected in ponds of different types. In a typical moorland peaty fishpond the yield of fish in a year is put at between 25 and 50 lb. per acre ; in a lowland pond with a hard water supply and a rich silted bottom 200-400 lb. of fish per acre may be grown in a year. These figures are similar to those of the farmer, who reckons that pasture will produce, according to its quality, between 5 and 300 lb. of meat per acre per annum. The data just quoted are based on observations on ponds stocked with one-year-old carp. The trout cultivator cannot hope to do as well, for, according to Schäperclaus, though the average yearling carp and yearling trout are both of approximately the same weight, about 2 oz., the carp will weigh some 14 oz. at the end of its second growing-season, and the trout only 7 oz.

The problem which interested the Germans was how to obtain 400 lb. of fish from a pond which, left to itself, would produce only 25 lb. It is significant that Germany had not only the biggest organization for the study of purely practical aspects of fresh-water fish production, but also, at least in Europe, the biggest organization of theoretical fresh-water biologists. But, before aspects of pond improvement involving some knowledge of the theoretical background are described, it will be convenient to dispose of the most straightforward method, which is to supply the fish with food not of aquatic origin. Meal made of lupins or of soya beans has been used for carp and tench, and horseflesh or offal is a standard diet for trout. In the present state of knowledge it is safe to say that this is the method which is most certain to yield results ; but it is not generally a commercial proposition and is rarely practised except, perhaps, by sportsmen with means.

The remaining methods of improving the crop of fish all depend on the same principle. The very basis of the food-chain is tackled and substances are added to the water in order to increase the number of primary producers—that is the algae and the rooted plants, the former being the more important.

From what has been said above in Chapter 2, it will be clear that the nature of the pond bottom is of paramount importance. A good bottom is a mixture of organic matter derived from the dead bodies of animals and plants and of inorganic matter in a fine state of division, that is silt, of which the importance was stressed on p. 106. On such a bottom decomposition proceeds more rapidly than on other types, and another characteristic of importance is that it absorbs chemical substances added to the water to increase the growth of living matter. They return to solution slowly and gradually. The other two types into which bottoms, broadly speaking, can be classified, the peaty and the inorganic, will not retain manurial salts, and most of the dose may be washed out of the pond before the plants have been able to make use of it.

The peaty bottom consists of plant remains which have undergone little or no decomposition. The absence of calcium is commonly one of the reasons why decay has not taken place, so that the addition of lime will usually bring it about, and produce a more satisfactory substratum. It is stated that 7-8 cwt. per acre is sufficient for a bottom which is just acid, but the dose must be increased with increasing acidity; the most extreme conditions, which will be a pH under 4, should receive 30-60 cwt. per acre of calcium carbonate or half that amount of lime.

Inorganic bottoms consist chiefly of clay, sand or gravel, and they may be improved by an addition of stable manure or sewage sludge.

Before we leave the bottom of the pond it may be remarked that the European practitioners are agreed that it is beneficial to allow the pond to dry out for a period of a few weeks each year; it is, of course, usually done in winter when the fish are not growing and are in special winter ponds where they can be kept closely crowded together. What processes take place is not known, but it is believed that exposure to the air causes oxidation of the mud to a depth greater than occurs under water, and that this has a beneficial effect on production when the pond is refilled. It is probable that in cold weather the soil will

retain enough moisture to keep many of the mud-dwelling animals alive. There is disagreement, on the other hand, about the advantages of the practice of leaving a pond dry for a whole year and planting leguminous crops on the bottom. Accumulation of nitrogen from the nitrogen-fixing bacteria associated with Leguminosae is one obvious advantage of this technique, but it may, perhaps, not compensate for the destruction of the bottom fauna.

The European workers emphasize that the best results from the application of the various manures which they have tried will not be obtained unless the lime requirements of the water have been met. They estimate that the lowest concentration for really good production is 65 parts per million of calcium carbonate. This is a little more than 20 parts of calcium per million, a figure which, as noted in Chapter 8 (p. 132), appears to be significant in the ecology of aquatic animals.

Of the various manurial substances which have been tried, phosphate has given the most satisfactory results, and increases in productivity of the order of 100% have been claimed. It may be obtained as super-phosphate, basic slag, bone meal, or di-calcium phosphate; the last three contain a certain amount of calcium, for which allowance must be made when the lime requirements of the pond are being calculated. Between 1 and 1½ cwt. of phosphate per acre is the recommended quantity, and it should be applied in two doses, the first in May or June, about a fortnight after liming, where this has been necessary, and the second in July or August. A larger quantity will produce a greater yield of fish, but the increase will not be proportional to the extra amount of phosphate applied.

The European workers find that the addition of half as much potassium to the phosphate is beneficial, but their results with nitrogen in the form of nitrates or ammonium salts have been conflicting.

The Americans have approached the problem from a different angle, and the attitude of the two countries reflects their respective positions in the world. The main German work started after the 1914-18 war when the country was exhausted and impoverished, and impressed with the need to gain the maximum return for the minimum outlay. The American work reflects a state of mind which demands slick, quick results, and does not need to give undue thought to the expenditure of resources. Swingle and Smith (1941) of the Agricultural Experimental Station, Alabama, are perhaps the two most familiar names in American fish-culture. These workers set out

to find what substances were required to produce a maximum growth of phytoplankton, and discovered that the most important elements are nitrogen, phosphorus and potassium mixed together in a certain proportion. These substances were available in a commercial artificial manure known as " 6-8-4 (N-P-K)," a title which denotes a content of 6% available nitrogen, 8% phosphoric acid and 4% potash, and could most easily be obtained in this form. The proportion of nitrogen in this mixture is too low to promote the maximum growth of phytoplankton and so 10 lb. of sodium nitrate should be added to every 100 lb. of it.

This manure is applied at intervals at the rate of 100 lb. to the acre. The first dose is put on in the spring when vegetation first shows signs of growth. The result is such a rich growth of phytoplankton that the water assumes a pea-soup appearance, and the bottom is not visible at a depth of 18 inches. As soon as it is visible at this depth, another dose is applied and this criterion is used to denote when further applications are required all through the summer. The effect of maintaining such a dense crop of phytoplankton is to deprive of light and so eliminate all rooted vegetation, an end which the Americans believe to be desirable.

Swingle and Smith estimate that untreated Alabama fish-ponds, according to their nature, produce as little as 40 or as much as 200 lb. of fish per acre per annum. This range is similar to that found in European waters ; the fish are quite different on the two continents, but all are " coarse " in the terminology of the fisherman. Addition of chemical manures to Alabama ponds leads to a production of 500-600 lb. of fish per acre per annum. This is rather more than the production in European ponds, but, then, the rate of manuring is considerably greater. When the applications are made according to the transparency of the water, between eight and fourteen will be necessary during the course of the season, the actual number depending on the natural salt content of the water. One acre will receive, therefore, anything from 800 to 1,400 lb. during the year. A recommended German dose is 1½ cwt. of phosphate and ¾ cwt. of potassium, which is a little under 250 lb. per acre per annum. The American dosage is, therefore, three to six times as great as the European.

A slightly different mixture, " 4-8-10 (N-P-K)," has been used in Canada in the Quebec region, where it is estimated that the average natural yield of trout is only about 6 lb. per acre. The manure was

added to three experimental ponds in different amounts, and the yield in three months was 65 lb. of fish with a dose of 64 lb. to the acre, 70 lb. of fish with three times this amount, and 121 lb. with five times this amount. The irregular results are attributed to the fact that the amount of water flowing through each pond was not the same. It seems likely also that the German finding that an increase above a certain dose does not lead to a commensurate increase in the production of fish may explain these results in part at least. The work is only preliminary but it does give a pointer to those who are interested in the production of trout.

In America less importance is attached to liming ponds deficient in calcium, and the only recommendation is that, for waters which are neutral or acid, 15 lb. of powdered limestone should be added to every 100 lb. of 6-8-4 (N-P-K) mixture. It is also recommended that ammonium sulphate should be avoided as a source of nitrogen in acid waters as it tends to produce sulphuric acid. It should be replaced by a nitrate salt.

Organic manures may also be used for increasing production in fish-ponds, and a variety of substances, such as farmyard manure, certain waste vegetable products, and even the weeds dragged from another pond have been applied. The Americans claim good results with cotton-seed meal, and state that the effect is nearly doubled if superphosphate be mixed with it. The addition of substances of this nature to a fish-pond must be carried out with caution, and frequent small applications are necessary; too large a quantity may, in the process of decomposition, use up so much of the oxygen dissolved in the water that the fish will die.

The organic matter in sewage has been used for many years in Europe to increase fish production, but the practice has never caught on in this country, and the health authorities react unfavourably to any suggestion that it should be tried; they remain unconvinced by the continental claim that there is no risk of infection with sewage-borne diseases. In Europe fish are kept for a week or two in clean water, between their removal from the sewage ponds and their despatch to market, and it is maintained that during this period they become free of all organisms which cause disease in man.

One of the best-known installations is at Munich, which possesses three features essential for the successful application of this practice. First there was available an area of ground which was suitable as a

site for the ponds and was of no great value for any other purpose; secondly, a clean river is available to dilute the sewage liquor with well oxygenated water; and, thirdly, the sewage effluent is not contaminated with any industrial waste-product toxic to fish. The sewage effluent is passed through the usual screens and sedimentation tanks and then, having been diluted with between four and ten times its own volume of well oxygenated water, it is run into the fish-ponds.

One acre of fish-pond six feet deep will purify the domestic sewage from about 1,000 people, and the production of carp in this volume of water is of the order of 500 lb. per annum according to the published figures. In the Munich fish-ponds rainbow trout have been cultivated successfully, in addition to carp and tench.

In hot still weather there may be a risk that decomposition will deplete the ponds of oxygen, and it may be necessary to cut off the supply of sewage liquor for a period of several days. There must, therefore, be an alternative method of sewage disposal at a time when successful disposal is at its most difficult, and this is a fourth condition which has to be fulfilled before the purification of sewage in fish-ponds is feasible.

One further obvious but nevertheless sometimes overlooked fact about fish growth, which requires notice before this discussion comes to a close, is that maximum production cannot be obtained if the initial stock is too small. In fact, the size of the best initial population has been the subject of a large amount of research. Rather detailed instructions are available to continental fish-farmers for stocking ponds which can be drained, and the following is an example. The stock for an acre of pond, of which the estimated production in a year is 100 lb., would be: yearlings, 45 carp, 50 tench and 35 trout; two-year-olds, 20 each of the same three species. It is estimated that deaths among the yearlings would carry off 20% of the tench, 10% of the carp and between 2% and 5% of the trout, but among the two-year-olds deaths would only amount to between 2% and 5% of all the species.

To summarize: in Europe the yield of fish has been improved by adding phosphate and potassium or organic matter to fishponds, but results with nitrates have been conflicting. Base-deficient ponds must be treated with lime before the other substances are added. In America a mixture of nitrogen, phosphorus, and potassium has been used successfully. There is no doubt that the addition of inorganic or organic

matter is a valuable way of improving the yield of fish in a pond or lake, but at present research is scarcely beyond the empirical stage. All the results so far relate the yield of fish and the chemical treatment directly, ignoring the intermediate links. The importance of knowing something about these will be evident from what has been written earlier about food-chains, and till these have been studied no final word on the best treatment for any particular pond or species of fish will be possible.

CHAPTER 14

IMPURE WATER

MAN has probably used streams and rivers to dispose of his refuse ever since he started to live in settlements. The practice, however, did not lead to really unpleasant results until he began to forgather in large towns and to dump into the nearest river not only his domestic waste material, but also that which emanated from the factories in which he was employed. Fitter (1945) records that the last salmon was taken from the River Thames in 1833 and, to judge from other rivers, this indicates that bad pollution had been affecting the river for several decades previously. In 1827 an anonymous pamphlet drew attention to the disgusting state of affairs whereby the Thames was used both as a sewer and as a water supply. Conditions over the rest of the country were no better though perhaps they did not get so bad quite so soon. The first step in any sort of retrenchment was the Public Health Act of 1875 and the Rivers Pollution Prevention Act of 1876, but neither achieved its full object and the battle for pure rivers is still raging to-day.

The commonest form of pollution is that caused by sewage. The important constituent is organic matter, which consists of carbon and hydrogen linked together in chains, attached to which are nitrogen and certain other elements, notably sulphur and phosphorus. As soon as it is released into water, this organic matter is readily attacked by bacteria, which find in it a rich source of energy and nourishment. The result of their activities is the breakdown of the complex organic compounds into simple inorganic substances such as water (H_2O), carbon dioxide (CO_2), nitrate (NO_3), sulphate (SO_4), and phosphate (P_2O_5). All these compounds, it will be noted, contain oxygen. When a sewage effluent is turned into a river the immediate result is, there-

fore, a rapid using up of the oxygen dissolved in the water. If there is still some organic matter left when all the oxygen has been used up, decomposition still goes on but now it is caused by a different set of bacteria which do not require free oxygen. Typical end-products are methane or marsh gas (CH_4), ammonia (NH_3), and sulphuretted hydrogen (H_2S). Some of these compounds are poisonous.

The speed of a biological activity increases with increasing temperature. If sewage is discharged into warm water, breakdown takes place within a short space of time and therefore within a short space of river. In colder water the decomposition will be extended over a greater length of river, the sewage will get mixed with a larger volume of water, and the chances of the oxygen supply being sufficient are improved.

If the amount of sewage is small and the quantity of water large, the reduction in the concentration of oxygen will not be great enough to harm any organism. It is likely, although it has never been demonstrated, that the discharge of some sewage has a beneficial effect on a river, since the productivity of a pond can be increased by running sewage through it. But a sewage effluent always brings in a certain amount of suspended matter, and this may settle in quiet parts of the river and form banks of sludge. If these overwhelm gravel stretches where trout are wont to spawn, fishery interests may be affected adversely.

More sewage and less water will lead to a state of affairs where the oxygen is reduced to a value at which some animals and plants will die. A further approach of the relative amounts will lead to the serious situation where oxygen is totally depleted and compounds which are toxic to life are produced.

The effect of an effluent must be considered not in relation to the average flow of a river but in relation to minimum flow and maximum temperature. The whole question was investigated very thoroughly by the Royal Commission on Sewage Disposal which, appointed in 1898, issued its final report, the ninth, in 1915. The Commission's recommendations were that, where there is a dilution of 1 volume of sewage to 500 volumes of water, crude sewage can be discharged without harmful result. Where the dilution is between 300 and 500 the effluent should conform to a standard which can, in effect, be attained by screening off the larger solid matter and allowing fine particles in suspension to settle. When the dilution is between 150

and 300, an effluent of the standard which they recommend can be obtained by some chemical precipitation in addition to screening and sedimentation. But if there is less than 150 volumes of water to 1 volume of sewage, then the sewage should be subjected to complete treatment.

Complete treatment is usually necessary, and there are many ways in which it can be done. The subject is a big one and its literature extensive, but an excellent summary of modern practice is given by Parker (1938). He describes five main methods. Septic tanks are now used only for small communities and single houses in the country. The sewage is run into an excavation in the ground and there it decomposes without oxygen. The liquor percolates away into the soil and the solid sediment is removed at intervals. This is quite satisfactory as long as the liquor does not run into a stream immediately, for it is a highly toxic effluent charged with the products of oxygenless decomposition. It is purified as it percolates through the soil.

In all the other methods there is some preliminary treatment in which solid matter is strained off and allowed to settle. The liquor is then passed on for further treatment. It may be subjected to precipitation by chemicals; this is a popular method in America, though it is not widely practised in this country except where certain trade effluents make it necessary.

An old-fashioned method still in use at some places, for example Oxford and Cambridge, is to run the sewage on to the land and allow decomposition by bacteria and other biological agencies to take place there. Provided that there is plenty of suitable land available—it should be flat with a porous soil—that the location is reasonably remote so that nuisance is not caused, and that there is no danger of polluting water supplies through fissures, this remains a satisfactory technique.

The most popular method to-day is the sprinkling or trickling filter, in which the organic matter is also broken down by biological agencies, but in a much smaller compass. A sprinkling filter with its squat cylindrical chamber and its rotating arms is, for some reason, a common object of the countryside near railway lines. The liquor, having been distributed by the rotating arms, trickles down through a bed of broken stone, coke or clinker. The very large surface exposed by these materials is colonized by a complex film of living slime consisting of bacteria and protozoa with higher animals, chiefly worms

and the larvae of midges and moth-flies, dwelling in it. The component organisms absorb organic matter and break it down, and the final effluent, after passing through a last sedimentation tank, may be pure enough to drink.

The most modern treatment is the activated sludge or bio-aeration process. It depends on the presence of certain bacteria which cause the organic matter to precipitate as a sludge or floc, on which they, protozoa, and other organisms cluster. The sewage liquor is agitated by compressed air or some other means at the beginning of the process, and then the floc is left to settle. A small amount of it is mixed with freshly introduced liquor to initiate the process of precipitation, and the rest is removed to drying beds.

Besides sewage, a number of trade wastes are commonly discharged into rivers, often with disastrous effect. Beet-sugar factories, places where milk is handled, breweries, distilleries, slaughter-houses, and flax-retting plants all produce effluents which are essentially similar to sewage, since the effective component is organic matter. The concentration, however, is usually greater. They can be treated in the same way as sewage and can be admitted to the local authority's sewage works without causing any difficulty, though allowance may have to be made for the higher concentration.

Redeke (1927), in a review of the subject, recognizes a second group of industries: leather, cellulose, textiles, and glue, which yield effluents containing poisonous inorganic substances in addition to organic matter. Special preliminary treatment is necessary before purification in an ordinary plant is possible. Factories where leather is produced emit an effluent tainted not only with the washings and scrapings from the hides but also with the compounds of arsenic and chromium which are used to cure them. After lime precipitation it can be treated in an ordinary sewage works. Effluents from places where cellulose is treated contain bisulphite of lime in addition to organic matter. It can be rendered innocuous if the effluents be allowed to ferment. Textile effluents contain both acids and alkalies. These will neutralize each other if present in equivalent amounts; actually lime is usually required to balance excess acid. If dyeing is also carried on, there are likely to be excessive amounts of sulphur compounds in the effluent. Finally, the manufacture of glue, size, glycerine and similar substances is associated with an effluent containing hydrochloric acid.

In Redeke's third group are industries which produce only a poisonous inorganic compound. Coke ovens, for example, give rise to cyanides as a waste product. Metal works give out acids and also metallic compounds of which some, such as those of copper and lead, are deadly to living organisms in quite small concentrations. Artificial silk manufacture involves the production of sulphides. Where china clay is worked the streams may become charged with fine particles, which eventually settle on the bottom and form a blanket which effects a purely mechanical suppression of life. All these effluents can be rendered harmless but each one requires a special treatment, and none can be discharged direct into the sewage works of the local authority.

Cole (1941) in an account which has the advantage of being more up to date than Redeke's, though the disadvantage of being concerned with American practice, which differs in certain details from British, classifies effluents according to their effect on fish. The primary division is into those which act directly and those which act indirectly. Those which act indirectly may do so either by using up oxygen, so that sewage and any effluent with organic matter are included here, or by destroying the fauna on which fish feed. Paper-mill effluents may contain fibrous material which settles on the bottom and stifles all forms of life by forming a mat, and sawdust may bring about the same result. There are also certain heavy fractions of oil and tar, which are insoluble and therefore not toxic, but destroy living organisms by forming a continuous layer on the bottom.

Cole's list of direct poisons includes acids, tar acids, ammonia, sulphuretted hydrogen, cyanide, arsenic from tanneries and sheep-dipping, and chlorine and chloramine from industries using bleaching powders. As far as is known all these substances enter the body and poison the tissues. Another class includes metals such as copper, lead, zinc, iron, cadmium, and mercury. Their action, which has been elucidated by Carpenter (1927) and later workers in Wales, is entirely upon the gills of fish ; no trace is to be found inside the fish. Carpenter showed that soluble salts of these metals precipitate an organic compound when they come into contact with the mucus on the gills and body of the fish. This is sloughed off, but, if there is a constant supply of the metal, there is constant reformation of the precipitate and the gills finally get clogged ; the fish show signs of respiratory distress and eventually die. A concentration of only one part of lead in three million is lethal.

New processes are always being introduced into industry, and a new process may mean yet another toxic substance discharged into streams and rivers. One example of a dangerous substance which has not been in use for very long is D.D.T. (dichlorodiphenyltrichlorethane), now used widely in sheep dips. It is highly toxic to insects and the accidental introduction of D.D.T. into a stream is likely to lead to serious depletion of the insect fauna, and so will affect the fish through their food even though it is not present in strong enough concentration to kill them directly.

Having catalogued the various substances which may be discharged into the country's streams and rivers, we may now turn to some of those streams and rivers and examine the effect of pollution on their fauna and flora. The Tees may be taken first, since a great deal is known about it as a result of thorough study by a team of competent investigators. The river itself, excluding the estuary, receives many sewage effluents, and the pollution is sufficient to cause marked changes in the composition of the fauna and flora, but this is such a common phenomenon that it has been included in Chapter 7 with the straightforward account of river life. The pollution is not sufficient to affect the fish and the trout-fishing is good. But one tributary, the Skerne, is very foul, and Butcher, Longwell and Pentelow (1937) wrote of it :

" The history of the fisheries of the Skerne is a striking example of the effect of pollution. In the early years of this century it appears that this river contained large numbers of trout and coarse fish, and that it was improving, for in 1901 the Report of the Fishery Board records that for the first time in living memory sea-trout ascended the river and spawned at Darlington. They continued to do so until 1903 but there is no record since of their visiting this river. Almost annually the Board records some pollution which killed fish in the Skerne, but in 1906 and 1907 it was still considered worth while to stock the river with trout. After that it appears that pollution increased and the Fishery Board gave up the unequal struggle. Now the capture of a trout is sufficiently rare to be recorded in the local newspapers. There is no doubt that in the absence of undue pollution the Skerne would support a large stock of fish."

Though the fresh-water reaches of the Tees are not seriously affected, the estuary is in a very different state, and this has a marked effect on the salmon which must pass through it. Alexander, South-

TABLE 6

Average number of fish caught at the mouth of the Tees in nets

Period	*No. of salmon caught*	*No. of sea-trout caught*
1904-08	6,411	5,229
1909-13	8,067	5,816
1914-18	5,122	1,825
1919-23	5,730	4,423
1924-28	2,850	1,274
1929-33	1,826	816

gate and Bassindale (1935) kept a watch on the smolt migration of 1930 and picked up 2,246 dead bodies stranded on the bank. It was impossible to estimate how many were washed out to sea unrecovered or overlooked for some other reason, or how many fell a prey to the gulls which could be seen taking a heavy toll of the smolts, presumably those in a moribund condition or at least suffering ill-effects to some degree. The figure 2,246 obviously represents but a small fraction of the total casualties.

The estuary receives the sewage from a population of some 280,000 persons in seven miles, and the oxygen may fall to 9% of saturation. But during the period of smolt migration the lowest concentration recorded was 50% of saturation, and it was found that this was not low enough to be lethal. And apparently the tar acids, which were present generally in a concentration of between 0·1 to 0·3, rising occasionally to 0·5 parts per million, were not causing the death of the smolts either. All the evidence pointed to the cyanides, of which there were about 0·2 parts per million parts of water. Experiments with invertebrates showed that some species were killed by this concentration and others were not. The fauna of the estuary was not greatly different from that of unpolluted but otherwise similar estuaries elsewhere, though a number of marine species did not penetrate as far into the Tees as into the unpolluted estuaries (Fig. 14, p. 117). In spite of the hazards provided by sewage, tar acids and cyanides, some smolts were evidently, at the time of the survey, making their way to the sea, and some salmon were returning and penetrating to the spawning grounds. But the number has been decreasing since the turn of the century,

and the tale is clearly told by the figures in Table 6. This shows the decline in the number of fish taken by nets at the mouth of the river ; the numbers caught by angling had shown a similar but even greater reduction.

Turing (1947) continues the story : " In 1937 the catch was 23 ; to-day it is nothing."

The Trent provides a classic study in the pollution and repurification of a river, and the result of Butcher's (1946) study of it are reproduced here in Fig. 19. He recognizes four zones :

1. The zone of foul pollution in which only the sewage fungus flourishes ; a few Tubificid worms represent the animal kingdom ; and plants, though the number of species is greater, are also few in individuals.
2. The zone of pollution, where Tubificids are numerous but other animal life absent apart from some red Chironomid larvae ; sewage fungus is still abundant but algae are now much commoner ; *Chamaesiphon* and *Cocconeis*, however, are very scarce and the population is made up largely of *Stigeoclonium*, *Nitzschia palea*, and *Gomphonema parvulum*, though the first of these three was not abundant in other polluted rivers examined.
3. The zone of mild pollution characterized by large numbers of the water hog-louse, *Asellus*, and a great abundance of all species of algae ; sewage fungus is rare.
4. The repurified zone where, other things being equal, the fauna and flora is similar to that found above the source of pollution. The total number of algae is less than in the preceding zone and *Chamaesiphon* and *Cocconeis* tend to be the most abundant species.

The highest point from which fish were recorded was just within the zone of mild pollution, and the point above which the local fishermen reckoned that angling was not worth while was about five miles downstream from the beginning of the repurified zone.

The animal figures were obtained by Mr. Pentelow, as the result of hand-net collecting, and therefore are not accurately quantitative. The figures for algae are the number growing on one square millimetre of a glass slide left in the river for 21 days.

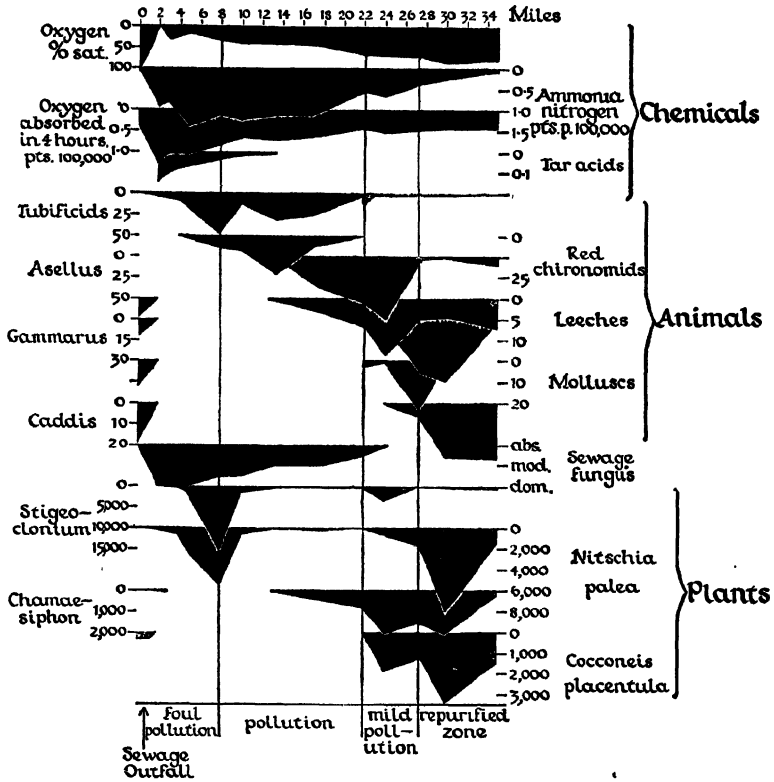


FIG. 19
Pollution in the River Trent

Fig. 20 shows a similar set of data for the River Churnet and the lower Dove. Over a stretch of ten miles not one single animal was found; plants were not affected so severely as this but in the first five miles they were very scarce. This was apparently due to a copper works, and analysis showed 1-2 parts per million of copper in the water.

The effect of lead-mining on the fauna of streams has also been studied carefully. The industry is a very old one in parts of Wales but, by the beginning of the century, most of the mines had fallen

into disuse as they could not compete with bigger undertakings elsewhere. Some were reopened during the 1914-18 war but closed down again soon after it was over.

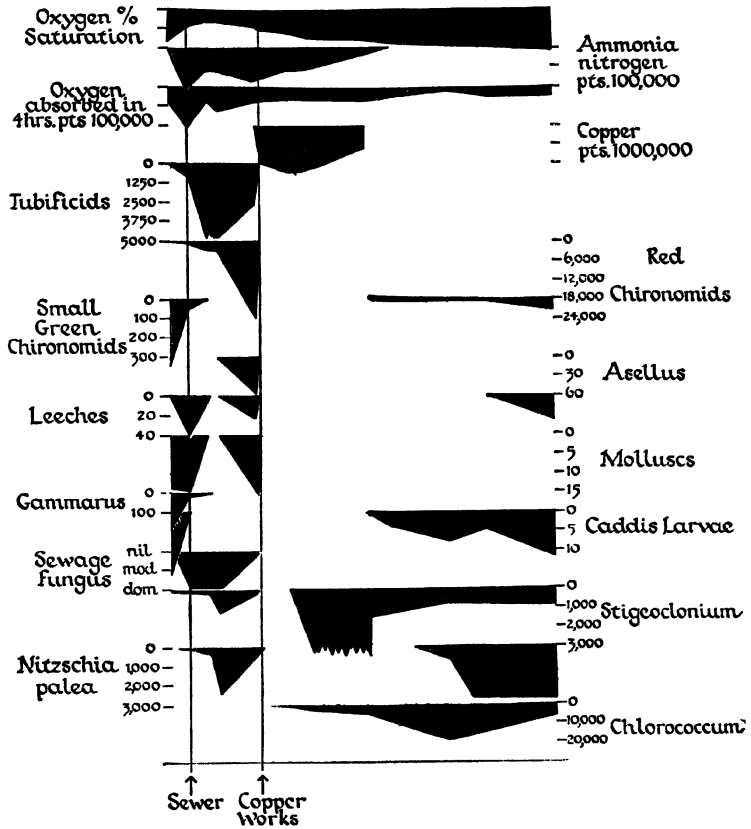


FIG. 20
Pollution in the River Churnet

The rock is crushed and ground and then elutriated so that the lighter particles of stone are carried away and the heavier particles of galena or lead sulphide remain. Originally the washings were carried away by the nearest stream and, as far as can be made out from the records, this caused no trouble until machinery was intro-

duced to do the crushing and grinding. Complaints then arose that the washings, which inevitably contain some metal, damaged pasture when they were deposited on the land by floods, and even caused the death of stock. To counter this the practice was adopted of sedimenting the washings before discharging the washing-water. This stilled the complaints but it gave no protection to the aquatic fauna, as the washing-water contains lead in solution. Furthermore the heaps of debris which accumulate from the sediment in the washing-tanks may yield enough lead, when rain-water seeps through them, to poison the stream for years after the mining has come to an end.

Laurie and Jones (1938) describe a survey of the lower reaches of the River Rheidol, in Cardiganshire, which drains an area in which there are no less than 43 derelict lead-mine workings. A few of these were opened up again during the 1914-18 war, and when Dr. Kathleen Carpenter surveyed the stream in 1921-22 she was able to find only 14 species of animals. The composition of the fauna was interesting. All the animals belonged to the phylum *Arthropoda* and most of them were insects ; among the insects the absence of caddis-flies (Trichoptera) was noteworthy. Analysis showed that there were 0·2 to 0·5 parts of lead per million parts of water.

By the following year there had been considerable recovery and Carpenter recorded 29 species, including Trichoptera and a flatworm, *Polycelis nigra*. The concentration of lead was less than 0·1 part per million, though it rose above this figure in floods.

Laurie and Jones made their survey in 1931 and 1932 and recorded 103 species, including molluscs and fish, which had been notable absentees in the earlier surveys. They believed this to be the normal fauna of a stream of the type of the Rheidol and accordingly concluded that recovery was complete. The concentration of lead was of the order of 0·02 parts per million rising to 0·1 part per million after heavy rain.

The authors point out that their figure of 103, which does not include the very small animals such as the Protozoa, is probably not completely accurate, since they were able to place many of the insect nymphs and larvae in the genus only and, in some genera, there may have been more than one species. They also adumbrate the possibility that the beds of these lead-polluted streams may contain silt and coarser particles, which are derived from the mine refuse dumps, and which would not be present in a stream-bed derived wholly from the

process of natural erosion. At present, however, faunistic knowledge is not sufficiently detailed to make possible an assessment of what effect this factor may have on the fauna.

Carpenter (1926) recognizes four stages in the pollution of a stream by a lead mine :

1. No life at all.
2. A sparse fauna composed almost entirely of insects, among which Trichoptera are notable absentees ; a sparse flora with such algae as *Lemanea* and *Batrachospermum* and a few mosses and liverworts.
3. A richer fauna, including Oligochaetes (worms), Turbellaria (flatworms), and Trichoptera ; flora including Chlorophyceae.
4. Fauna completed by the appearance of molluscs and fishes ; flora by the appearance of higher plants.

These four stages may be seen in one river with increasing distance from the source of pollution, or at one point in a river with the passage of time.

These are examples of what pollution may do to the living organisms in a river. The rivers chosen are those in which detailed observations have been made and put on record by experienced biologists. A survey of the state of all the main British rivers is, at the time of writing, being carried out under the auspices of the British Field Sports Society. This survey is bound to be more superficial than those just referred to, but it leaves no doubt that what has been described is the rule rather than the exception throughout England and Wales.

The study of the effect of pollution leads on to the important matter of assessing pollution. A bacterial test is often carried out, and the purity of the water judged by the number of bacteria whose real home is the human intestine. This is a simple and reliable method of detecting pollution from sewage, and it has the advantage that it also gives a measure of the degree of contamination. But the drawback to it is that a negative result tells nothing. There may easily be intermittent pollution which is sufficient to harm the fauna but which will not be detected by the bacteriologist if his sample is not taken at the right time ; and perhaps the offender is releasing his effluent only after dark or at some other time when he has reason to suppose that no-one with a sampling-bottle is prowling near the river. Moreover it is

practicable to mix sewage with some bactericide, usually chlorine, so that decomposition is delayed for a period. This practice is not uncommon when, in the interval, the sewage is carried out to sea, but it is also available to the unscrupulous person seeking to avoid a summons for pollution. Further, the bacteriologist will not detect pollution from sources other than sewage; though possibly, since copper is a good bactericide, the extremely pure condition of the Churnet (see Fig. 20) below the copper works might have led an astute observer to suspect something unusual.

The chemist can cover a wider field. He tests for pollution with organic matter in various ways. First, and most important, is the amount of oxygen in solution in the water; but it is not always possible to test for this, because certain reagents must be added to the sample immediately after it has been collected. The actual amount of organic matter may be determined. In a sample of water left to stand, organic matter will be decomposed and the process will use up oxygen. The chemist measures the amount of oxygen which disappears in a given time at a given temperature, and assumes that it is proportional to the amount of organic matter. He calls his answer the B.O.D., which stands for biological or biochemical oxygen demand. The amount of oxygen taken from potassium permanganate in a given time at a given temperature is a chemical reaction giving some indication of the amount of organic matter present; it is found to be a useful test in practice though little is known about what exactly does take place. The amount of ammonia is also an indication of the degree of pollution. How the concentration of oxygen rises, and the B.O.D. and ammonia concentration fall as a polluted river gradually repurifies itself is shown in Fig. 19.

The chemist can also test for other known toxic substances such as metallic salts, and a chemical analysis to examine for the presence of every substance known to have a harmful effect on fresh-water life is well within the bounds of possibility; but it is a lengthy process. Moreover it can never be ruled out that some hitherto unknown substance is causing the trouble; and the chemist may be misled in the same way as the bacteriologist by a sample not taken at the proper time.

When the source of pollution is known, bacteriological and chemical analysis is the best way of following its fluctuations and discovering whether it is getting better or worse. But, if the question is whether

or not pollution is taking place, then, ideally, tests based on an examination of the fauna and flora should be made. We have already referred to the four zones of sewage pollution of Butcher and to the four zones of lead pollution of Carpenter, and it is not necessary to pursue description further. But, except where there is a big growth of sewage fungus, detection by biological means will never be quite as straightforward as by bacteriological and chemical tests. The composition of a fauna and flora varies widely according to conditions. The biologist who is investigating pollution must have behind him a rather wide range of experience, so that at any place he can say with confidence what sort of fauna he would expect, assuming that there was no pollution. The number of such people at present is very small, and this is the main disadvantage of the biological approach to pollution detection; bacteriologists and chemists with the requisite knowledge and skill may, on the other hand, be found all over the country.

It must be emphasized that conditions are not indicated by the presence of one individual of one species; it is the composition of the whole population which provides the clue. *Asellus*, the water hog-louse, for example, is not by any means confined to places where there is pollution, and the finding of one specimen is no indication that sewage or organic matter from any other source is entering the river. In fact, as recorded in the next chapter, *Asellus* is one of the animals which, in the days before filtration, colonized water-mains rather readily. But, if *Asellus* is the commonest animal, the existence of pollution is likely. Even so the biologist would be unwilling to commit himself without further examination of the animals and plants, both upstream and down.

Although law is a subject best left to persons with a legal training, no account of the pollution of our rivers would be complete without at least an outline of the measures which have been taken to curb the evil and some indication of why they have not curbed it. At common law a riparian owner has a right to receive water unaffected by the activities of persons higher upstream. But it is often difficult to obtain conclusive evidence that pollution is taking place, and the expense of seeking an injunction or damages in court is greater than most private individuals are prepared to risk.

The Rivers Pollution Prevention Act of 1876 applies to all non-tidal waters and to any tidal waters which have been declared a stream

by the Minister of Health. It makes it an offence to discharge into a stream solid matter so as to interfere with the flow of the stream or to pollute it with sewage or factory waste. But there is an escape clause to the effect that no offence is committed if the best practicable and reasonably available means are being used to render the discharge harmless. Any measures to render an effluent harmless will cost money, and it was successfully argued that an expensive outlay for this purpose did not come within the meaning of " reasonably available." This was a cogent argument in the seventies—the heyday of industrial expansion and free competition—and to-day the whole populace is conscious as never before of the vital part which industrial production plays in the life of the nation and of the importance of low costs. None the less it is difficult to resist the conclusion that the Act of 1876 weighted the scales unduly against those interested in keeping rivers pure ; and that many concerns used the escape clause to avoid installing purification plant which they could very well have afforded.

The enforcement of the Act was placed in the hands of the local authorities, most of whom made little use of the new power bestowed on them. One may surmise that they were unwilling to burden the rates with the expense of installing a sewage-purification system in response to what they perhaps stigmatized as a new-fangled whim. It is interesting to note (Frankland and Morton, 1874) that in 1874 the Commissioners, appointed in 1868 to inquire into the best means of preventing the pollution of rivers, came to the following conclusion about cholera and typhoid, now of course known to be caused by bacteria : " The existence of specific poisons capable of producing cholera and typhoid fever is attested by evidence so abundant and strong as to be practically irresistible. These poisons are contained in the discharges from the bowels of persons suffering from these diseases." The Commissioners were enlightened men, and their advanced theories probably did not impress local councillors, who possibly were not. Furthermore, if the pollution of a river led to difficulties over water supply, that was a problem for the next local authority down the stream and no concern of the one responsible for the trouble.

The duty of enforcement was transferred to County Councils when these were formed under the Local Government Act of 1888, and this did produce some improvement, as the jurisdiction of a County Council extended over long stretches and sometimes over the whole of a river. The Local Government Act also made provision for the setting up of

joint committees to administer the Rivers Pollution Prevention Act, and where these were formed they did achieve a measure of success.

The general position, however, remained highly unsatisfactory, and in 1898 the Government appointed a Royal Commission on Sewage Disposal. This set about its duties in a thorough manner and initiated original research when it could not obtain from any other source information which it considered important. The final report was issued in 1915. The commission recommended certain standards, for example the desirable dilution for sewage described above, and gave an account of methods by which different kinds of effluent could be rendered innocuous. The middle of a war was, however, an unfortunate time for the issue of a report of this sort.

The Salmon and Fresh-water Fisheries Act of 1923 made it an offence to discharge into tidal or non-tidal waters any substance liable to injure fish or affect adversely their spawning-grounds or food. Local fishery boards can institute proceedings under this Act, but they seldom have the financial resources to employ scientifically trained staff or to embark on litigation which might prove costly. And so rivers are still polluted.

Various persons and bodies interested in river purity campaigned vigorously between the wars. In 1921 the Salmon and Trout Association convened a meeting at Fishmongers Hall and the outcome was a deputation to the Minister of Agriculture and Fisheries, who appointed a Standing Committee on River Pollution. This committee, which was allocated no funds, made surveys and could call on the technical experts of the Ministry of Agriculture and Fisheries, which, at about this time, equipped a laboratory and appointed some scientific staff. The committee aimed to prevent pollution wherever possible, by amicable arrangement when this could be arranged and by legal action through the Fishery Boards when it could not. They were concerned with preventing fresh pollution rather than with an assault on the entrenched strongholds.

In 1926 the Salmon and Trout Association and the British Waterworks Association drafted a memorandum and sent it to Mr. Stanley Baldwin. In the following year, with the Fishmonger's Company, they organized a deputation on which almost every one of the many diverse interests in water was represented. The result of this deputation was the setting up of a Central Advisory Committee and a Water Pollution Research Board, the latter to continue the work of the Royal Com-

mission which had dissolved in 1915. This was a particularly necessary step, not only to investigate ways and means of dealing with effluents of various kinds and to seek continually ways and means of improving existing methods, but also to keep on terms with advances in industry and possible new sources of pollution. Some idea of the scope of the Water Pollution Research Board may be gained from the fact that it issues monthly a summary of current literature, each number summarizing between 100 and 200 papers.

But the central problem of how to enforce the use of the known methods of purification still remains. At the present time the British Field Sports Society is in the vanguard of the campaign for pure rivers, with a series of reports intended to cover eventually every river of any note in England and Wales.

Local authorities faced with the problem of sewage to dispose of and industrial concerns which have waste products to get rid of are on one side, and on the other water-supply undertakings, fishermen, and presumably any member of the community who derives pleasure from nature. Almost every authoritative opinion voiced has stressed the need for an over-riding authority with power to weigh the claims of the conflicting interests and issue judgments which cannot be ignored.

At the time of writing new river boards are being set up, and a report by the Central Advisory Committee recommends that they should be equipped with new legal powers under an Act repealing that of 1876. It is suggested that each should lay down standards with which effluents discharged into its streams and rivers must comply. These standards should be incorporated in bye-laws, subject to confirmation by the Ministry of Health after interested parties have had opportunity to raise objections, or put forward arguments in support.

CHAPTER 15

PURE WATER

THE subject of water supply can be approached in two ways by the naturalist : how do the inhabitants of fresh water affect the engineer ; and how does the engineer affect the inhabitants of fresh water ?

The congregation of population in great conurbations, coupled with ever advancing ideas about hygiene and cleanliness, has made water supply one of the major features of modern civilization. It is easy to imagine that, if in a thousand years' time our civilization is represented by nothing but ruins, great concrete reservoirs, or vast masonry dams blocking valleys, or even the conduit tunnels bored through the hills, will be among the more imposing of the remains.

Water supply is not only a matter of conveying water in the required amount to the required place at the required time. The water must also be purified, for it can be a dangerous substance to drink. The traveller who, in tropical lands, is not careful about where his water comes from, runs the risk of contracting a number of serious diseases. Notoriously rampant in Egypt is a small worm of the fluke type known as *Bilharzia*, a name which has been simplified to " Bill Harris " by the British Army, sometimes to be relatinized into " Billharrisia " by persons who wish to parade a show of knowledge. *Bilharzia* lives in the abdominal veins of man and there it lays its eggs. These work their way through the tissues to the bladder or the rectum, according to the species, and are passed to the exterior. There is no further development unless they reach fresh water, but the chances of this happening are high in a country where the local populace has no knowledge of hygiene. A larval stage comes out of the egg and swims off in search of a certain kind of snail. If the search is successful, it enters the snail, penetrates the liver, and there repro-

duces asexually, giving rise to a great number of young. A small swimming stage emerges from the snail and it reinvades the human host, penetrating any part of the body if it is not taken in at the mouth. Another disease, also interesting to the zoologist, is caused by the guinea-worm which, when adult, lies in the tissues in a tube which communicates with the surface for egg-laying through a small ulcer. The creature, which may reach a length of 40 inches, is commonly removed with the aid of a matchstick on which it is rolled, a little bit being extracted each day. Its other host is a small water-flea, and the life-cycle is completed only when a human swallows an infected water-flea while drinking or bathing.

Then there are the diseases caused by bacteria : cholera, fevers of the typhoid group (which are not to be mistaken for typhus, a disease carried by lice), and the complex of complaints which goes by the name of dysentery. Recently some evidence has been brought forward that certain disease-causing viruses may pass from man to man in water, and this possibility is under investigation.

In Britain the only diseases known definitely to be water-borne are due to bacteria and there is nothing higher in the biological scale which will harm human beings. Of the three mentioned, cholera is now unknown in these latitudes and has been so for more than fifty years, though as recently as 1874 it carried off 20,000 people in an epidemic. Danger from typhoid and dysentery is never completely absent, though both are now rare. Even a few cases of typhoid provide headline news to-day, though a century ago epidemics with a death-roll of thousands were only just beginning to excite comment. Water, therefore, is safe to drink in Britain if it is free of disease-bearing organisms. But the waterworks engineer has to go further than this, for what is good for the consumer and what the consumer wants are not identical. The layman seldom worries unduly about bacteria, for what the eye cannot see the heart does not grieve about, but he does demand that his water shall be colourless, tasteless and free of any living thing which can be seen. Nothing, we understand, leads more quickly to an angry letter or to an enraged caller at the waterworks office than the emergence of something alive from the domestic tap. The waterworks engineer must, therefore, solve the problem of rendering water free of taste, colour, and all visible matter, dead or alive. The customer is always right.

Water may be taken from three main sources—underground

supplies, lakes or reservoirs, and rivers ; and there is a different set of problems associated with each one. Underground supplies are usually free of bacteria and all other forms of life, for percolation through soil is an efficient method of filtration. But it is a mistake to suppose that underground water, even though it comes from quite deep down, is necessarily pure. Sometimes there are cracks and fissures through which water polluted at the surface may run straight down into some subterranean reservoir without any percolation through soil.

Modern methods of testing the purity of water depend on ascertaining the number of *Bacterium coli* per litre. *Bacterium coli* is an inhabitant of the human intestinal tract and can live for quite a long time in water. Although itself harmless, its presence, therefore, indicates contamination with human excreta and implies a potential risk that bacteria which cause disease may be in the water too. A standard assessment of purity is :

Under 20 *Bact. coli* per litre—good					
20-100	,,	,,	,,	,,	fair
Over 100	,,	,,	,,	,,	bad

Complete absence is not demanded, as a certain number are derived from animals other than man.

The engineer who can tap a subterranean supply of water is likely to be faced with the problems of hardness, oxygen deficiency, and richness in nutrient salts. Hardness is a purely chemical problem. The chief effect of oxygen deficiency is to bring into solution any iron present in the soils through which the water has come. Certain bacteria oxidize soluble ferrous compounds back to insoluble ferric iron, and, if there is much organic matter present, they may be extremely abundant. When water rich in organic matter and ferrous iron is led through pipes, a gradual blocking up of the pipes by the deposition of ferric iron will be caused by the activities of the iron bacteria. Furthermore, the water which reaches the consumer will be stained a rusty colour, and a dripping tap will leave unsightly stains on bath or wash-basin.

If underground water is rich in plant nutrients it should not be brought into an open reservoir or there will be a crop of phytoplankton to be coped with.

Many large towns within reach of Scotland, Wales, the Lake District, or the Pennine Chain derive their water from some reservoir in the mountains; either utilizing an existing lake, which is often increased in size by a dam, or by blocking a valley and creating an entirely artificial reservoir. Some of the lakes are "primitive" and yield almost pure water; the dissolved substances in Thirlmere, Manchester's supply, are similar to those in Ennerdale Water given in Table 1, on p. 16, and the water could safely be supplied straight to the consumer without any treatment at all. Actually, to guard against remote possibilities, the water is chlorinated. Other lakes are more productive and accordingly less ideal as sources of water, for the greater amount of life means that the water must be filtered as well as chlorinated; the richer the lake the greater the work and therefore the higher the costs at the filtration plant.

When a reservoir is to be created on a site where there is no standing water already, there are various questions with which the biologist, if asked, can help. The first has to do with the choice of the site itself. Usually engineering considerations are paramount, for the number of places where a dam could economically be located are very limited. Nevertheless there are examples known to the authors where two sites have been available, one nearer and one farther from the town to be supplied. Choice has fallen upon the nearer site on account of the shorter and therefore cheaper supply line, with the result that a reservoir which might have been sited in barren moorland has been sited in lower land, which is cultivated and enriched annually by the dung-spreading activities of the farmer. The expense of filtering the richer water have soon exceeded the sum saved on the shorter supply line.

On the shape of a reservoir also the biologist has definite ideas, though well aware that the ideal is not a feasible engineering proposition. Biologically, a reservoir is a lake and subject to all the phenomena characteristic of lakes. In Chapter 4 a fundamental difference between a eutrophic and an oligotrophic lake was described. The eutrophic lake is rich and the richness leads to a depletion of oxygen in the lower colder layer of water or hypolimnion. This increases the richness still further. But eutrophy is not entirely a function of the richness or the amount of nutrient salts available. If a lake be deep, it will have a big hypolimnion and there will be so much oxygen available that total depletion in the course of a summer

is unlikely. Conditions are then said to be morphometrically oligotrophic. If a reservoir must be built in country which is likely to yield eutrophic conditions, there will be considerable advantage to be gained from making it so deep that it is morphometrically oligotrophic. The ideal reservoir is deep and has a small surface area so that the volume of water receiving sufficient light to make plant growth possible is small. Productivity, therefore, is low. But in practice the shape of a reservoir is likely to be determined chiefly by the height to which it is possible to build the dam.

Theoretical studies of lakes lead to a third point which is of practical importance in water supply. Every lake is continuously evolving at a greater or slower rate. Primarily this depends on changes in the surrounding land but the lake itself tends to accumulate material and accordingly to become richer in the course of time. The big lakes of the Lake District have been changing extremely slowly in the centuries which have elapsed since their formation; but smaller bodies change more rapidly, and there are records of great changes in reservoirs within the space of fifty years. Clearly the retarding of the rate of evolution is of fundamental importance in waterworks practice.

Pearsall (1947) suggests three ways in which this may be done. The first arises from a consideration of what is known to have happened in natural waters. Evolution in the Lake District lakes has been associated with weathering of the rocks, with cultivation of the land, and with human settlement. Reservoir interests will desire to restrict all three as far as may be practicable. Weathering is obviously beyond human control, but soil erosion, which also leads to the enrichment of water, may be regarded as part of the process. It can be arrested to a considerable degree by planting trees, particularly on steep slopes near the water.

Control of agricultural practices is not feasible, and in this small and crowded island compromise between conflicting interests is often unavoidable; wherefore if agricultural land has been selected as the site for a reservoir there is not much that can be done. But one of the authors can recollect seeing a farm right on the edge of a reservoir and, just beside the farm, a large manure-heap. A strip of dark green luxuriant grass stretched from the dung-hill to the water's edge and indicated plainly that a rich supply of nutrient material was seeping from the one to the other. A slightly different site for the manure

would have made quite an appreciable difference to the reservoir, but probably none to the farm. Some authorities fly to the other extreme and seek to banish even the sheep and the hiker from the whole of the catchment area. This is certainly going to unnecessary lengths, and it is difficult to understand the reason for it. The increase in productivity due to man and sheep will be slight and will not make a big difference to the load on the filter beds. To postulate risk of pollution with disease-bearing organisms is illogical, since precautionary chlorination is already a standard practice.

There will always be some matter in suspension in the streams whatever is done in the drainage area, and this will be deposited in the reservoir. Pearsall suggests that each inflow of any size should run into the main reservoir through a small shallow basin. Much of the matter in suspension would settle in this basin, and periodically the water could be run out of it and the sediment on the bottom removed.

The third measure concerns the vexed question of cropping. Water undertakings often exclude anglers from their reservoirs for fear that the water might become contaminated with the bacteria of some disease ; but this is a specious objection as has just been shown. The advantage of angling is obvious. Some nutrient salts will enter any reservoir, however perfect the site or thorough the measures already described, and part of what comes in will not go out. The accumulating matter is constantly circulating. It is built up into plant bodies at the base of the food-chain and may then pass through a succession of animal bodies, culminating in fish. At all stages there is death and decay, and the breakdown of dead bodies into simple constituents completes the cycle. If fish are continually being removed, matter is being withdrawn from this cycle and the accumulation of nutrient material is retarded. Theoretically it is possible to check it completely.

In south and east England it is not practicable to bring water from large rain-filled reservoirs, since suitable gathering-grounds are too far away. Nor is there always a suitable or sufficient supply of water available underground. There is then no choice but to take water from some large river. Such water will certainly be rich, because the river will have passed through fertile agricultural land and will have received the effluent from many sewage works. A copious production of life cannot be avoided, and the engineer must seek ways

and means of ridding his water of organisms before letting it into the supply mains.

Large reservoirs are an essential feature of a water-supply system derived from rivers. They store a reserve which can be drawn upon at times of greatest demand and they also have an important function as sedimentation tanks for the mineral matter which every river carries in suspension. Some intestinal bacteria can survive for a period in fresh water but they cannot reproduce to any great extent, and consequently storage in a reservoir greatly reduces their numbers. But the still, clear conditions, with a big surface area, are ideal for the growth of phytoplankton. Phytoplankton leads to zooplankton and to larger animals as well, though, in a reservoir with sides running down sheer to a depth of several feet, conditions are not very good for these last, provided that rooted vegetation is not allowed to grow.

These living organisms must be strained off before the water is fit for domestic supply, and this is generally done by passing it through a bed of sand. Pressure may be applied (either by means of a big head of water or a pump), or it may not. These two methods, rapid and slow sand filtration respectively, are almost always augmented by some other process.

Chemical precipitation is often associated with rapid sand filtration. The water is first treated with alum or some other substance which, on contact with water, gives rise to a colloidal hydroxide of iron or aluminium. A jelly-like net is formed in the surface layers and sinks to the bottom, taking with it all particulate matter, living and dead. The water is then passed through the sand bed.

A slow sand filter is commonly used in conjunction with biological filtration and purification. The process takes place in a rectangular basin not unlike a swimming-bath to look at. Gravel is placed on the bottom and above it a graded series of sands, 2-3 feet deep, the finest being at the surface. Water is run into the basin and allowed to stand for a few days. The result is a rich living growth. Various algae particularly diatoms, bacteria, and protozoa form a carpet on the surface of the sand, and larger animals, particularly Chironomid larvae, may inhabit this carpet in great numbers. Underneath it bacteria grow on the sand grains, which they surround with a gelatinous covering. This complex of living organisms is the effective part of the filter. It exerts a mechanical effect and planktonic algae and animals are strained out on its surface. It also oxygenates the water and this

is an advantage for several reasons, not least because water with plenty of oxygen dissolved in it has a sparkle which is pleasing to the palate of the connoisseur. Much organic matter in the water is oxidized and broken down into simple compounds, and these, with inorganic substances already present, are removed by the algae. It seems likely that some part of the system, possibly the gelatinous envelope round the bacteria in the sand, is absorbent, for traces of substances such as copper which have been used to kill algae in the reservoir are removed by a slow sand filter.

After filtration the water is chlorinated, for there is always a chance that a few bacteria may pass the filter ; and then it is ready for supply to the consumer.

A filter-bed clogs up sooner or later, sooner if the water contains many diatoms, for the skeleton of these plants is relatively indestructible. Some species appear to be a good deal worse than others. The surface layers of sand are then removed and cleaned and the whole process starts afresh. Pearsall, Gardiner and Greenshields (1946), to whom reference may be made for a fuller account of biology in relation to waterworks, give some figures which bring home vividly the problem which the waterworks engineer has to solve. A reservoir receiving water from the Thames and holding about 7,000 million gallons might, at certain times, contain 110 tons dry weight of the alga *Fragilaria crotonensis* ; the wet weight would be of the order of 1,000 tons. It is interesting as a sideline to make a comparison here with Windermere, in which a similar volume would contain less than 3 tons, dry weight, of *Asterionella* at the height of the season. The engineer supplying water from this reservoir at a normal rate would have to remove about 10 tons wet weight of *Fragilaria crotonensis* every day.

In actual fact the engineer would seek to avoid this load upon his filters, but in order to take full advantage of all the circumstances he requires the collaboration of a biologist. When a water-supply system has been installed, many of the problems with which the engineer has to contend are biological ; it is therefore surprising that only one water undertaking in the country, the Metropolitan Water Board, has a biologist on its staff.

In any reservoir there will be some species which, like *Asterionella* in Windermere (Fig. 2, p. 22), increases rapidly to a peak and then decreases again to a relatively low level of abundance. If a record is kept of the rate at which cell-division is taking place, and if the amount

of certain substances in solution in the reservoir is known, it is possible to calculate with reasonable accuracy when a peak will be reached, what the numbers will be at the peak, and how rapidly they will fall again to a low level. If this information is available to the engineer he can regulate his operations accordingly. It may be possible to leave the reservoir out of use during the period of the algal "flowering," if an alternative where phytoplankton is at a different stage of development is available. If this is not possible it may be decided to destroy the algae with poisons. Obviously the attack must be launched as soon as it is known that a flowering is impending; the poisoned algae fall to the bottom and their components return to circulation, so the fewer of them the better. Copper sulphate is most commonly used and quite low concentrations are lethal to algae. Any copper left over is apparently removed by sand filtration, though the sulphate may lead to trouble later, for, if all the oxygen is used up, it may give rise to sulphides.

Algae are troublesome to the engineer not only because they block his filters; some impart a distinct taste to the water, usually an unpleasant one. Sometimes it is highly resistant to treatment but usually it can be removed fairly easily, by aeration, by the use of oxidizing agents such as ozone, or by passage through special charcoal screens.

The rusting up of pipes by the action of iron bacteria is a danger if filtration is too rapid. It is also likely to happen if the water is withdrawn from the lower layer of a reservoir. This practice has the advantage that the water comes from a zone where plant growth is not taking place because there is not enough light, but, if the reservoir is stratified and the hypolimnion is depleted of oxygen, it may be rich in ferrous iron and this is a substance which should not be introduced into pipes. The withdrawal of compensation water from the hypolimnion of an oxygen-depleted reservoir is an excellent way of getting rid of nutrient salts which, if left in the reservoir, would increase the crop of algae to be filtered in the following year.

An account of the animals which inhabit pipes is now largely past history as far as water supply is concerned, though accidents happen occasionally. It is, however, of interest to the naturalist. The most detailed study was that made of the Hamburg supply system; this is briefly summarized by Dr. A. B. Hastings (1937) in a British Museum pamphlet on *The Biology of Water Supply*. The frequent but never

excessive flow makes the inside of water pipes a particularly suitable place for those animals which are sedentary and which obtain their food by filtering particles out of the water. Since such forms usually have a motile stage early in the life-history, their chances of attaining this environment are good. The Polyzoa, or moss-animalcules, live in branched colonies not unlike certain corals, and have been found in great numbers inside pipes. Sponges, too, which at certain times of the year produce resting spore-like bodies known as statoblasts, used to find their way into pipes where, once established, they flourished. *Dreissensia*, the zebra-mussel, can attach itself to a hard substratum and is not essentially a mud-dweller as the other bivalves are, and it is another common species in pipes. It is interesting to note that *Dreissensia*, which has invaded fresh water from the sea quite recently, still has a planktonic larval stage. This is common to all bivalves which live in the sea but has been lost in every other fresh-water species.

Once the walls of the pipes are well lined with Polyzoa, sponges, and *Dreissensia*, there will be an abundance of nooks and crannies in which other animals can find harbourage, and various Crustacea, particularly *Asellus*, the water hog-louse, may become established. It is a debris-feeder, and presumably finds a good supply of food lodged in the many holes and crevices which the overgrown surface of the pipe now presents. The basis of a food-chain is thus firmly established, and in the Hamburg water system even eels were abundant. The Hamburg water pipes supported a rich and varied fauna until sand filtration was introduced when it died off and disappeared.

These are some of the many ways in which the inhabitants of fresh water impinge upon the engineer. How does the engineer affect the inhabitants of fresh water? On the whole his activities are beneficial. We cannot do better than quote two sentences from Fitter's (1945) *London's Natural History* to support this statement: "The creation by the Metropolitan Water Board of an extensive series of large lakes in the valleys of the Thames and Lea has been one of the major events in the recent development of London's avifauna. In an average winter practically every duck, grebe and diver that visits the British Isles regularly may be seen with tolerable certainty on one of the reservoirs within twenty miles of London." Obviously this is also true for many invertebrate animals. The all-concrete storage reservoir has no counterpart in nature, and will therefore harbour only a portion of the fresh-water fauna and flora, but the impounding

reservoir formed by damming a valley may differ in no important respect from a natural lake in the same surroundings. Water supply therefore leads to a greater number of pieces of water for aquatic animals and plants to live in. But sometimes the amount of water drawn off from a reservoir leads to a great fluctuation in the water level ; there will be a large and irregular rise and fall depending on the rainfall, and there may be a smaller diurnal rise and fall caused by a fluctuating demand during the twenty-four hours. The result is that wave-action may extend over a greater vertical range than in a natural lake, and the establishment of rooted vegetation in the deeper parts of the shallow-water region cannot take place. This has far-reaching repercussions, and the result of the fluctuation is an impoverishment of both fauna and flora.

CHAPTER 16

SUMMARY

AN ATTEMPT has been made in these pages to compose a well-balanced unified picture; in this, the summary, we shall stress the gaps and empty spaces existing within the framework of the title LIFE IN LAKES AND RIVERS.

The underlying theme is based on four interrogatives, *what*? *where*? *why*? and *how much*? Chapter 6 is devoted to answering the question *what* occurs in fresh water, though within the scope of a dozen pages or so only the most superficial sketch can be given. An exact identification of the species concerned is required as a preliminary to most types of work, and at this early point the first main gap in our knowledge becomes apparent. The greater part of the fauna in some places is composed of insect nymphs and larvae, but only a certain proportion of these can at present be identified with certainty. All, except perhaps those belonging to a few big groups, probably are distinct, but the differences between them still await the worker who will seek them out and describe them. For the most part such identifications of fresh-water animals as are possible must be made from French or German keys, which inevitably include some species which do not occur in Britain and omit others which do.

The question *where* do the various species occur can be tackled from two points of view. The first is to take some particular habitat and discover as many as possible of the species in it. Since many nymphs and larvae are unidentifiable, the work is bound to be incomplete, and since it is difficult to name, or get named, some of the other groups, it has been found that this line of approach is less attractive on close acquaintance than at first sight. Most of the surveys which have been brought to a successful conclusion have been the work of

teams. The most thorough faunistic and floristic surveys in this country are those of the Ministry of Agriculture and Fishery teams, who have studied rivers. Small streams, too, have been fairly well investigated, and a number of Welsh workers have described stream faunas. Lakes and ponds have received less attention. Something is known about the fauna of the lakes in the Lake District, where the Fresh-water Biological Association has been working for nearly twenty years, but, when in these pages we wished to describe a calcareous lake by way of contrast, we were forced by lack of knowledge about our own waters to seek an example outside Britain. Brackish water has not been wholly neglected, but the information for other small bodies of water is scanty and incomplete.

The alternative approach to faunistic work, the approach which is recommended to anybody who cannot give a great deal of time to the subject, is to select one group, master the systematics, and then study the biology of each species and the range of conditions under which it is found. Investigation along these lines ultimately leads to the experimental laboratory.

The question *how much* has immediate practical interest to the fisherman and to the waterworks engineer, but the data still remain scanty, chiefly because the examination of only a few samples involves the time-consuming counting of a great many specimens.

All this so far is groundwork. When we try to answer the question *why*—why does species A occur in locality B, but not in locality C, or why does lake D support so many more animals than lake E—we quickly pass far beyond the confines of water and of biology. Chemical problems present themselves first and immediately lead on to others. Circulation in a lake affects the distribution of nutrient substances, and therefore the study must branch out to include the sun and its heat, the wind, and the properties of the water. But the nutrient substances are derived mainly from the drainage area, and search for their origin leads out of the water into the realms of geology and climate. Bound up with geology are agricultural practice and industrial practice, both factors which may exert a major influence on fresh water. Professor Pearsall and Dr. Pennington, whose interpretation of the bottom deposits of Windermere was described in Chapter 4, have gone further still and brought archaeology and history within the orbit of the fresh-water naturalist.

The answer to many of these *why* questions is to be provided only

by a well-equipped laboratory and a team of research workers with a wide knowledge of physics and chemistry, and a flair for designing and constructing elaborate apparatus. But the territory is not by any means closed to the amateur, and the complicated answer is not necessarily the correct one. The mosquito which deserted the rice-fields at a certain stage of development because she liked to fly over the water and drop her eggs from the air is a good illustration (p. 138).

It is probably true to say that there is not a single piece of water in the country unaffected by man. Mountain torrents and high tarns and pools might be put forward by some to dispute this statement, for few of them are directly influenced by man to-day. But, had not man cut down the trees around them long ago and prevented regeneration by running his sheep over the land, they would not be exactly as they are to-day. Therefore fresh-water natural history becomes inextricably mixed with the social organization of the country, regrettably no doubt, because many, both fishermen and naturalists, look to fresh water to provide them with an escape from the conflicts and worries of everyday modern life. But the issue must be faced.

In these pages we have dealt with the claims of four interests in the lakes and rivers of this country, claims which coincide and conflict in a complex pattern. First there are the suppliers of water, seeking new sources of supply as the demand rises. Subterranean water is showing signs of having been exploited to capacity, and attention is now increasingly directed towards new reservoirs, utilization of existing lakes, and tapping of rivers. The daily rise and fall in a reservoir may have an unfavourable effect on fish food, and the compensation water compelled by law may not satisfy the fisherman whose river water is taken for domestic supply; on the other hand a new reservoir may provide a new fishing-ground. Fishermen and water-works officials are therefore sometimes friends and sometimes foes. The local authority disposing of sewage and the industrialist disposing of trade wastes are popular with few; but we depend on the industrialist for our very bread to-day and the pros and cons of adding to his costs by demanding extensive purification schemes must be carefully weighed. The fisherman will alter a river on his own account if he can, but he will not come into serious conflict with any one, apart from the polluter, except perhaps over the question of access. The naturalist, if he is not also a fisherman, is probably interested to leave a place as little altered as possible. Nobody's claim is paramount;

a compromise is the only solution, and it behoves the fisherman, the waterworks official, the waste products disposer, and the naturalist each to acquaint himself with the claims and problems of the others. But, now that such questions as the location of industry and the establishment of national parks are decided at Westminster, the utilization of our water amenities and resources should be decided at the national level. At the risk of sounding like a Royal Commission we conclude by advocating a national water authority.

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FOR those who read German there is an extensive literature ; most of the main journals devoted to fresh-water biology are in this language, and of the books we may mention Thienemann (1925) and Ruttner (1940), two textbooks of limnology ; Demoll and Maier's (1924) comprehensive handbook on inland fisheries ; and Wesenberg-Lund (1943) on the biology of fresh-water insects. In Britain Carpenter (1928) and Mellanby (1938) correspond to the first and last of these, though both are on a very much smaller scale. In America there is a general textbook by Welch (1935), but it is a work to refer to and not to read. Whipple (1927) contains much useful information. Hubbs and Eschmeyer (1938) and Needham (1940) deal with practical matters of interest to the fisherman, though much of the American work on this subject is still in pamphlet form.

References to handbooks for identification are outside the scope of the present work, though mention may be made of Smart (1942). It is perhaps also worth pointing out that the American fauna is quite different from the European and therefore American keys and handbooks are of no value in this country.

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