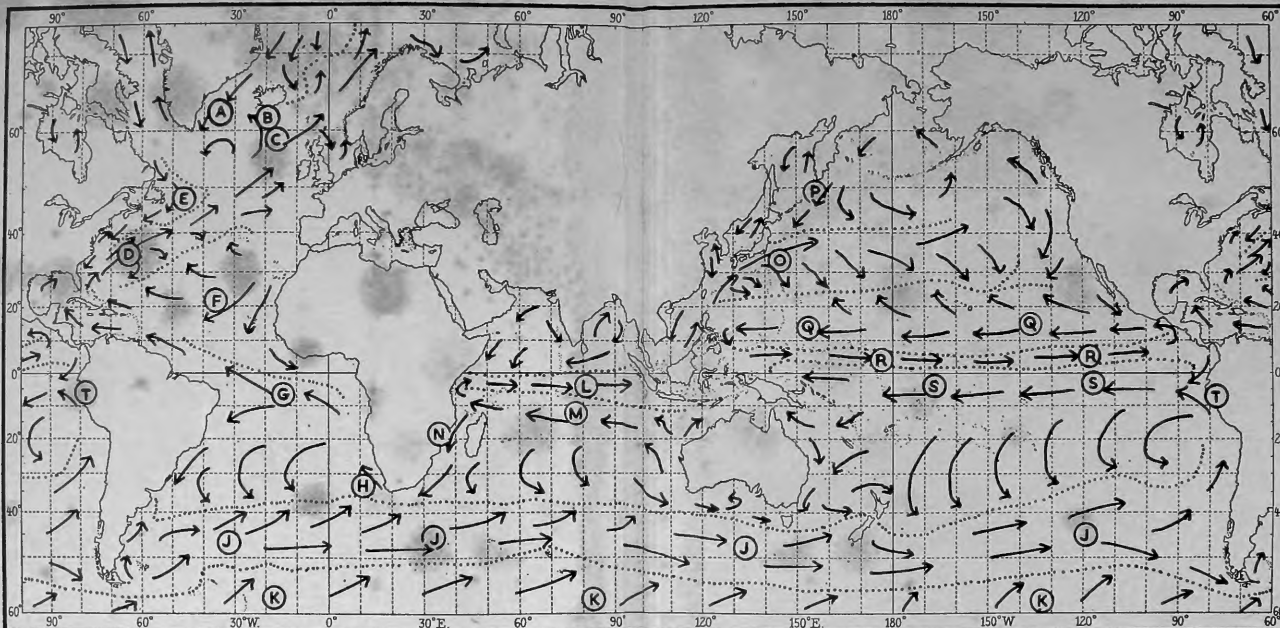
Richard H. Backus
Nov. 8, 1966



The surface currents, simplified after Erich Brun. The dotted lines represent where they diverge some of the major discontinuations: where currents converge the water sinks, there is upwelling.

A East Greenland Current
B Irminger Current
C North Atlantic Drift
D Gulf Stream
E Labrador Current
F North Atlantic Equatorial Current
G South Atlantic Equatorial Current
H Benguela Current
J West Wind Drift
K South Polar Drift

L Indian Equatorial Counter Current
M South Indian Equatorial Current
N Mozambique Current
O Kuro Shio
P Kuril Current (Oya Shio)
Q North Pacific Equatorial Current
R Pacific Equatorial Counter Current
S South Pacific Equatorial Current
T Humboldt Current (Peru Current)

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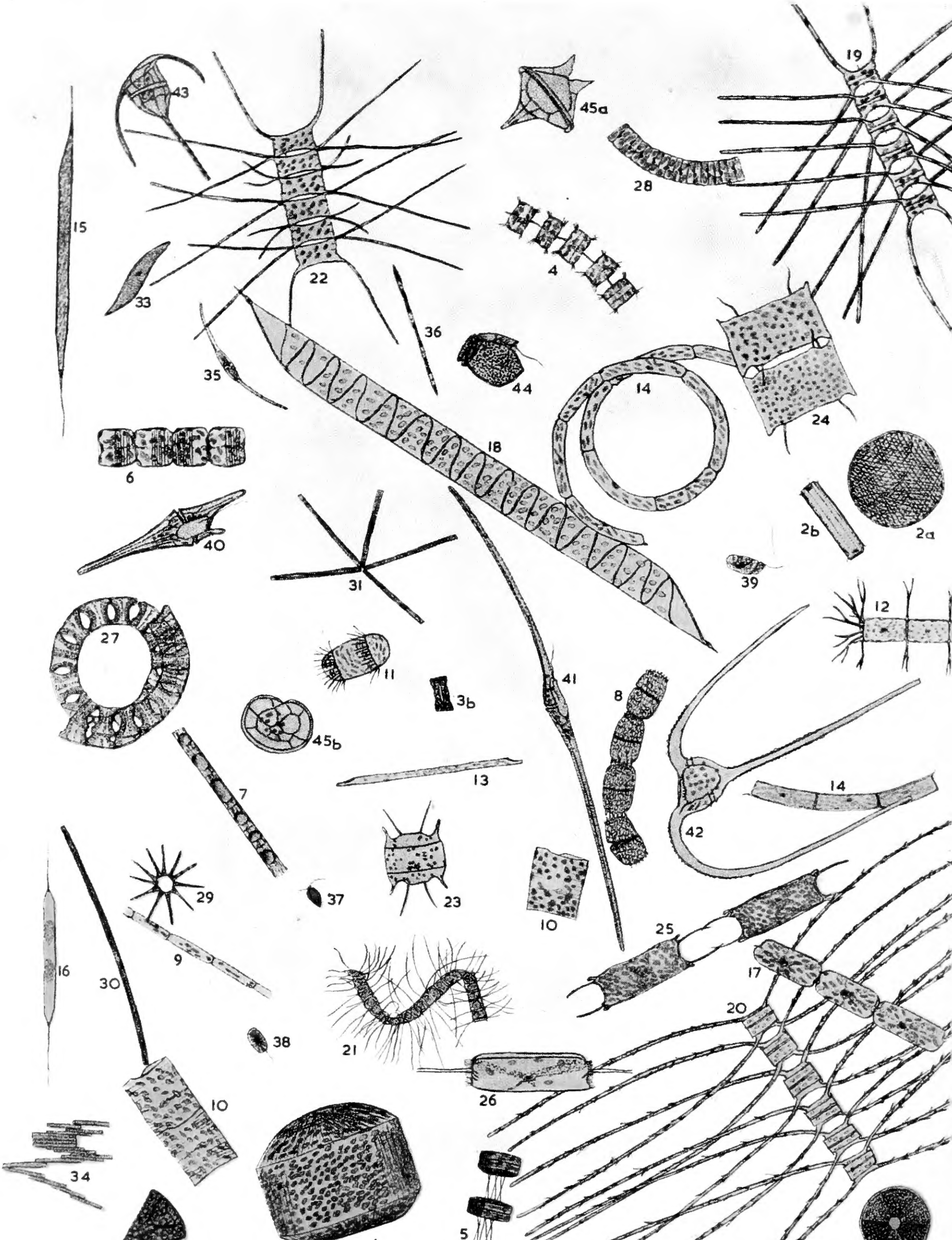
43
22
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28
19
15
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33
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14
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2b
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14
42
7
10
23
29
37
25
9
17
16
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20
38
21
26
10
34
1
5
3a
32

NATURE ADRIFT

The Story of Marine Plankton

JAMES FRASER
D.Sc., Ph.D., F.R.S.E., M.I.Biol.
*Senior Principal Scientific Officer at the Marine Laboratory,
Department of Agriculture and Fisheries for Scotland, Aberdeen.*

Those living gems 'of purest ray serene',
Oft frail, fantastic, strange and rare,
Whose lives sheer mysteries have ever been,
But need not be — with care.

Professor Walter Garstang
1943

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CONTENTS

FRONTISPIECE. Some examples of plants—the phytoplankton.

Diatoms

1. *Coscinodiscus concinnus*
2. *Coscinodiscus radiatus*, (*a*) valve view, (*b*) girdle view
3. *Actinoptychus undulatus*, (*a*) valve view (*b*) girdle view
4. *Thalassiosira gravida*
5. *Coscinosira polychorda*
6. *Lauderia borealis*
7. *Skeletonema costatum*
8. *Stephanopyxis turris*
9. *Leptocylindricus danicus*
10. *Guinardia flaccida*
11. *Corethron criophilum*
12. *Bacteriastrum delicatulum*
13. *Rhizosolenia alata*
14. *Rhizosolenia faeröense*
15. *Rhizosolenia hebetata*
16. *Rhizosolenia setigera*
17. *Rhizosolenia stolterfothii*
18. *Rhizosolenia styliformis*
19. *Chaetoceros atlanticus*
20. *Chaetoceros borealis*
21. *Chaetoceros debilis*
22. *Chaetoceros decipiens*
23. *Biddulphia mobiliensis*
24. *Biddulphia regia*
25. *Biddulphia sinensis*
26. *Ditylium brightwelli*
27. *Eucampia zoodiacus*
28. *Fragillaria islandica*
29. *Asterionella japonica*
30. *Thalassiothrix longissima*
31. *Thalassiothrix nitzschioides*
32. *Lycmophora lyngbyei*
33. *Gyrosigma sp.*
34. *Bacillaria paradoxa*
35. *Nitzschia closterium*
36. *Nitzschia seriata*

Dinoflagellates

37. *Prorocentrum micans*
38. *Amphidinium britannicum*
39. *Pouchetia polyphemus*
40. *Ceratium furca*
41. *Ceratium fusus*
42. *Ceratium macroceros*
43. *Ceratium tripos*
44. *Dinophysis acuta*
45. *Peridinium depressum*, (*a*) side view, (*b*) from the top

Colour drawing by T. Lovegrove

LIST OF PLATES

LIST OF TEXT FIGURES

AUTHOR'S PREFACE

TODAY THERE is a remarkable interest in the living things of the sea, partly due to a real desire for increased general knowledge especially about things not too commonplace. Science leaps forward during wars, many new tools and techniques are discovered and developed, and after this hectic stimulation there follows a period during which men set out idealistically to search for truth and self knowledge. That the sea and the life in it has received its share of this interest is thus also in part due to the frogman's equipment and the underwater camera, which provide an opportunity to see so much more of these creatures in their natural homes. Not only have those benefited who themselves venture into this field, but through films and television a greater number can now experience this very real thrill for themselves. Such an interest is both receptive and questioning, and centres largely on the desire to know more of the 'how' and the 'why' of the myriad living creatures, how they live and depend on each other, and how their existence has its effect on us. The drifting plankton, as the basis of life in the sea, including of course the fish, certainly has a greater effect on us than a casual thought would suggest.

These are the kind of things this book is intended to convey. It is not a handbook to help identify the organisms of the plankton. That would indeed be a colossal effort, like producing a single volume to cover all the flowers, grasses, mosses and moulds, all the insects, spiders, worms, slugs and snails and goodness knows what else besides. Such information is available in thousands of scattered tomes and papers in all sorts of scientific journals and in dozens of languages. If this book stimulates anyone to collect plankton for himself, whether as a passing dip into a strange living cosmos or as a real pastime, or helps to show him the advantages of marine biology as a career starting with a university course, then it will have served an additional and very worth-while function. In Chapter 2, you will find some hints on how to start, and Chapters 3 to 7 should give you an idea of the type of creature being looked at. But this is not the book's main function, which is to open a window on to a vista that few can explore for themselves, if they wish to uncover more than the merest fringe, as it needs a sea-worthy ship, expensive gear and a large specialist library. Many of us find exploration so much more comfortable from a favourite armchair than from the deck of a storm-tossed ship! Nevertheless the readily accessible fringe offers joys enough if you have a good hand lens—though a microscope, even a very cheap one, would be much better.

It is hoped that as you, the reader, explore this underwater world through this book some of your desire for knowledge will be satisfied and some of your questions answered. If it makes your appetite the keener and you want to ask questions you had not thought of before, then it will be even better. If you get interested in these creatures, either alive or from your armchair, and would know more of their personalities and their behaviour, exploring as it were the same country by another route, then you should read Professor Sir Alister Hardy's book, No. 34 in the New Naturalist series (Collins), and after that you can delve farther and deeper as your fancy dictates. It is an excellent book, written by another plankton enthusiast; if you enjoy mine you are sure to enjoy his also. I recommend it to you.

In the production of this book, I have written partly from my own experiences but necessarily even more from the researches of others. These I have taken from their published works in journals from all over the world and I gratefully acknowledge this here, as to make the book easily readable by the nature lover I have not included detailed references. I must thank H.M. Government through the Department of Agriculture and Fisheries for Scotland for permitting me to write it, yet this is a personal book and is in no way an official document and I must clearly state that nothing written in it makes any claim to be the official view of this or any other Government Department. I particularly wish to thank Dr. C. E. Lucas, C.M.G., my colleague with Professor Hardy and now my Director at Aberdeen, for his advice and help that made this book a possibility and my job at the Marine Laboratory, Aberdeen, just about the most interesting one that I could have found.

To those who have helped me with the illustrations I am deeply grateful, for without them this book would not be worth the writing. They include those who have drawn figures, those who graciously let me use their excellent photographs or permitted me to copy published figures.

My friend and colleague Mr. J. D. Milne has drawn for me Figures 1, 2, 3, 4, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 24, 25, 26, 30, 31, 32 and 37; a number of these are copies—Figures 8 and 32 with the kind permission of Professor Hardy, 24 and 25 with that of Dr. Gunnar Thorson and Dr. C. Barker Jørgensen of Denmark, 13, 14, 15, 30 and 37 with that of Dr. F. S. Russell of Plymouth, and 35 of R. S. Glover of Edinburgh. Many others are adapted from figures published in various books and papers, too many to cite in detail in this 'Nature Study' book, and in acknowledging this I express my debt and thanks. Figures 5 and 6 were drawn for me by R. S. Glover and Figure 38 is by A. J. Lee of the Fisheries Laboratory, Lowestoft. The coloured frontispiece is by my colleague Mr. T. Lovegrove, and the half-tone drawings of fish larvae in Plates XXVIII, XXIX and XXX were also drawn

by a colleague, Mr. N. T. Nicoll, whose photograph of *Explorer* is given in Plate II.

All photographs are acknowledged in their legends, but it is a privilege to record my gratitude to Dr. D. P. Wilson of Plymouth for so many excellent pictures taken of the living creatures, both black and white and in colour; to Mr. Peter David of the National Institute of Oceanography for his beautiful colour photographs; to Dr. H. G. Stubbings of the Admiralty for kind permission to use their Crown Copyright photographs in Plate XXXIII which are reproduced by permission from the *Journal of the Royal Naval Scientific Service.* Also included are several excellent photographs by Lennart Nilsson, reproduced by kind permission of the publishers, Messrs Tidens of Stockholm from the book *Life in the Sea* (English edition by G. T. Foulis & Co.) The lower picture in Plate XXXV is by D. F. S. Raitt and in Plate XII by Margaret Nyblad. To the following publishers I also acknowledge my thanks for permission to copy certain figures: Cambridge University Press (13 and 14 from *The Medusae of the British Isles* by F. S. Russell); The British Association for the Advancement of Science (35); Messrs Frederick Warne and Co. Ltd (30 and 37 from *The Seas* by Russell and Yonge).

As a professional biologist working on plankton, I have had access to materials and facilities that I would not otherwise have had, and chances to meet fellow workers from all over the world. By courtesy of the Department of Agriculture and Fisheries for Scotland, I have been able to use these opportunities to the advantage of the reader.

The verse on the title page is from the poem 'An oceanographer's dream' (with apologies to Tennyson) by Walter Garstang, which is included in his book *Larval Forms*, Blackwell, Oxford, 1951.

The index includes references to scientific terms explained in the text and subsequently used without further explanation.

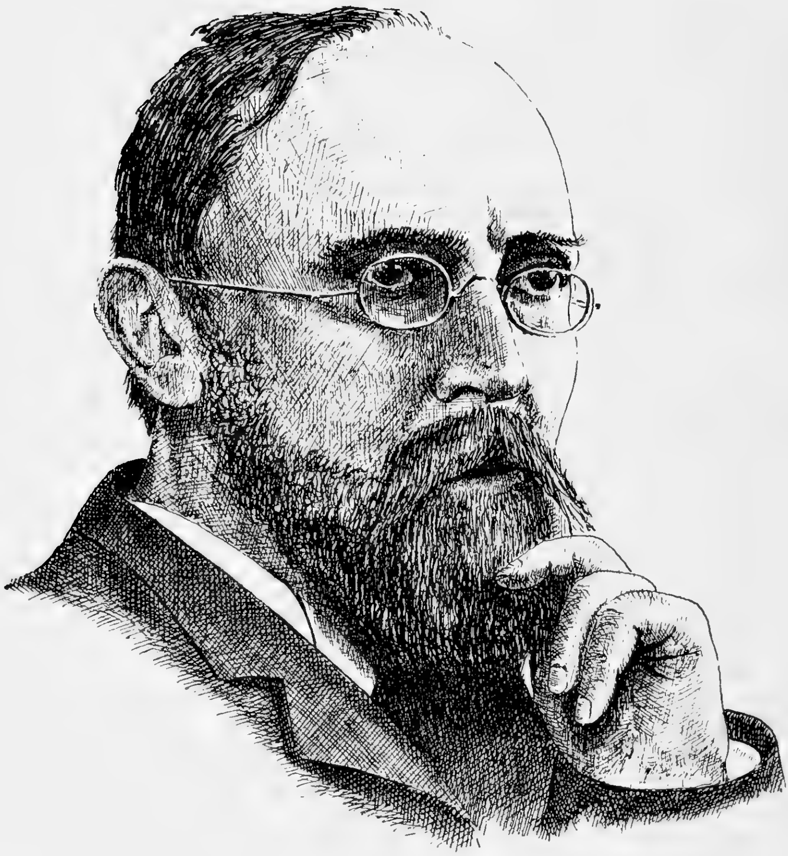


Fig. 1. Victor Hensen, 1835–1924. Professor at Kiel University, and leader of the German Plankton Expedition, July to November 1889. Drawn by J. D. Milne from a photograph.

CHAPTER 1

Introduction

UNTIL RECENTLY, the use of the word 'plankton'—a term of scientific 'shorthand'—was confined to the specialists' jargon, but with the greatly increased spread of knowledge it has gradually crept out until it is now a recognized term for what was previously called 'feed' by the fisherman, and often just 'life' by the layman. It is not so many years since the word did not exist at all; it was coined by Hensen (Fig. 1), a German, in 1887 and more critically defined by another German, Haeckel, in 1890. In brief, it is a comprehensive term to include all those living things, plant and animal, that are drifted about by the water movements. It is a most expressive term derived from the Greek *πλανκτον*, i.e. that which is passively drifting or wandering. Its constituents range in size from the minute plants that are about 1/10,000 inch to the largest jellyfish which may be a yard or so across. Many of the animals can, of course, swim, but their movements are small compared with those of the water itself. Although they can move up and down through appreciable and often great distances, their general distribution, both locally and geographically, is determined by their environment. By this definition plankton includes also the young free-living stages of many animals which are relatively sedentary as adults, such as the molluscs and barnacles, the young stages of bottom-dwelling animals such as crabs and worms, the floating fish eggs and the young fish after they hatch and before their own swimming powers are sufficiently developed for them to choose their own whereabouts.

Plankton thus takes its place with the two other main aquatic communities, the 'benthos' living on the bottom, and the 'nekton' which swims about freely.

There is plankton in fresh water as well as in the sea and the term is no longer confined to its original aquatic field; 'aerial plankton' is sometimes used in referring to insects, seeds and spores windblown from place to place, out of control, as it were, as distinct from deliberate migrations.

The existence of marine plankton has been known in a vague way almost since time immemorial, but its detailed study is one of the more recent scientific disciplines, and is barely more than 100 years old. In 1845 a German, Johannes Müller, towed a conical net of fine-meshed cloth behind a boat and so became the first research worker on plankton. His catch revealed an entirely new sphere for biological investigation, and it is small

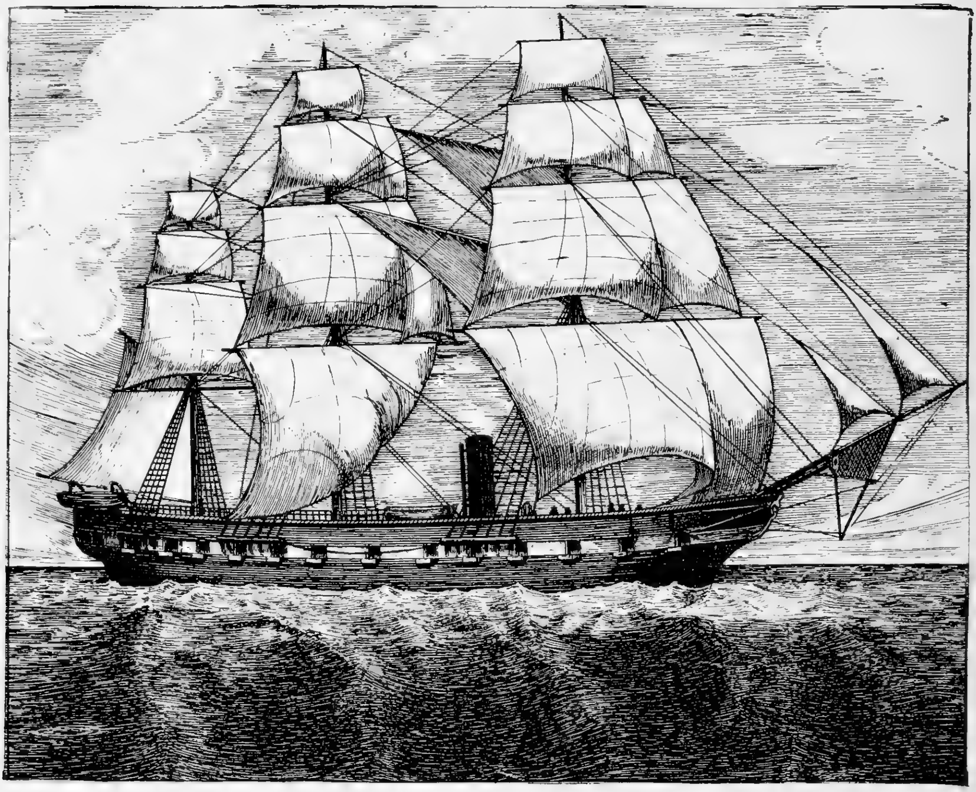


Fig. 2. H.M.S. *Challenger* drawn by J. D. Milne from various sketches in the Challenger volumes.

wonder that many other zoologists and botanists eagerly followed Müller's lead. Thirty years later a great deal had been learned, thousands of organisms, both plant and animal, had been caught, studied and named according to the Linnean system of nomenclature and the stage was set for the first and still perhaps the greatest marine expedition of discovery. This was the voyage of H.M.S. *Challenger* (Fig. 2) under the leadership of Sir John Murray, which set out from Portsmouth in December 1872 for a voyage round the world to investigate all kinds of life in the sea, plankton, nekton and benthos from all depths from the Arctic to the tropical seas. She returned after four years with an enormous wealth of material which was written up with tremendous zest. The biological reports—the most extensive—were the work of sixty-two authors who produced eighty-seven parts, bound in forty-two larges tomes, in only nine years. Since then there have been numerous major expeditions and some hundreds of minor expeditions, too many for individual mention, examples are the great German Plankton Expedition under Victor Hensen (the Hensen who first used the name 'plankton'), the German *Valdivia*, and the Danish *Dana*. There are, too, the great cruises of exploration by H.M.S. *Discovery* chiefly in the Antarctic, by the

PLATE I. Fishery Research Ship *Explorer* from the Aberdeen laboratory of the Department of Agriculture and Fisheries for Scotland.

Photograph by N. T. Nicoll

Princess Alice of Monaco, by the recent Danish *Galathea* in 1950–52 which found life six miles down in the Philippine Trench, and many other investigations, into polar, temperate and tropical waters by British, Norwegian, Swedish, German, American, Japanese, Russian and other scientists. There are also the now countless numbers of cruises of the research vessels of the various biological and fisheries laboratories, owned by almost every country, big or small, that has a sea coast. These vary from the small rowing or motor boat attached to the smaller marine biological laboratories and used only for local work, to the bigger and more fully equipped sea-going ships of the larger laboratories. There are a great many of these, their number and their equipment would indeed surprise the pioneers like Sir John Murray or Victor Hensen, such is the modern realization of the need to understand the wealth of the sea and to conserve it when necessary. There are few countries with a real interest in marine fisheries that do not possess at least one research vessel; many have several. Their structure and equipment vary according to the work they are intended to do and the areas in which they do it. The Arctic-going ships from Icelandic, Norwegian, Russian, English, Scottish, German and Danish laboratories, for example (see Plate II), have to operate in different conditions from those confined to the tropics. In addition, many naval ships are doing special survey work and there are the weather ships keeping a watchful eye on weather conditions from their oceanic stations. Almost all of these, big or small, collect plankton for one purpose or another. Small wonder then, that all that is known about plankton could fill a full-sized library and that this book is just a fleeting glimpse.

The methods of catching plankton will naturally vary according to the kind of plankton being investigated, the purpose for which the information is required and the working conditions. In Chapter 2, some of the methods are briefly surveyed, beginning with a simple strainer that the beginner can himself use. The next logical step is to look at what is caught and Chapters 3 to 7 cover some of the range of types. In the next chapters we discuss these creatures in their environment, their dependence on each other and their importance in the economy of the sea. This leads to the closing chapters in which something of their more subtle physiology and behaviour is described, ending with a discussion of what we can do for our own good with this immense larder of the sea.

It is hoped that the serious student will get some benefit from this book, though it is not written primarily for him, and there are, therefore, in most of the chapters details that should make his way clearer but which can be ignored by the general reader to the degree he chooses.




Plate II.

(*Top left*) The one metre tow net being hauled from the stern of the research ship *Scotia*.
(*Top right*) The flowmeter in the tail-piece of the Gulf III plankton sampler.
(*Bottom left*) The stinging jellyfish, *Cyanea*, left by the tide in a rock pool.
(*Bottom right*) The Portuguese Man o' War, *Physalia*, just after capturing a fish.

Three photographs by N. T. Nicoll,
Physalia by D. P. Wilson

CHAPTER 2

Methods

THE INDIVIDUAL constituents of plankton, even when abundant, only occupy a small part of the total volume of water, so that their collection is essentially a method of separating them from the water in the most convenient way. The method chosen will depend on what is required, and from where; it is a matter of selection and extraction. As we have seen in the introduction, plankton consists of a very wide range of forms from minute plants of some 1/10,000 inch to the larger jellyfish, and quite obviously what is suitable for selecting from one end of this range would be hopeless for the other. If we want to concentrate our organisms by passing the water through some sort of net or filter we must choose a suitable mesh, and this can range from the finest microfilters to the coarse mesh of a fishing net. The finer the filter the longer it takes the water to drain through it, so that whereas filter paper can be used to filter about a cupful of sea water—which might well contain 50,000 of the minutest plants and fifty of those about 1/100 inch—if we want to sample the large jellyfish as much water as possible must be filtered. To do this as big a net as one can handle with a large mesh must be used. The larger the mesh the less resistance to the water and the faster we can pull it using the same energy, thus filtering more water.

By far the most diverse in form, and thus the most interesting, of the plankton organisms are those towards the middle of the range, i.e. from about 1/200 inch to 1 inch and for these we want neither a filter paper, which will not deal with the quantity of water we want fast enough, nor a large coarse net. Except for very casual sampling, we need to choose the size of mesh required for our special purpose, and to be satisfactory our net must have a reasonably constant mesh. If one looks at a linen handkerchief through a microscope (Plate III) the strands are fairly regularly placed but they occupy more space than the holes which are small and extremely irregular. A coarser net of stramin (jute) or a 'cheese cloth' (Plate III) has a much larger ratio of holes to material but again the holes are unsatisfactory, this time due to the fluffy nature of the strands so that small fibres extend into the spaces and choke them. Fortunately for the planktologist just the right material is commercially available; the flour millers use it to sift their flour into various degrees of fineness. It is called 'bolting cloth' and is made of silk or nylon; the meshes are remarkably constant and the strands are kept the right distance apart by the special twists put in during manufacture

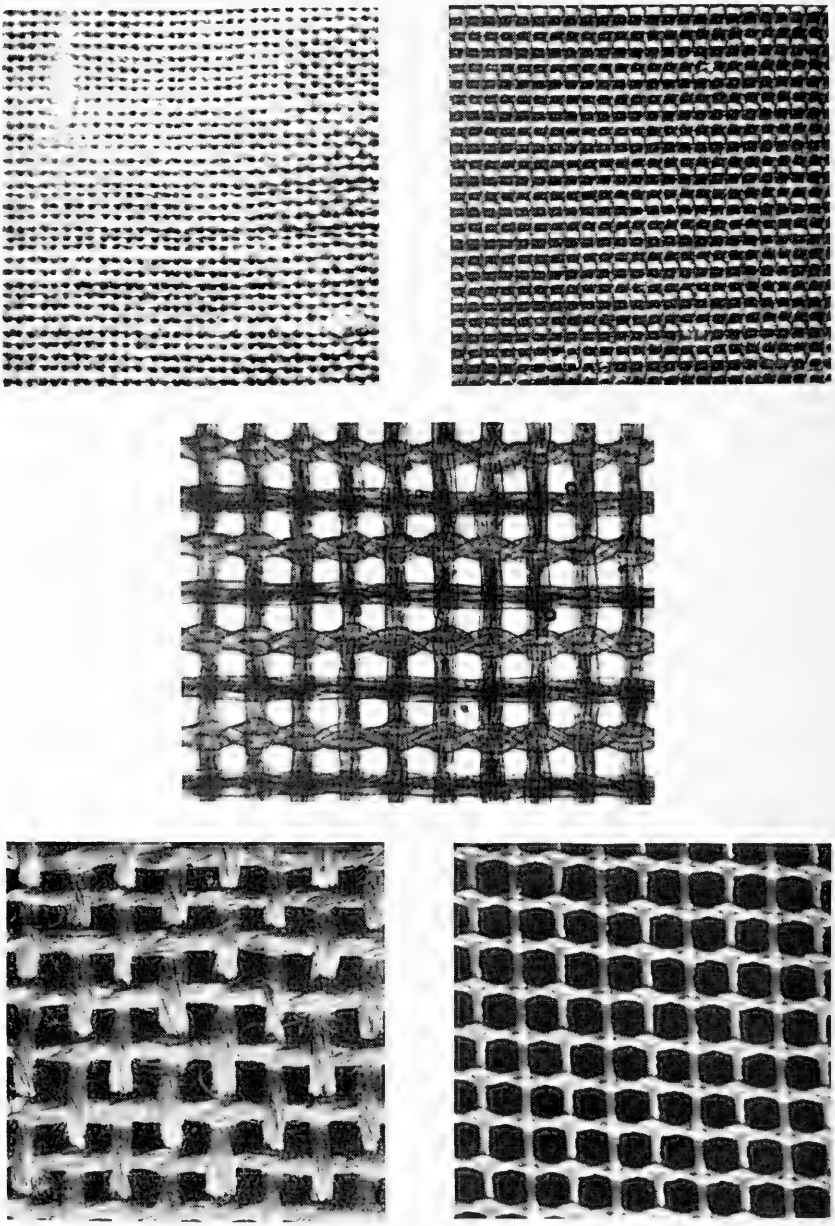


Plate III. Enlarged illustrations of meshes.

(*Top left*) A linen handkerchief; the holes are irregular and the strands of material are bigger than the holes so that filtration is poor.

(*Top right*) Bolting cloth No. 3 with 60 meshes per inch; the holes are regular and filtration is good

(*Bottom left*) Stramin (open sacking); the jute fibres are coarse and fluffy so that the holes are irregularly and badly choked.

(*Bottom right*) A coarse bolting cloth of 26 meshes per inch; the fibres are tightly twisted and woven to give rigid square clear holes.

(*Centre*) Fine bolting cloth of 180 meshes to the inch. The specially woven meshes interlock to give a remarkably regular and clean mesh in spite of its fineness.

Photographs by James Fraser

(Plate III). There is a wide range of meshes made, but the most practical ones for plankton work are (*a*) the finest with about 180 to 200 meshes to the inch for fine work, (*b*) 'No. 3' with 60 meshes to the inch for most of the small creatures of the zooplankton, and (*c*) a 'grit-gauze' of about 26 meshes to the inch if you want to lose nine-tenths of the smaller and commoner forms and only look for some of the larger varieties in a lot of water. The finer the net the smaller the organisms retained, but the water will pass through it only slowly and a fine net is easily clogged. Because of its greater resistance it must be towed more slowly or the water in its path will not pass through the net but spill round its edges. The larger animals capable of darting about will be able to avoid such a net and their numbers in the sample will not be representative. There is thus no ideal mesh for all purposes.

However, for casual interest one does not want representative samples, but merely a diversity. An irregular mesh of cheese cloth or muslin will give a nicely mixed sample—but do not use too delicate a fabric or it will burst under strain. A simple plankton net is illustrated in Fig. 3; 1. It is merely a conical net attached to a light metal or cane ring, the size of the opening depending on the size of sample wanted and the facilities for using it. One foot diameter will give quite a strong resistance behind a rowing boat and 6 or 9 inches would be preferable. Power driven research ships use larger ones of 1 or even 2 metres diameter (Plates II, IV*a*). Because the flow of water through the net depends on the ratio of total area of the holes to the opening, the finer the mesh the longer the net in relation to the diameter, and a net from three to seven times as long as the diameter is usual. This shape also has the advantage of washing the catch during towing down to the tip where it is concentrated and so the more easily extracted. To keep the catch in the best condition, it should be protected as far as possible from the strain of being pressed against the meshes, and so a 'bucket' or small jar is usually attached to the end (Fig. 3; 1*c*). A metal one is less fragile than glass, but a clear plastic one has the advantage of both. The bucket also keeps the catch from drying before it is transferred to the sample jar. If the condition of the organisms is less important than their numbers, as it so often is in plankton survey work, then a small detachable silk bag is more efficient and more convenient than a 'bucket'. It should be of the same or slightly smaller mesh than the net itself. Most plankton organisms collected in such a bag are in remarkably good condition but the delicate siphonophores (p. 54) and similar fragile forms can be rather badly damaged.

A net of this sort usually needs to be handled from a boat, which adds to the pleasure of collecting if it is a nice day, but an equally effective way near the shore is to let the tide provide the energy and to stream the net from the

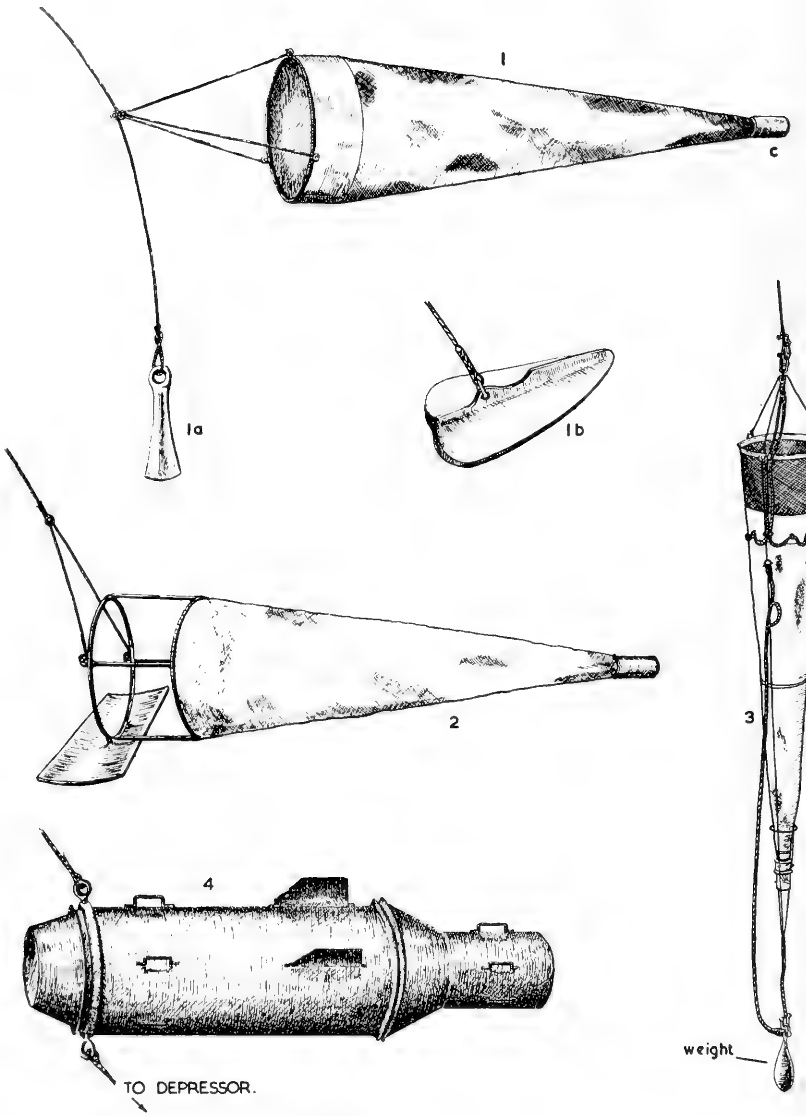


FIG. 3. Some types of nets, etc., for catching plankton.

1. The simple townet: it can be kept below the surface by a weight (*a*) or a depressor (*b*); the bucket (*c*) retains the catch in good condition.
2. The paravane net: the diving plane acts as a depressor and the opening is not obstructed by bridles.
3. The Nansen net, rigged for vertical hauls, as used by the research ship *Discovery*.
4. The Gulf III high-speed plankton sampler.

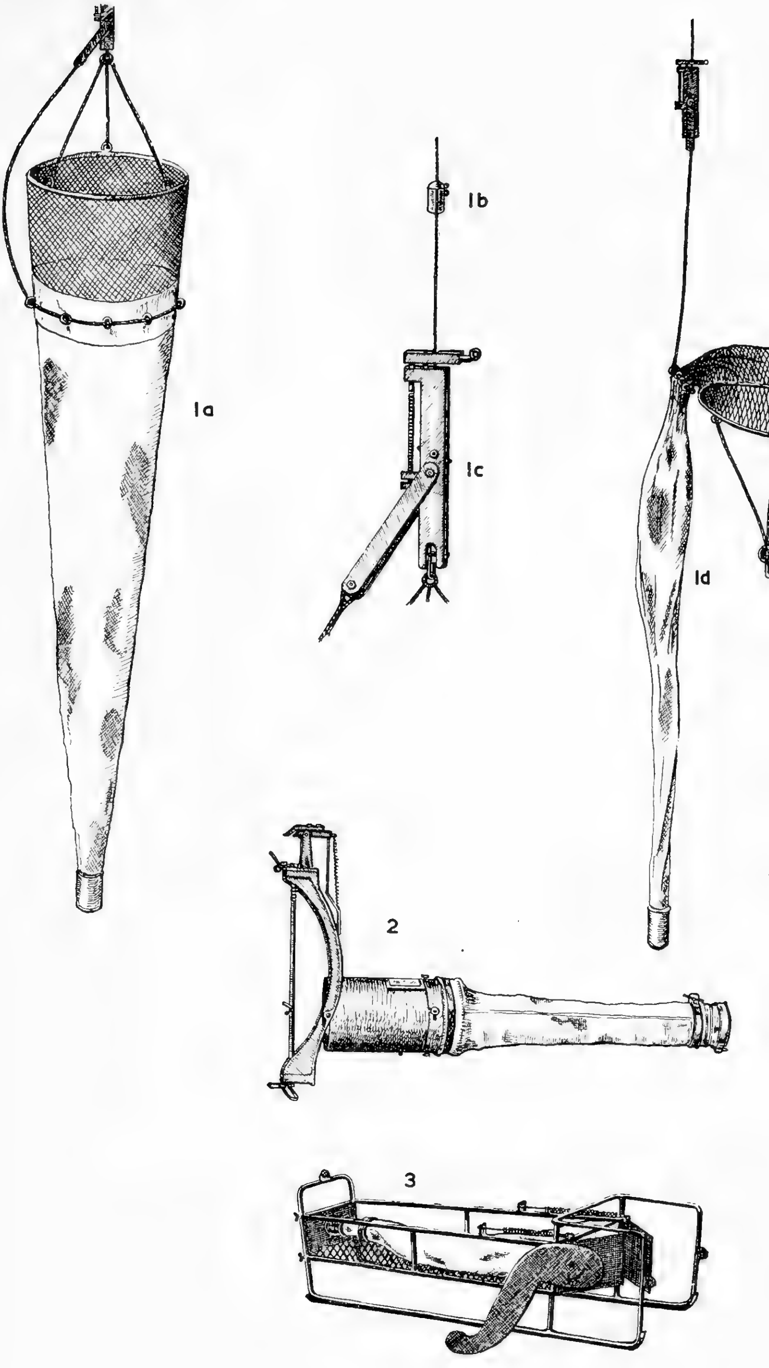


FIG. 4.

1. The vertical closing net: (*a*) hauling the net vertically, (*b*) the messenger on its way to trip the closing mechanism (*c*). The triple bridle is then released and the net is throttled (*d*) and hauled the rest of the way closed.
2. The Clarke-Bumpus net: a small net mounted on a special frame incorporating opening and closing mechanisms. These rotate a close-fitting metal disc about a pivot at the mouth of the cylinder which opens and closes the entrance.
3. The Bossanyi net: for sampling the plankton close to, but not actually on the bottom. The doors are kept shut by springs except when the arms drag along the bottom. The net lies on a frame to prevent chafing on stones and shells.

end of a jetty. If the ring is light and the speed of towing about 2 knots, the net will rise to the surface due to the resistance of the water. If a sub-surface or deep water sample is wanted you must attach a weight, using a short length of cable (Fig. 3; 1*a*). If the net is over-weighted or the speed too slow and it goes to the bottom, the weight touches first, it then no longer pulls the net down and this prevents the net from tearing on the rocks or sharp shells.

If, however, you want as a first trial to do something much simpler, try this. Take to a rock pool a small muslin bag a few inches across (a cheap 'tiddler' net from the local seaside shop will do if it has a fine mesh) and a jar. Use the jar to scoop the water from amongst the small weeds in the pool and filter it through the bag. After about ten scoops fill the jar with clean pool water and empty into it the contents of the bag. Strictly speaking this will not be true plankton because most of the organisms you have will normally live amongst the weeds and not drift about, but they will be the first cousins of plankton and you will be able to recognize their relationships from a study of Chapters 4 to 6.

Now let us consider the equipment used by the marine biologists. Basically the most used apparatus is the simple net illustrated in Fig. 3; 1, with various additions and modifications. If the biologist does not need accurate figures, then he uses such a net unmodified because of its simplicity and cheapness. While such a net is being towed through the water, the plankton organisms caught are partly washed down to the tip and partly lie against the meshes. The more plankton there is the sooner the net becomes clogged so that it cannot pass all the water in its path and its catching power is gradually reduced. This means that the exact amount of water filtered cannot be known and careful counts of the organisms caught mean very little. If the filtration of the net is improved, the counts mean more. Increasing the length of the net improves the filtration but makes it all the more difficult to handle and more difficult to ensure that the catch is taken out of the net and not left to spoil the next sample. A better way is to reduce the size of the opening with a cone of canvas or metal as in the Hensen net (Plate IV*b*). A much better way, but a more expensive one, is to use a flow-meter in the net, an instrument which works in the same way as the meter in a petrol pump. It can be calibrated by towing it and the empty ring, with no net, through a known length of water and assuming a complete flow through the ring. There are of course snags to this too; if the vanes of the meter were big enough to fill the whole of the opening it could be very accurate, but it would increase the warning effect of the net, so spoiling the sample; it would also be extremely liable to injury when being hauled aboard in bad weather. As the net gradually chokes, some of the water that enters is forced out again as an

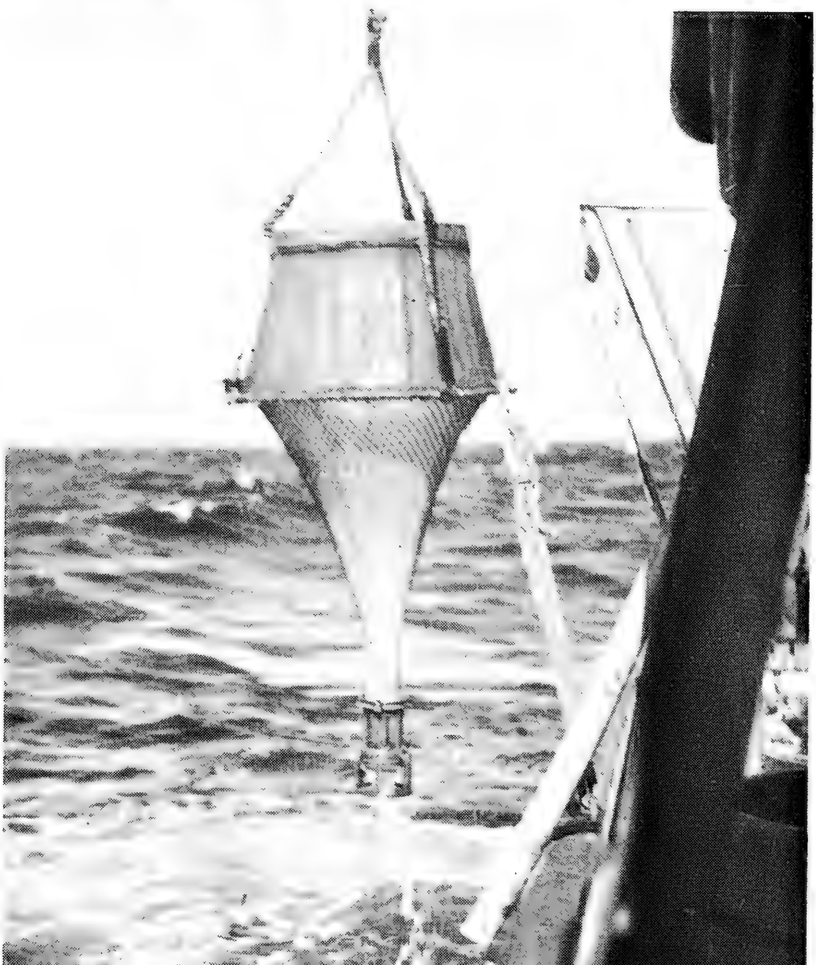


PLATE IV. Plankton nets at sea.

(*a*) The 1-metre townet; it is fastened by a non-slipping knot in a chain to a wire cable that continues to a similar net at a greater depth.

(*b*) The Hensen net after being hauled vertically.

Photographs by (*a*) N. T. Nicoll, (*b*) James Fraser overspill at the edges and this results in inaccurate register in a small meter. Expense is quite an important factor as the loss of a net, which can often happen in a heavy sea, can mean the loss of the meter also. Meters are therefore not used if only the proportions of the various organisms or a very rough estimation of numbers is all that is required.

To take the net below the surface a weight is needed and, although a couple of pounds is adequate for a small net behind a rowing boat, it rerequires an 80 lb. lead to take a 1-metre net down at 2 knots, using a wire: depth ratio of about 2 to 1. The accuracy of the depth reached may be important and small variations in the speed of the ship, caused by wind or tide, not easy to correct by adjusting engine speed, can make big differences to the wire: depth ratio. Instead of a weight, it is therefore better (but again more expensive) to use a depressor (Fig. 3; 1*b*). This is like an underwater kite and is attached to a line in such a way that the water pressure forces it down, just as wind pressure forces the conventional aerial kite upwards. The greater the speed the greater the downward pull and, within a resonable range of speeds, the net stays at about the same level. For accurate depth location, a depth-recording flow-meter is used (Plate II). The water pressure, increasing with depth, works a pressure gauge calibrated in depth. In its simplest form it will merely register the maximum depth reached, but linked with a revolving drum worked by the flow part of the meter it can be made to give a continuous record of the depth of the path of the net. This very useful instrument costs the best part of £100!

A simpler depth indicator, but one recording only the maximum depth, is the Kelvin Tube. This is a length of glass tubing closed at one end and coated inside with a water soluble stain. As the depth increases the air inside the tube is more and more compressed, and water enters at the open end of the tube and dissolves the stain. On recovery it is easy to see just how far the water has penetrated and the tube can be compared with a gauge calibrated to give the depth in fathoms or metres. As glass tubes are delicate these Kelvin tubes are usually sent down protected by an outer brass case.

Now let us return again to our basic net (Fig. 3; 1). It is towed by three or four bridles which keep the ring correctly opposed to the water-flow and these in turn are attached to a single towing warp. For sampling at different depths at the same time several nets can be attached to the same warp if the weight or depressor at the end is big enough. This arrangement of bridles means that the water just in front of the net is disturbed and those creatures capable of a quick dart away can see or feel the approach of the net in time to dodge it. One way of avoiding this when using a single net is to fix a paravane to the lower edge of the ring and attach the towing warp only to upper edge (Fig. 3; 2). Nevertheless, fast moving creatures with good eyesight like young fish can see the net and still dodge it. Catches of young fish are thus usually much bigger in night hauls than in day hauls, irrespective of their diurnal depth distribution (see Chapter 12). One way to help overcome this difficulty is to increase the towing speed, but this is not a straightforward answer. The net is incapable of filtering water at more than a certain rate, so to tow it faster merely means more overspill, and unless the aperture is reduced the increased pressure may be more than the silk can stand and the net will tear away. Faster towing also means a greater pressure cone in the water immediately in front of the net which frightens more plankton away.

A modern net, such as the Gulf III (Fig. 3; 4), is an attempt to get over all these difficulties at once: fundamentally it is still the same basic cone of net though it hardly looks like it. So that it can be towed at high speed, the net is now a rigid structure of fine mesh wire adequately supported at both ends, and to protect it from damage it is totally enclosed in a large metal tube. To give a proper filtration ratio the mouth opening is reduced, and behind the net the outer case is also reduced in diameter to give a venturi effect. This reduction affects the passage of water flowing over the instrument, causing a partial vacuum which helps to suck the water through. This now means that the flow meter, or depth/flow meter, can be fitted in this narrow tail part where it is protected and where it will register the water-flow that has actually passed through the net—a much more accurate way. It is towed by a line attached only to the upper front edge of the drum and kept down in the water by a depressor attached by a line to the lower edge. As in our simple net and weight system, this line means that if the depressor touches bottom its downward pull is no longer effective and the relatively delicate net and housing will not be damaged. If the bottom is very jagged the depressor may be lost, the net will then come to the surface and the loss will be comparatively slight. The water passing the drum, aided by stabilizing fins, keeps the whole structure facing directly into the water-flow and the opening is thus clear of hindrances. The whole is somewhat streamlined to reduce towing resistance and to limit the turbulence in front of it.

Because of the different depth distribution of the various planktonic forms, and because this varies according to the light (see Chapter 12) horizontally towed nets will not give representative samples of the plankton in any one place, but they are used to investigate depth distribution. If one wishes to sample the whole depth range then a vertical haul is required. Theoretically, assuming perfect filtration etc, if a net with an opening of 1 m^2 is hauled vertically from the bottom to the surface it will sample the total plankton living under 1 m^2 of surface. This kind of information is essential when trying to assess total plankton crop at any one time. But nets are far from 100 per cent efficient, 30 per cent is about average, but it frequently ranges from 10 to 70 per cent, so that a flow meter is still necessary. If the organisms one is to count are not very abundant and the sea at that part is not very deep, a vertical haul may give too small a sample for satisfactory results. A vertically hauled net cannot make use of all the bright ideas that have gone into the making of the high speed tow net, and an oblique haul is therefore usually made. This means that a high speed net, with all its advantages, can be hauled at a steady speed from the bottom to the surface whilst being towed; the resultant catch is then equivalent to a very elongated vertical sample with the actual water-flow properly assessed by the flow-meter.

When attempting to do accurate quantitative work at known depths some sort of a closing net is necessary to prevent the capture of plankton from other depths during shooting and hauling. If the sample from a vertical haul is likely to be big enough for the purpose the problem is easier to solve. The net can be lowered vertically and if it is weighted at the tip (Fig. 3; 3), it will sink end first and so not catch anything on the way down. After hauling for the necessary distance, a special weight, called a messenger (Fig. 4; 1*b*), can then be attached to the line. This is merely a weight, usually of brass, so constructed that it can be clipped over the line so that it cannot come off, yet is free to run easily down it. The messenger, on arrival at the net, triggers off the closing mechanism (Fig. 4; 1*c*). The simplest of these is merely a throttling device, so that the net instead of being hauled by the bridles is now hauled by a loop round the elongated canvas collar of the net itself (Fig. 4; 1*d*). Another method is to use a hinged ring hauled by four bridles; to close it the two bridles attached near the hinges are released putting all the strain on the other two, thus closing the opening like a lady's handbag. Horizontally hauled nets must be sent down closed, opened at the right depth and then closed again. To do this, a system of metal doors is used. These are held by a spring across the mouth of the net until released by the first messenger, when they swing through 90 degrees to a horizontal position no longer impeding the water-flow. After the desired distance has been covered, a second messenger is sent down which further releases the catch and the doors swing through a second 90 degrees to close the net again. One example often used is the Clarke-Bumpus net (Fig. 4; 2).

Various modifications of these patterns have been adopted for special purposes. A plankton net can be fixed to a sledge and fitted with doors that are kept closed by a light spring but which open as the apparatus is drawn along the sea bed. Such a net captures only the plankton found in the few inches immediately above the bottom (Fig. 4; 3—the Bossanyi net). There are, too, varieties of detail in the construction of plankton nets of all kinds, developed in different countries for slightly different purposes.

In 1931 Professor Hardy of the University of Hull (now Sir Alister

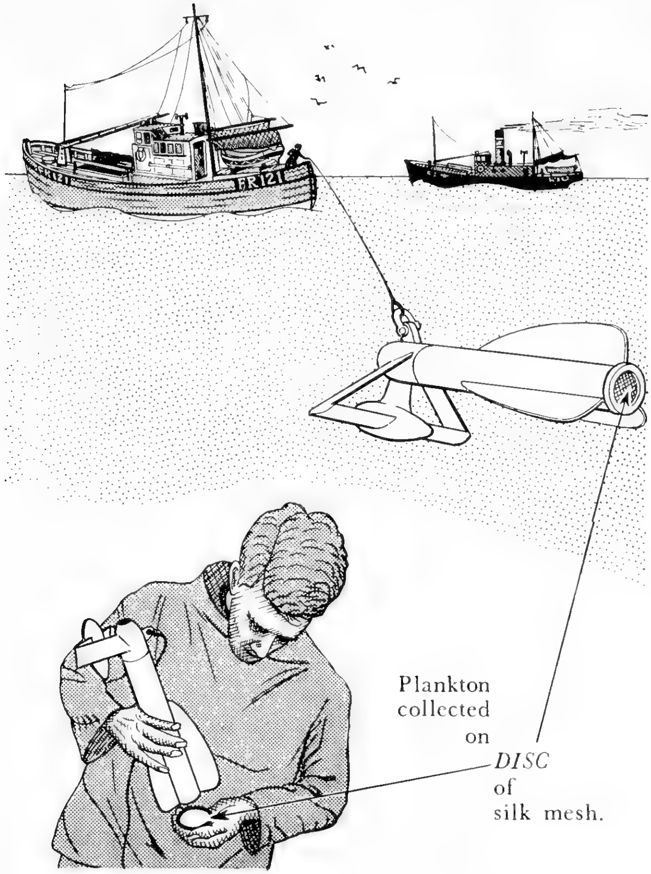


Fig. 5. The 'Hardy' Plankton Indicator, as used to sample plankton by fishing vessels working on the herring grounds.

Hardy of Oxford) started an oceanographic department whose main function was to sample the plankton over as broad an area as possible using commercial vessels, either fishing vessels or the larger ships used on the normal steamship lines. Two different types of apparatus were developed. The first of these, called the Plankton Indicator, is a high speed net reduced to its simplest terms (Fig. 5), being merely a metal tube with a constricted opening, a fixed diving plane instead of a weight or detachable depressor, and stabilizing fins. The net is merely a disc of 60 mesh silk attached to a ring placed inside near the tail. It was designed for easy handing aboard herring fishing vessels, and to be towed when the skipper was near the grounds chosen for his night's fishing. If the disc showed plenty of herring food his chances of a good catch of herring were increased, as discussed in more detail in Chapter 10. With the modern development of the echo sounder a more positive indication of the presence of herring is given and the 'Indicator' has gone

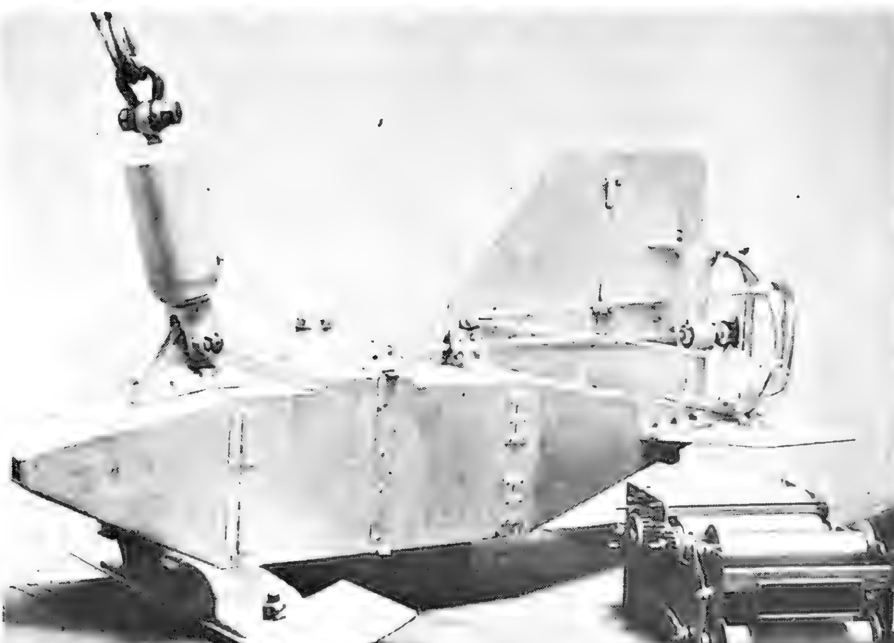


PLATE V.

(*Top*) The Icelandic high speed sampler on board the Scottish research vessel *Explorer*.
(*Bottom*) The 'Hardy' Continuous Plankton Recorder, for continuous towing behind commercial ships on passage.

Photographs by James Fraser

out of service for this purpose. However it is still a simple and excellent small sampler and is now used, in a slightly modified form, by a number of research laboratories. In particular, the staff of the Edinburgh Oceanographic Laboratory (under the Scottish Marine Biological Association) still use it for their regular surveys of the plankton of the herring grounds: I say 'still' because the Edinburgh laboratory is the present thriving continuation of what was originally Professor Hardy's Hull laboratory.

An essentially similar instrument to the 'Hardy' Plankton Indicator has been made and used in Japan and is called instead the 'Handy Plankton Indicator'! Japanese workers, especially Professor Motoda, have designed many interesting and useful additions to the range of our plankton samplers. A larger version of the 'Hardy' Indicator is the Icelandic sampler (Plate V), designed to give a rather bigger catch but with the maximum simplicity.

The second type of gear designed by Professor Hardy was first used on F.R.S. *Discovery*. An improved model is now used by the Edinburgh Laboratories and is towed from commercial ships at their normal cruising speeds. It is called the 'Continuous Plankton Recorder' (Fig. 6 and Plate V). This instrument samples continuously, mile after mile, the plankton on the steamship route. Basically it is the high-speed net again—a metal tube, streamlined, constricted at the front, with stabilizing fins and a 'paravane' diving plane rigidly fixed to it. As the instrument is towed the water-flow over it drives a small 'propeller' which acts through a gear-box and slowly winds on a long length of plankton silk which is drawn across the path of the inflowing water. The aperture is small, only $\frac{3}{4}$ inch square, to keep the sample to reasonable proportions. A column of water $\frac{3}{4}$ inch square and 100 miles long would contain $3\frac{1}{2}$ million cubic inches of water or 15,500 gallons = 70,000 litres. The area of silk exposed to the passage of water is 4 inches × 2 inches to give a relatively large filtration area and to help prevent clogging. As it collects the plankton the silk, graduated in numbered divisions, is gradually wound on exposing a fresh surface. The silk is then met by another roll of ungraduated silk and both silks wind on together, with plankton safely sandwiched between the two, into a tank loaded with formalin preservative. The speed of the silk can be varied from about 2 inches to 1 mile to 2 inches to 10 miles according to the length of tow and degree of precision required in the knowledge of the plankton distribution. The paravane is designed to take the Recorder to depths of about 10 metres (33 feet) within quite a range of towing speeds, 8 to 16 knots. It is first loaded by the scientists and then it can be handled by the crew and collected on the return of the ship to its base port or sent to Edinburgh from a distant port. It thus has to stand heavy weather and heavy treatment in transit and is therefore very robust, weighing about 156 lb. The regular surveys initiated at Hull and developed in

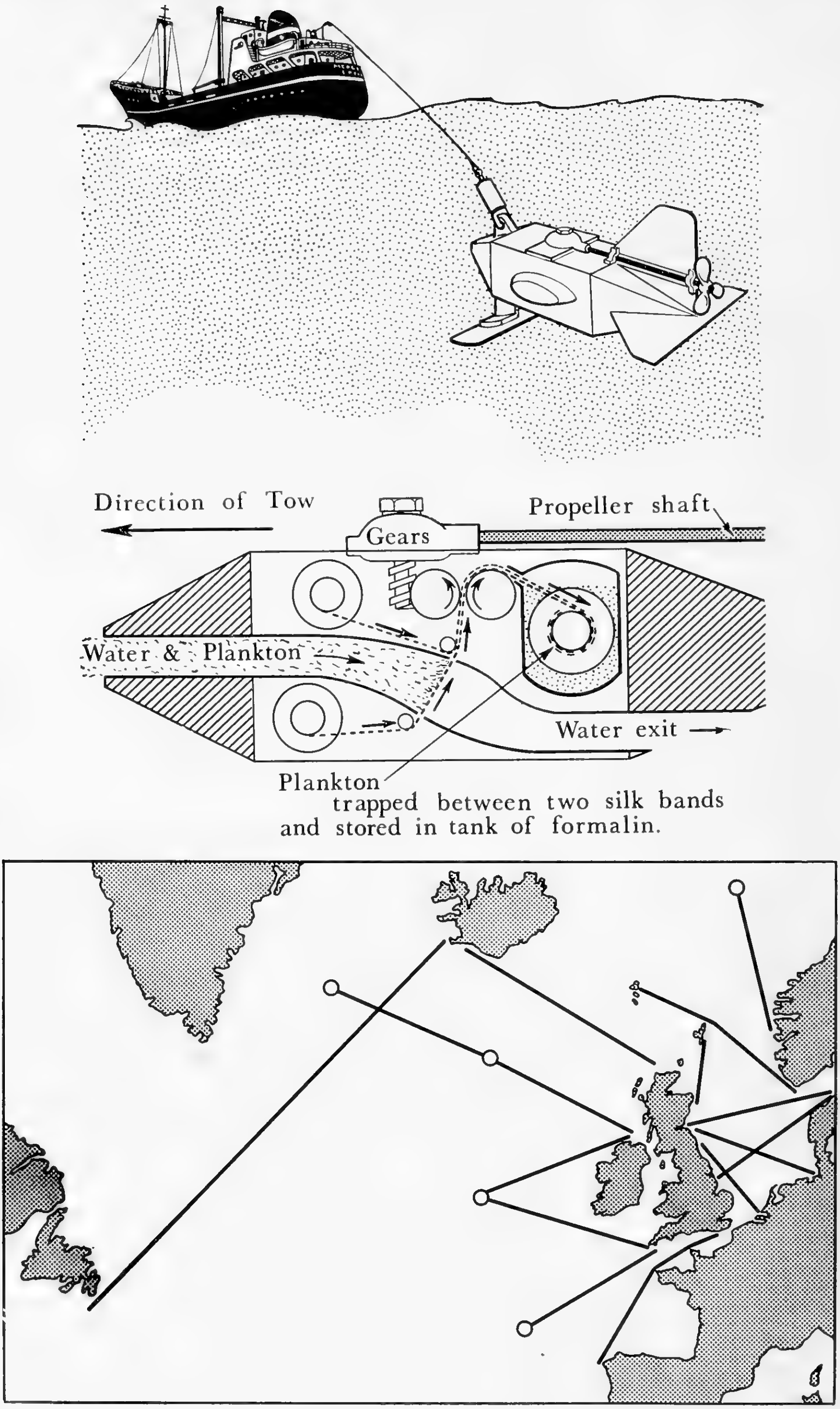


FIG. 6. The 'Hardy' Continuous Plankton Recorder, used to sample plankton along the routes of commercial and other ships on passage. The upper figure depicts the recorder being towed by a cargo vessel, and below it is a diagram showing the internal mechanism of the instrument. The chart shows the lines of regular monthly sampling as at 1 January 1961 organized by the Edinburgh Oceanographic Laboratory of the Scottish Marine Biological Association. The open circles show the positions of the Weather Ships.

Edinburgh now cover annually many thousands of miles, as may be seen from the route chart, Fig. 6.

To sample the bigger and usually more infrequent species much larger nets are used with a correspondingly coarser mesh, the idea being to filter the maximum amount of water possible under the circumstances. Here the development of techniques has been largely towards decreasing the difficulties of manhandling and storing large nets. A fixed ring to keep the mouth of the net open is therefore dispensed with and its place taken by a flexible rope framework kept apart by the water pressure. The principle is the same as used for the kite, the depressor and the otterboards of a trawl net, i.e. an impervious surface is kept at an angle to the water-flow which thus pushes it to the side. In the 'Corbin' net this is a continuous canvas sheet kept rigid at the correct angles by struts attached to the lower half of the mouth of the net; in the 'Isaacs-Kidd' net there is a 'kite' attached to the footrope. As we saw earlier the difficulty is to get the net to go down and it is therefore usually unnecessary to have any special 'kite' arrangement on the upper edge. The construction of the nets unfortunately necessitates the use of bridles attached to the struts or kite that disturb the water in front of the net, a serious disadvantage when we are trying to capture the faster moving creatures. Alternatively, the net may simply be of a pattern similar to a commercial fishing net but with a 'cod end' of particularly small mesh—about $\frac{1}{4}$ inch mesh.

If a pump is used, all the water can be passed through a net or filter on board the ship and accurately measured. As the length of suction tube is known, the precise depth of origin of the sample is also known. Small pumps are adequate for the finest plankton, a 2 or 3 inches diameter pipe with a power driven centrifugal pump of about 6 h.p. can give sufficient water for estimating the small to medium sized organisms but only a very powerful pump could deliver the large volume necessary for the rarer and fast swimming species. A 1-metre net, towed at 2 knots ideally would cope with nearly 3,000 cubic metres of water in an hour, or 640,000 gallons an hour which would indeed require a large pump! Although pumps are suitable for some surface or sub-surface sampling, they become quite unwieldy when long lengths of tubing of large diameter have to be handled in order to reach to the deeper layers.

At the other end of the range we have to sample the smallest organisms that pass through the finest of our silk meshes. There are three possible methods. The first is to use fine filters, the chemical filter papers are not fine enough for this purpose and we use 'membrane filters'. These are composed of incompletely cross-linked polymer molecules, as the chemist says, and can be had in a variety of pore sizes from 1 μ upwards (1 μ = 1 micron =

1/1,000 millimetre). They look like discs of opaque white cellophane. These of course, pass water very slowly indeed even when the speed is increased by applying a vacuum pump below or air pressure above the filter. As the numbers of these smallest organisms are so great, this is not usually a severe drawback, and small samples of water are sufficient. The difficulty is to get them off the filter for later examination! This is virtually impossible so that one looks at them on the filter by making it transparent with a medium of the same refractive index 1·47, or one dissolves away the filter. Neither is completely satisfactory and the method is mainly used for chemical or optical assessment of the amount of pigment, usually the chlorophyll, that can be chemically extracted from the organisms left on the filter. A recent method that complements rather than replaces the chlorophyll estimation makes use of radioactive isotopes; the chlorophyll method indicates what is there, but the isotope method reveals what is being produced. Of these the most useful is carbon-14; and the amount of C^{14} present can be asssessed with a Geiger counter. If we add a known but very small amount of C^{14} to a sample of sea water with a known amount of ordinary carbon, C^{12}, there will be a measurable amount of radioactivity, but not enough to kill the organisms. The carbon is not, of course, in the solid black state, but as part of a soluble compound like a carbonate or as dissolved carbon dioxide. All living plants absorb carbon during their metabolism (see also Chapter 9) and will absorb C^{14} at just about the same ratio as the ordinary carbon C^{12}. The ratio of C^{14} to C^{12} absorbed by the organisms will therefore be about the same as it was in the sea-water sample. After a carefully timed period of exposure to a constant light and at a constant temperature, we can then filter the sample through a membrane filter and measure the radioactivity of the filter. If no living plants were present all the C^{14} would go through the filter; the amount of activity shown by the filter thus represents the anount of plant metabolic activity during the period of the experiments. Under constant conditions we can relate this to the productivity of the water.

If we want to examine our smallest organisms microscopically, we can adopt a different technique, the second, which is by centrifuging the water. Centrifuging is a method of spinning a sample at great speed, up to about 20,000 revolutions per minute, in a series of carefully balanced glass tubes—they need to be carefully balanced to avoid the shatter that would result from unbalance at high speed. Plankton, particularly dead plankton, is slightly heavier than water and, after a few minutes centrifuging, the organisms are concentrated at the tips of the tubes. After gradual slowing and stopping of the spin they can be extracted with a fine pipette. Such pressure tends to distort fragile and delicate organisms and make identification difficult, so the third method is the one now mostly used. This is just a patience-demanding variation of the previous method. A sample of sea water, after adding a preservative (see page 26), is placed in a vertical glass or plastic tube open at the top but attached at the bottom to a shallow trough of the same diameter which has been fixed to a microscope slide. The join is made lightly with 'Vaseline' or a similar waterproof seal, easily broken. The whole column is carefully set aside and the sample gradually sediments out into the shallow trough. This may take hours or days, according to the length of the tube. After settling out has been completed, the surplus water is removed (usually by sucking it out from above) leaving only the small amount of water in the trough with the sample of plankton. The tube is then broken off at the seal and the slide ready for microscopical examination.

Methods of observation of the living plankton in its natural environment are now possible with special modern equipment, and extend from the simple underwater camera and the frogman, to closed circuit television, and to special underwater observation chambers like the French bathyscaphe *Trieste* and the Russian research submarine, *Severyanka*.

All these methods have their limitations, which are mostly serious, but are of a different kind from other sampling methods. The obvious one is, of course, that the small size of most planktonic organisms makes naked eye or near-natural size observation difficult, if not impossible, so that it is confined to the larger species only, except to record an undefined 'soup' which can vary in its 'soupiness'. Visibility under water, even in the best conditions, is poor compared with that in air. A further difficulty is the extreme transparency of so many of the organisms while they are alive, though they rapidly become opaque after death. Using photographic methods, a great deal depends on chance, especially if the camera is operated from the deck of a ship and not by a diver in person. The camera cannot be orientated and must be focused beforehand. Only those organisms in actual focus can be seen whilst the others tend to blur the picture.

One advantage of the unaccompanied camera is that it can be operated in conditions where a diver cannot work, because of depth, or darkness, or weather. Underwater photography at night or in depths below adequate light penetration must be accompanied by its own lighting unit. This can be continuous flood lighting—which might radically change the natural distribution by attracting or repelling the plankton—or by flash. Flash, however, is a very concentrated form of light and this has its own peculiar but severe limitations. Most plankton organisms are fairly transparent, some extremely so, and what one sees in a flash photograph is often merely the high-lights reflected from their curved surfaces, a series of minute replicas of the flash and its reflector, varying in clarity with the accuracy of the focus

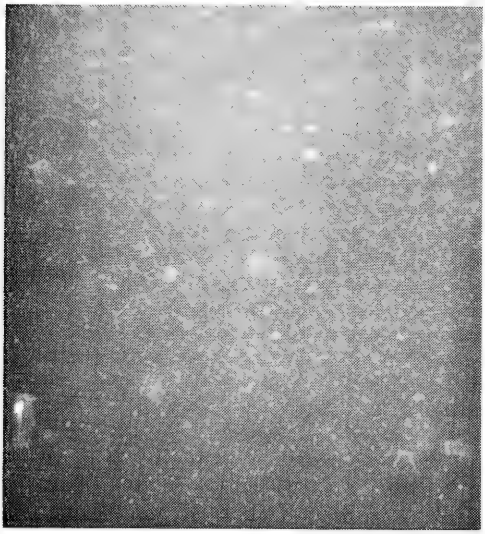


PLATE VI.

Photograph of living plankton taken at sea by underwater flash. Only a few organisms can be recognized—3 medusae, *Solmaris* (cf. Fig. 14; 4) and a salp (cf. Fig. 23; 6)—the rest form an undefined 'soup' reflecting only highlights mostly out of focus and blurred. About 1/12 natural size.

so that accurately focused organisms appear as bright pin-pricks and the others as round blurs, the size depending on how far they are out of focus. The result is a 'soup' which gives an idea of the abundance of the plankton but only rarely anything identifiable (Plate VI). Sometimes an opaque organism can be seen, if it happens to be in focus. Some can be identified because their shape gives a characteristic series of high-lights—for example the tentacles of a jellyfish which are not simple hair-like threads but a series of bulges each of which has its high-light as would a string of beads. Some organisms are sufficiently opaque to be photographed quite successfully.

The closed circuit television has special advantages in that it can be controlled in direction, focused, and especially because the actual movement so often gives the organism away.

Observations from underwater chambers can give valuable information from places otherwise beyond reach; some details of plankton distribution at great depths deduced from the observations made from the bathyscaphe are given in Chapter 8. These methods are mentioned here, but few indeed will have the opportunity to use them.

This chapter must end with a short account of preservatives. An unpreserved plankton sample, at the concentration convenient for examination, will not remain alive long, and on death it will encourage a fast and very obnoxious growth of bacteria. The simplest method of preservation and one of the most satisfactory, is by formaldehyde. A concentrated solution is about 40 per cent formaldehyde, and this solution is known as formalin. This is diluted in use to about 4 or 5 per cent formalin (= about 2 per cent formaldehyde), but allowance must be made for the water content of the plankton itself. For example, a fish, or a jellyfish, if it is to be preserved in a volume of formalin about equal to its own bulk, would require 10 per cent formalin, which would after penetration be 5 per cent. A sample with numerous small organisms should preferably have a free volume of preservative of several times its own volume. Colours are gradually bleached and as formalin is slightly acid, calcareous shells are gradually dissolved, but this can be reduced by 'buffering' with borax, sodium bicarbonate or preferably with an excess of powdered calcium carbonate which neutralizes any acid as it forms.

The minute organisms are best preserved with Lugol's iodine, as some of them are so fragile that the addition of formalin causes them to 'explode'. The expert histologist in his study of the actual cell structure needs special preservatives for his work, but he needs no advice about his methods from this book.

With a little forethought and ingenuity, the beginner can make his own nets, using a small hoop or similar ring and some butter muslin, mosquito netting or cheese cloth. Silk is, of course, better and can be obtained from John Staniar & Co., Manchester Wire Works, Manchester, or from Henry Simon Ltd, Cheadle Heath, Stockport. It is usually sold in lengths 40 inches wide; grade 3 costs about 30s. and the finest about £4 per yard. Nylon is cheaper, does not rot if left damp, but the meshes are also less rigid and it is not easy to sew the seams satisfactorily. The complete nets suitable for schools, etc. and for work in fresh water, can be bought at various scientific instrument suppliers (e.g. Flatters and Garnet Ltd, 309 Oxford Road, Manchester, 3, or P. K. Dutt & Co. Ltd, 1 Alfred Place, London, W.C.1) and larger nets from the Marine Biological Association, Citadel Hill, Plymouth or from the Freshwater Biological Association, Far Sawry, Ambleside, Westmoreland.

Two last hints: always label your collections, and include the date, the exact locality and the type of gear used. Write the label in soft pencil on a good quality paper and put it *inside* the jar. The formalin will preserve the paper and it will not get lost. If you wish, of course, use an outside label too, but do not omit the inside one. The second hint concerns magnifications. Never just say 'three times as big' without defining the meaning. 'Three times linear' is clear, or '× 3 diam.', but a piece of paper three times as big, or × 3, could mean three times the area, or three times the length and width which is nine times the area. A ball, × 3, could mean three times the volume or weight, or three times the diameter which is twenty-seven times the volume. A convenient method used with drawings is that used in this book, where a line representing a stated length is drawn to the same scale.

CHAPTER 3

The plants of the plankton—the 'phytoplankton'

There is an old, well-worn adage that 'all flesh is grass', and this is just as true in the sea as on the land, but here the 'grass' is the phytoplankton, the floating plants that are drifted by the water movements from place to place.

Green plants containing chlorophyll are able to utilize dissolved carbon dioxide, nutrient salts and the sun's energy to produce carbohydrates, proteins and oils, the basic food materials of the animals. The main difference between the terrestrial and aquatic environments is that on the land the water is in dark interstitial spaces between fairly stable soil particles and the light and carbon dioxide are in the air above; in the sea there is no such division and no stability. Light can penetrate sea water sufficiently for photosynthesis to be effective at the bottom in only a very small fraction of the total area of the sea, at depths less than 20 or 30 fathoms in the latitude of the British Isles, too small a fraction to be worth considering in the general chain of food production in the sea, and we can thus ignore the familiar seaweeds attached round our sea coasts. There can be no holdfast in the open sea and the plants must float in the light zone, and floating, be carried by the water movements from place to place, both horizontally in the currents and vertically in areas of turbulence.

If one looks at a sunbeam in a room one can see the dust particles floating about, and the smaller the particle the easier it floats. So it is with the plants of the open sea and they, too, are small, usually between 1/10,000 inch and 1/50 inch (Frontispiece, Plate VII and Fig. 7). Many have spines which increase their surface area and this helps flotation, others produce oil globules which reduce their specific gravity. Because of their small size, only the largest can be seen without a microscope, and just as a mere speck, and they cannot therefore be studied by the reader with only a general interest. Nevertheless, skipping some of the details if he so wishes, he should be able to get an idea of the types of plants that exist in the sea and so appreciate to advantage their importance, as discussed later in Chapters 9 and 10.

In brief, there are three main kinds of plants in the plankton, the nanoplankton, the diatoms and the dinoflagellates.

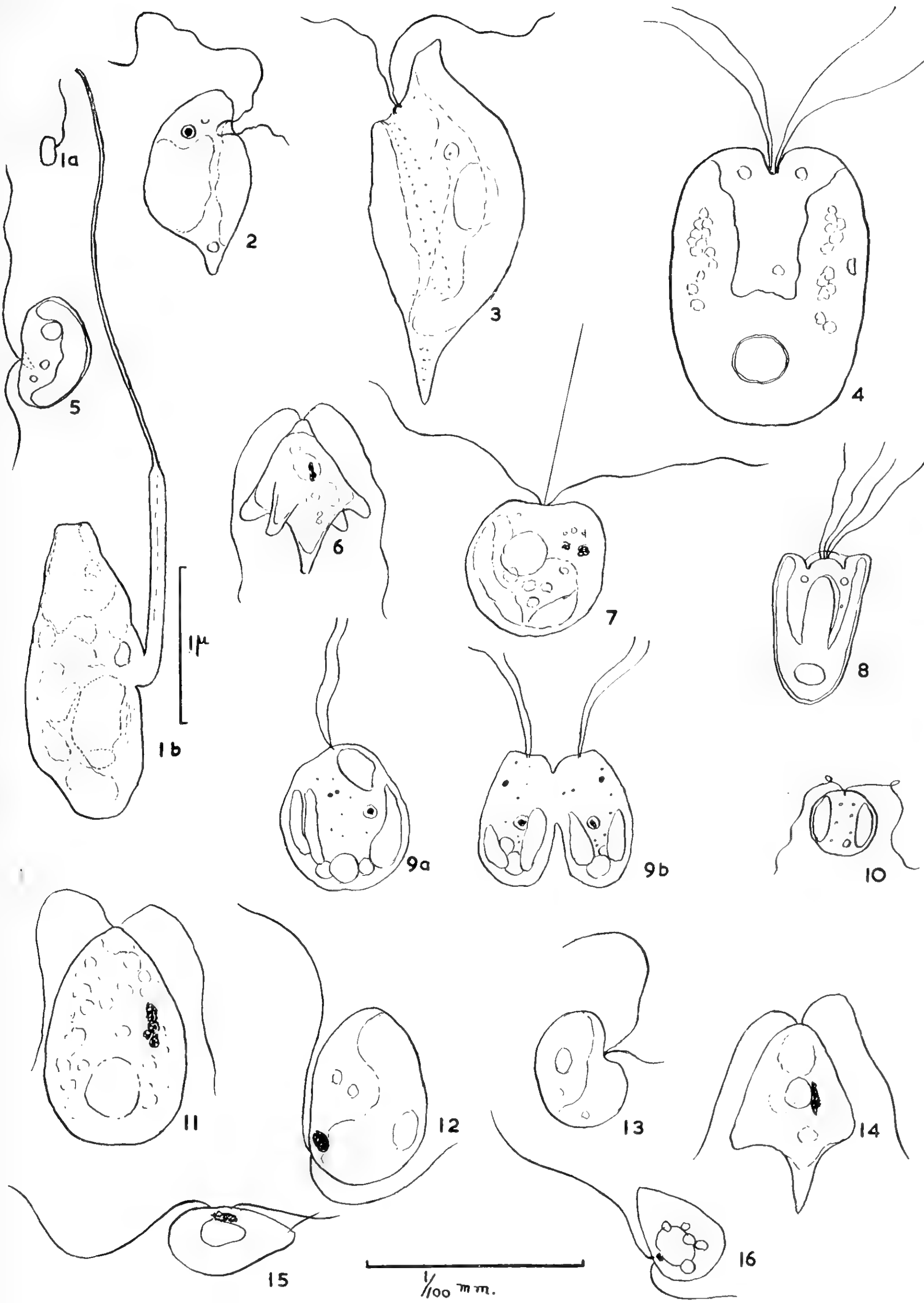


FIG. 7. Some organisms of the nanoplankton.

1, *Chromulina pusilla;* 2, *Pavlova gyrans;* 3, *Cryptomonas acuta;* 4, *Platymonas apiculata;* 5, *Hemiselmis rufescens;* 6, *Brachiomonas submarina;* 7, *Chrysochromulina minor;* 8, *Pyramimonas grossi;* 9a, *Isochrysis galbana;* 9b, the same dividing; 10, *Dicratena inornata;* 11, *Dunaliella parva;* 12, *Bipedimonas pyriformis;* 13, *Thalassomonas pusilla;* 14, *Brachiomonas simplex;* 15, Male spore of bladderwrack (*Fucus*); 16, Asexual spore of oarweed (*Saccorhiza*).

All to approximately the same scale, except 1b which is from a photograph taken with an electron microscope.

(a) *The Nanoplankton* *

These are extremely tiny plants, mostly between 1/10,000 inch and 1/1,000 inch, very delicate and capable of swimming often several times their own length in a second. As they are so minute, they are measured in 'μ' units ($1/\mu = 1/1{,}000$ millimetre). Those with one or more flagella are often termed 'μ flagellates' or hekistoplankton. A flagellum is a whip-like hair which lashes the water in one direction and flexes as it returns for the next beat, so enabling the organisms to swim in any direction. Planktonic organisms, bacteria excepted, less than 10 μ are included in the nanoplankton. The smallest known are only about 1 μ and are thus difficult to study even with an extremely good microscope. Electron microscope studies have, however, improved our knowledge of their structure considerably. Drawings of some are given in Fig. 7.

In spite of their small size, the nanoplankton is of great importance in the sea and it has been estimated that their total volume is at times about equal to and sometimes greatly exceeds that of the diatoms and dinoflagellates together. This will be more fully discussed in Chapter 9.

Because the discovery of nanoplankton is fairly recent and has been studied by only a very few experts, we still know very little about it. If you yearn to discover and name new species you should choose this field, for the numbers may well be limited only by the time given to them! We know so little about their physiology too, a most important field of study. Their very simplicity of structure makes it possible to investigate in pure cultures some of the little-known but highly complicated problems of vitamin requirements and vitamin production that could give clues to similar problems in higher plants and animals.

One of the best known is probably *Chromulina pusilla*, one of the smallest, only $1\text{–}1\frac{1}{2}\ \mu$; it was first named as one of the Chrysophyceae (orange or yellow plants) in 1952 by Butcher from studies made with the ordinary microscope. Research in 1959 with the electron microscope and biochemical tests have shown that it is not a member of the Chrysophyceae at all, but its affinities are nearer the Chlorophycae (green plants) to which most plants belong. *C. pusilla* is extremely abundant in coastal and open sea waters near the British Isles and probably in a much wider area. Figure 7; 1*a* and *b* show its general shape, a single cell with its one nucleus and a highly

* The term nanoplankton is not based on botanical characters but is merely a convenient size grouping. It is derived from the Greek 'nanos' meaning dwarf, and was coined by Lohmann in 1911 as 'nannoplankton', thus introducing a misspelling which should surely be corrected, although some purists argue that the way Lohmann spelt it should be the valid term even if wrongly derived.

refractive pyrenoid which may be a food reserve. There is a single flagellum. Its movements are delightful to watch and it often spins rapidly on its own axis. Indeed this dancing effect prompted Butcher to call one of his most graceful finds *Pavlova gyrans*; this has two flagella of unequal length (Fig. 7; 2).

These organisms reproduce by simply dividing into two halves (Fig. 7; 9*a* and *b*). When conditions are bad, they can form 'resting spores' which can withstand very severe drying, or cold, and grow again into the active form when things become normal again.

(b) The Diatoms

These plants rarely exceed 1/50 inch in size. They cannot swim in the accepted sense and have thick shells of silica.

Until the importance of the nanoplankton was realized diatoms were considered to be the main source of the productivity of the sea and the fundamental food supply of the animals including the fish themselves. Even considering the nanoplankton, their importance is immense. They are big enough to be caught by the finest grade of plankton nets and can be studied with a good microscope. Their hard shells or frustules of silica can be chemically cleaned with acid, and mounted for microscopical examination revealing a vast range of minute detail of form which has been a valuable aid to classification.

They belong to the class of Algae called the Bacillariophyceae and each consists of a single cell, although these may remain attached to each other after reproductive division, so that chains of cells are formed (Plates I and VII). Each cell has a skeleton composed of two valves that fit into each other like a pill-box and its lid (Fig. 8). When seen from the surface or bottom of

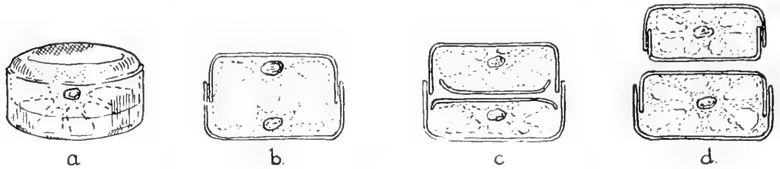


Fig. 8. Diagrams showing the simple division of a pillbox-like diatom: (*a*) the normal cell, (*b*), (*c*) and (*d*) sections through a dividing cell. Note that the new lower cell in (*d*) is the same size as the original but the upper cell is smaller. (From Professor Hardy's book, by kind permission.)

the box we get a 'valve view' which is primarily circular (e.g. Plate I; 2*a*) but may be a variety of shapes. When seen from the side we get a 'girdle view', which is primarily rectangular (Plate I; 2*b*) but also varies. It may be a 'flat' pill-box or a 'tall' one, even needle shaped, and there are indeed many

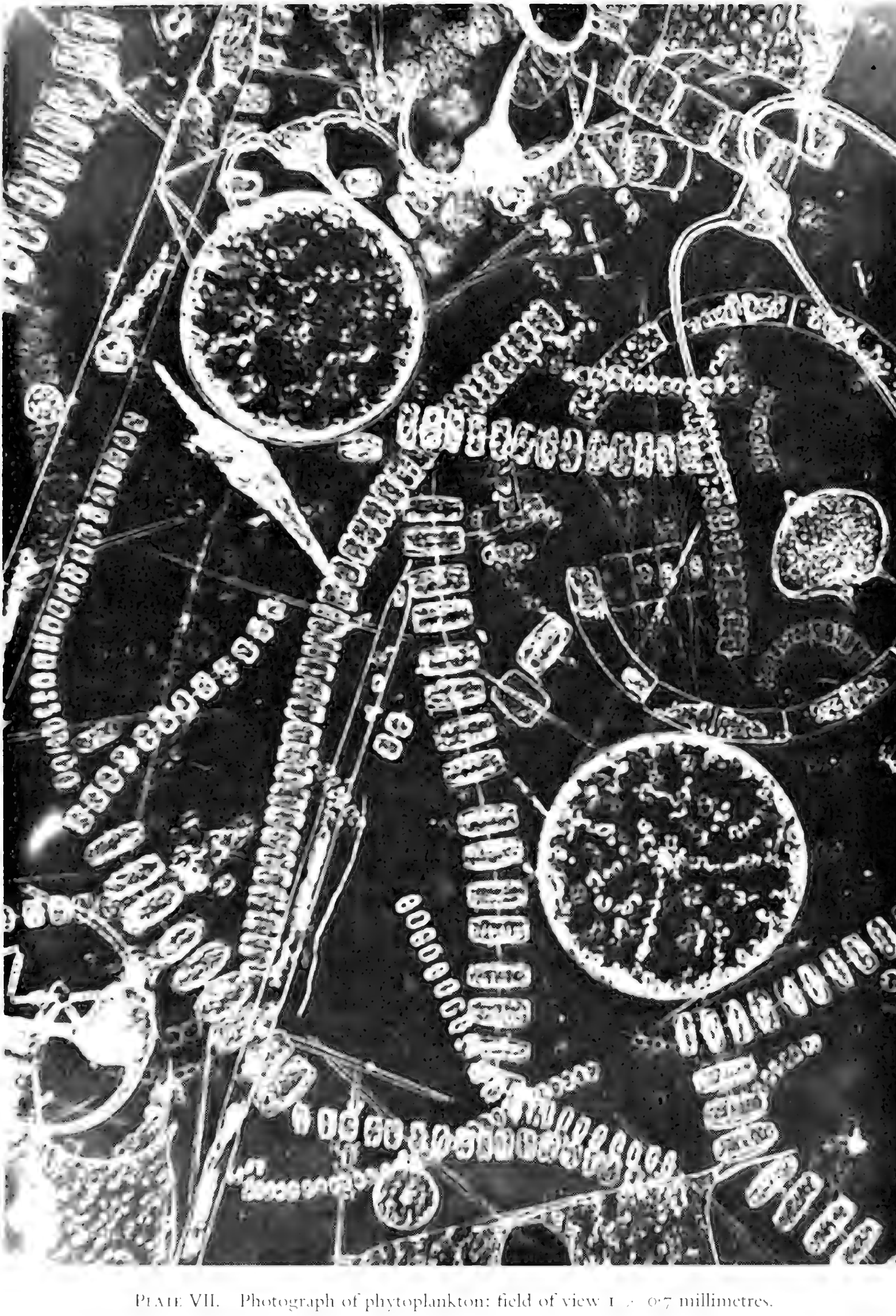
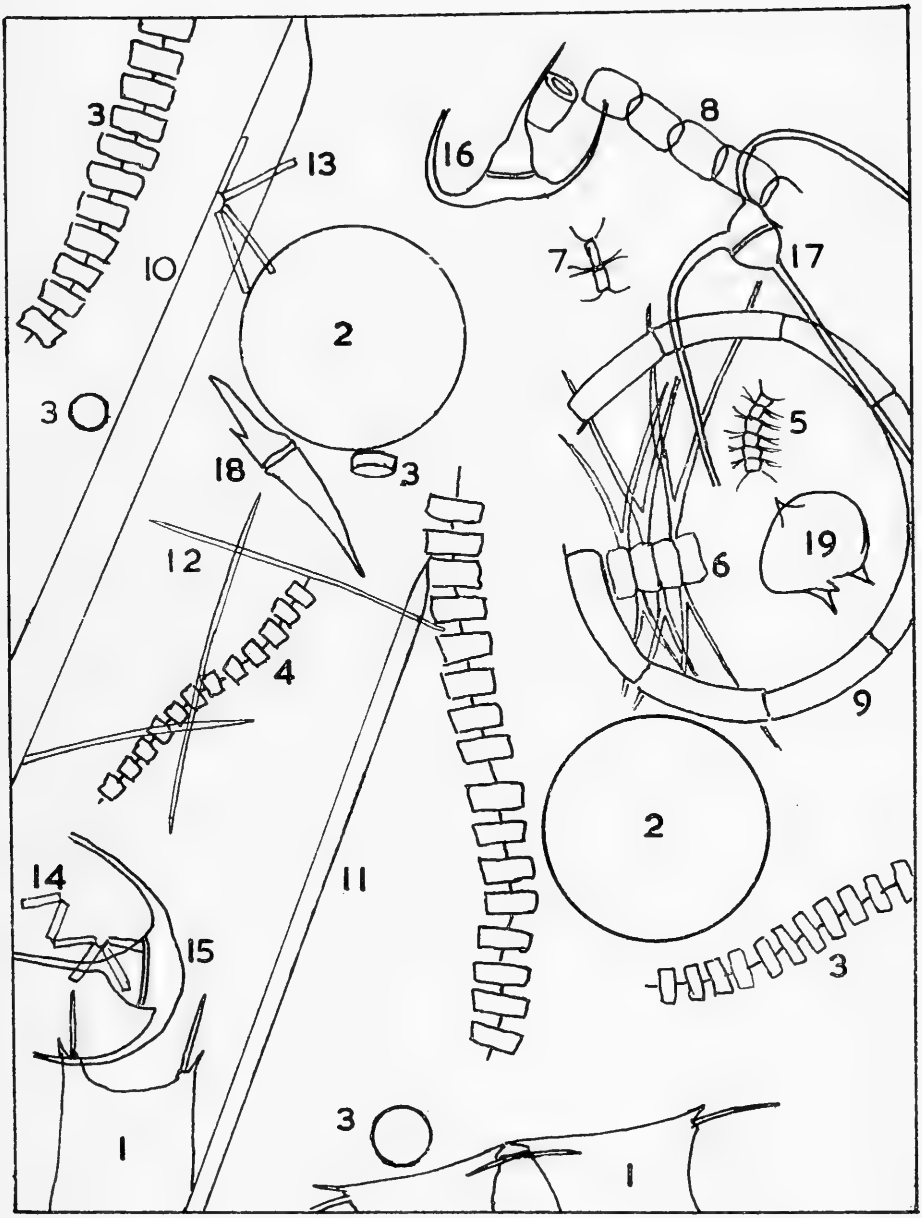


PLATE VII. Photograph of phytoplankton: field of view 1 × 0·7 millimetres.



Key to species:

1, *Biddulphia sinensis.* 2, *Coscinodiscus concinnus.* 3, *Thalassiosira gravida.* 4. *Thalassiosira nordenskioldii.* 5, *Chaetoceros curvisetus.* 6, *Chaetoceros decipiens.* 7, *Chaetoceros densus.* 8, *Melsosira borreri.* 9, *Rhizosolenia stolterfothi.* 10, *Rhizosolenia styliformis.* 11, *Rhizosolenia alata.* 12, *Nitzschia delicatissima.* 13, *Thalassiothrix frauenfeldii.* 14, *Thalassiothrix nitzschioides.* 15, *Ceratium tripos.* 16, *Ceratium longipes.* 17, *Ceratium macroceros.* 18, *Ceratium furca.* 19, *Peridinium depressum.*

Photograph by James Fraser

variations (Plate I). The shells (Plate VIII) are sculptured in various ways by the addition of spines and small holes—'puncta'—in strict patterns, through which the internal cytoplasm of the cell, the living part, has contact with the water outside. Some diatoms, chiefly those that live on the bottom, have one or both valves pierced by a slit called a raphe (Fig. 9) and these forms can

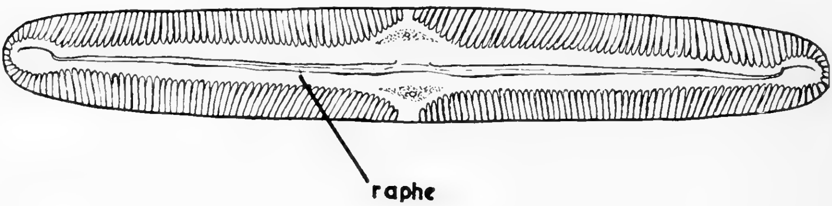


FIG. 9. A naviculoid diatom, *Pinnularia*, showing raphe, ×1200 diameters.

move slowly along, invisibly propelled by slight pressure differences caused by the minute chemical differences between the two ends of the cell. The movement is reminiscent, in fact, of the toy paper boats propelled by adding a small piece of naphtha into a slot in the deck. These kinds of diatom are sometimes carried into the plankton from the bottom by turbulent currents or wave action near the shore and will be amongst the most frequent kind if samples are collected from rock pools in the way described on page 14.

Diatoms have been abundant since Cretaceous times and their shells of silica have fallen to the sea bed, gradually accumulating through geological and recent times to form a diatomaceous ooze which predominates in a virtually continuous belt around Antarctica and in a band across the North Pacific Ocean. The dried ooze is also mined in places now above sea level and used as a polishing and insulating material. The most famous are the Kieselguhr mines of Germany; and there is a flourishing mine in the Hebrides in Scotland, only opened in 1960, although an older one in Skye closed in 1959 as to continue mining there became uneconomic. There are many others dotted over the world. Other planktonic marine organisms also form oozes on the sea bed and these will be dealt with later in the book.

But to return to the living diatoms! They are mostly (and the planktonic ones all are) *holophytic* or *autotrophic*, i.e. they live entirely by the process of photosynthesis using dissolved salts and gases and utilizing the sun's energy. This produces a large proportion of carbohydrate, with oils and proteins. As long as there is sufficient food present as dissolved salts, and sufficient light, diatoms continue to thrive and reproduce. This they do by simple division, the two parts of the pill-box separate and each grows a new half inside (Fig. 8). It thus follows that the two daughter cells are of

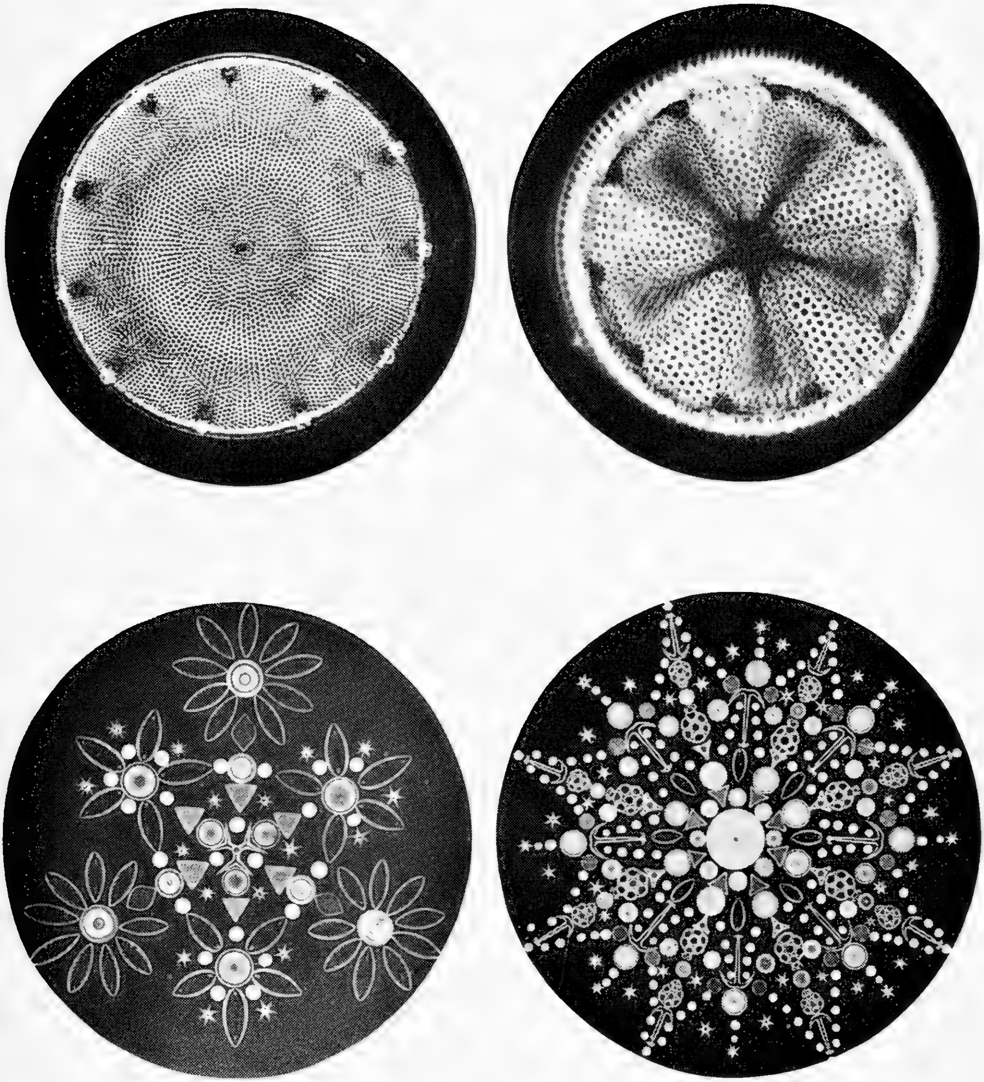


PLATE VIII.

(*Top*) Skeletons of diatoms; (*left*) *Aulacodiscus margaritaceous* (related to *Coscinodiscus* Plate I, 1 and 2); (*right*) *Actinoptychus heliopelta* (related to *A. undulata* Plate I, 3); both about 200 μ. (*Bottom*) 'The old microscopists playground'; geometric arrangement of diatoms and spicules; the groups are about 2 millimetres (*left*) and $3\frac{1}{2}$ millimetres (*right*) across.

[Photographs prepared by the author from negatives made in 1892 by the late J. Ogilvie, tea and coffee merchant, Dundee. The original mounting of the arrangement in the bottom right was by E. Thum of Leipzig and consists of 329 pieces.]

slightly unequal size, one being the same as the original, but the other, formed from the previous inside half, will be slightly smaller. On re-division the same thing occurs, and this can be useful information to the marine biologist as the detailed examination of the size range of any species in a diatom 'patch' in the sea helps him to identify the patch and gives a clue to the number of generations that have gone into its making. When cells become too small, they form auxospores which are aggregations of the cell contents in a large thin-walled swelling formed from the parent cell. These grow and form much larger cells of the normal shape and so the process starts again. These auxospores can be, but are not necessarily, involved in the production of resting spores which can survive conditions, such as the cold winters, which might be fatal to the normal cells.

Some diatoms are almost always found singly, or in pairs immediately after division (Frontispiece; 23, 24). Others cling in chains in which the cells show several different types of attachment; closely joined by the cell walls, interlacing of spines, ribbons of mucilage, or cytoplasmic threads formed from the actual living cell structure. The chains may be simple like strings of beads, ribbons coiled spirally or twisted in various directions, or as rods attached at one end only or at alternate ends. A series of pictures of some of the common types is given in the Frontispiece and a number of these can also be seen and recognized in the photograph, Plate VII.

Most of the diatoms are between about 1/200 inch and 1/50 inch, but they range from about 2·5 μ (1/1,000 inch) to 1,800 μ (1/14 inch). One of the smallest that is abundant in the coastal waters around the British Isles in spring is *Skeletonema costatum* (Frontispiece; 7) which has cells of about 7–15 μ across. Later in the year we find *Rhizosolenia styliformis*, (Frontispiece; 18) a large needle-shaped species that may be as much as 1/200 inch across and 1/20 inch long. An occasional visitor in our Atlantic water is *Ethmodiscus gazellae*, a relatively enormous round pill-box species similar to *Coscinodiscus* illustrated in Frontispiece; 1, but 14 inch in diameter. More about the abundance and succession of these diatoms throughout the year is given in Chapter 9.

A diatom from eastern waters, *Biddulphia sinensis* (Frontispiece; 25) named from its Chinese origin, was found in the southern North Sea near Heligoland in 1903 and assumed to have been brought in the ballast of some ship to the Elbe. Finding conditions suitable it multiplied there and became quite an abundant species in the southern North Sea and indeed was for a time conveniently used by planktologists as an indicator of this water. It gradually spread farther and by now it has far outgrown this restriction and is found in the English Channel, Irish Sea and northern North Sea.

Because of the very fine sculpturing of the diatom frustules they have been used as objects for testing the resolving power of microscope lenses. For example, *Pleurosigma angulatum* can be resolved with a lens that can separate about 45,000 lines per inch, but *Amphipleura pellucida* needs a better lens, one that separates 93,000 lines per inch. During the period 1880 to about 1920, there were many microscopists who delighted in using their instruments for the sheer joy of it, not particularly keen to make any new contribution to science but to obtain the ultimate optical perfection. To them the diatoms were favourites, not as a rule the planktonic ones, but the bottom-living species from rock pools, fresh water and bogs. They spent many happy evenings with their paraffin lamp, their expensive instruments, changing lenses etc., and arranging their minute 'collections' in strictly geometrical patterns such as those illustrated in Plate IX. Ready prepared slides of these fancy patterns could also be purchased. So also could slides of named diatoms to help the microscopist to identify his own collections. One such slide prepared in 1869 by Möller of Weden in Holstein contained about 400 different species beautifully arranged in a square of about 5 millimetres, and he provided a printed catalogue of their names. Few of us these days have the leisure for such academic pleasures!

(*c*) *The Dinoflagellates*

Dinoflagellates are of two main kinds, the 'naked' forms (Fig. 10 and Frontis.; 37–39) and the 'thecate' forms, 40–45, which have a strong exoskeleton built of plates of cellulose. These plates are of constant shape for each species and can therefore be used as characters for identifying them. All have two flagella, one free, and the other wrapped round a groove called the girdle (Plate IX). Many naked forms live on the sea floor in shallow water amongst the sand grains and mud, though quite a number are planktonic. There are several hundred planktonic thecate species, one of the commonest being *Ceratium tripos* (Frontis.; 43, and Pl. IX).

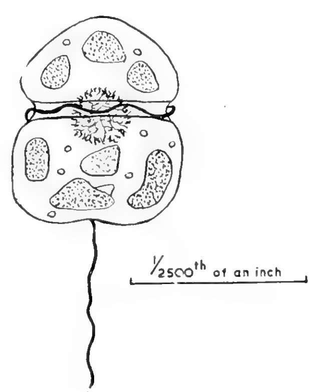
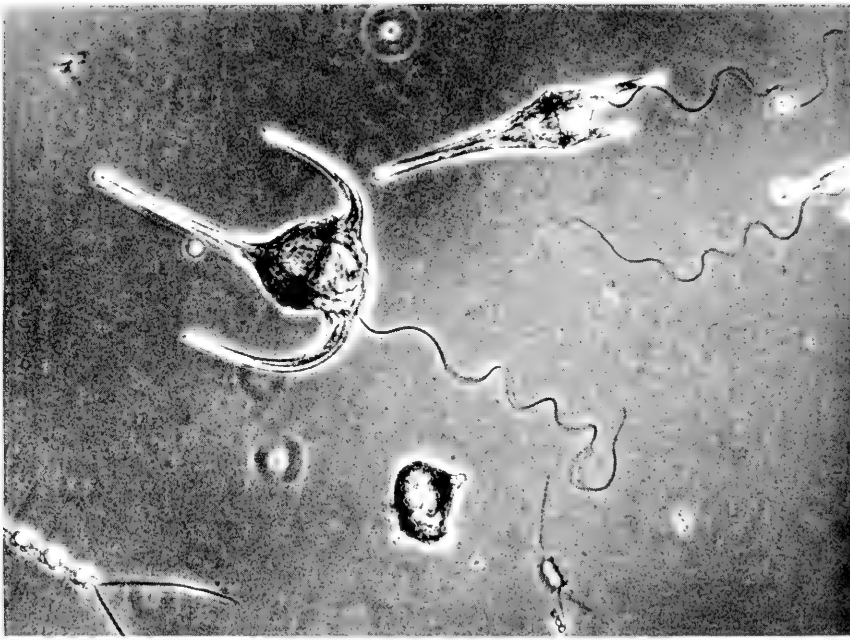


FIG. 10.
Gymnodinium veneficium, a dinoflagellate that produces a poison.

Like the diatoms they mostly contain chlorophyll but it is masked by other pigments giving them a brownish colour instead of green. They can thus utilize the dissolved salts and gases with the aid of sunlight, and in turn form the food of the animals. Many live only this way, i.e. they are autotrophic, but some can feed, like the protozoa, on minute organic particles in



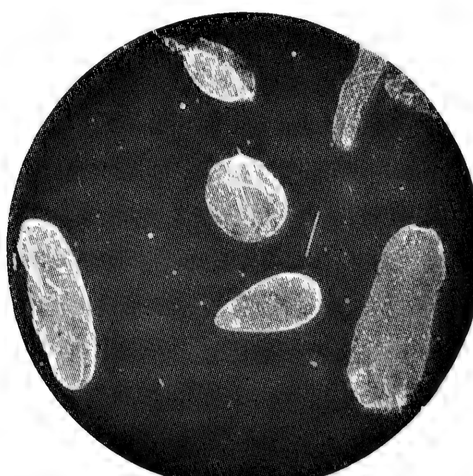


PLATE IX.

(*Top*) *Ceratium tripos* with *C. furca* and *Peridinium sp.*, showing especially the flagellae.
(*Bottom left*) *Noctiluca scintillans,* a phosphorescent dinoflagellate.
Photographs by Lennart Nilsson (from *Life in the Sea*)

(*Bottom right*) *Phaeocystis*, photographed alive by D. P. Wilson.

the water (i.e. they are heterotrophic), or on dissolved organic food. It is probable that some of the bottom-living forms, which have no chlorophyll, feed only in this way, but many of the planktonic ones can probably feed in both ways. The planktonic dinoflagellates can thrive in waters with less nutrient salts than can the diatoms so that they are generally most abundant after the diatoms die out, and indeed the heterotrophic ones may be partly utilizing the disintegration products of the diatoms—but more about this succession of species in Chapter 9. Like the other plants previously mentioned they reproduce by simple division, but the two new cells nearly always break away so that they continue to live singly. Sometimes, however, in the genus *Ceratium*, they remain attached to each other to form a chain when they are said to be 'in catena'.

Many dinoflagellates are phosphorescent, but as they are so small and often so numerous, the light they emit is like an undefined 'cloud of light' rather than the brighter easily defined pinpricks of light caused by a number of planktonic animals. One that deserves special mention in this connection is called *Noctiluca scintillans*. It is an unusual dinoflagellate, so swollen that it is almost spherical, relatively common, and about 1/15 inch across with the typical dinoflagellate part a mere fraction of the total (Plate IX). This is a producer of the well-known phosphorescence in the sea and hence its name. It is entirely heterotrophic and it feeds on diatoms and the smaller animals in the plankton which can sometimes be seen whole inside it.

Other members of the phytoplankton are the threadlike filaments of some of the blue-green algae (Cyanophyceae or Myxophyceae) such as *Oscillatoria* and *Anabena* which are found more often in inshore waters than in the open sea, and indeed the members of this group are much more typically freshwater than marine. Two other important marine organisms of the phytoplankton are *Phaeocystis* a member of the Yellow-green Algae (Chrysophysae), and *Halosphaera* one of the Xanthophyceae. *Halosphaera* is a bright green sphere, big enough to be seen by the naked eye as it is the size of a pin's head; it is an oceanic species often brought into the northern North Sea in great numbers in early spring. It does not just divide into two as do so many of the other species of phytoplankton, but the living tissue inside divides and redivides until the whole sphere is full of minute spores each with flagellae. These burst free and swim about—as members of the nanoplankton—until they eventually grow into new spheres. *Phaeocystis* (Plate IX) is similar in many ways but instead of being a very rigid sphere it forms a large gelatinous capsule of no particular shape. Numbers of these stick together to form a gelatinous mass, and if this is sufficiently dense makes the water unpalatable to herring which may change their course to avoid patches of it. Sometimes it is abundant near the shore and becomes deposited as a slime on the beach, and in July 1958 it was severe enough to adhere to bathing suits at the Danish resort of Fanø. Luckily such occurrences are very rare.

One feature of the phytoplankton, of whatever type, is that so long as conditions suit it perfectly, it can reproduce extremely rapidly to form denser and denser masses. The denser the mass, the more nutrient required so that the limit is reached very suddenly and the patch disintegrates even faster than it formed. Such patches, which occur in fresh water as well as in the sea, are called 'blooms', referring to the sudden burst of activity, and not to any analogy with the flowers of the higher plants. These blooms have their importance in the economy of the sea (Chapter 10) and may also show interesting side effects. One of the Blue-green threads called *Trichodesmium erythraeum* has a red colouring matter as well as the green. It lives in warm waters and on blooming forms mucilaginous balls of about 1/32 inch in diameter, which give the whole water a red appearance. It is responsible for the name of the Red Sea. Similar red-coloured plants, of various species, bloom suddenly and give rise to the stories of converting water into blood, and another is responsible for the colour of 'pink icebergs'. Such blooms depend on the simultaneous presence of several factors of which an abundant supply of nutrients is one. This supply can come from the upwelling of nutrient-rich deep water, drainage from richly fertilized land, mining operations or decay of a patch of other organisms which may themselves have taken a long time to concentrate the nutrients from a wide area. Sometimes a bloom occurs of a toxin-producing species forming a 'red tide', and although these occur mostly in warm water they can occur locally in cooler areas, but mostly in brackish waters where there is little tidal mixing. Red tides are mostly associated with dinoflagellates, such as *Gymnodinium brevis* and *Goniaulax monilata*; about a dozen are known. In a bloom sufficient toxin can be produced to kill off large numbers of fish within the affected area, and the poison carried ashore in wind-blown spray, can cause irritation to the people living there. Sometimes fish are killed merely by lack of oxygen when the bloom decays, the bacterial process of decay having used up the available oxygen. Red tides in New Zealand have been found to be due to minute animals called rotifers which have a bright red eye spot, but these are non-poisonous.

A poisonous dinoflagellate lives in British waters; it is *Gymnodinium veneficium*, which has been grown in culture at the Marine Biological Station at Plymouth (Fig. 10). It has never been known to 'bloom' here and is so unlikely to, that any danger of large-scale destruction of fish from this cause is quite remote. Nevertheless, a reporter got hold of the story and in a short article headed *Deadly plant found in the sea* he said 'Marine biologists have discovered a particularly deadly sea plant in Plymouth Sound. If the plant bloomed it could kill every living thing in the sea around it.' Such a story, based on fact, but made sensational and distorted by the omission of other facts, can cause mischief. Indeed, this story eventually led to a question in the House, with the best intention of attempting to forestall trouble for the fisherman. With the constant mixing of the waters round the British Isles by both tides and currents, there is little chance of any sudden concentrations of nutrients forming and even if they did the chance that a rare poisonous dinoflagellate would bloom instead of one of the thousand other non-poisonous species is indeed remote and no cause for the worry so sensationally expressed by the reporter. Some further details of this type of effect on the fish and fisheries are given in Chapter 10.

Some dinoflagellates are parasitic, living inside other organisms in the plankton, particularly radiolarians (p. 48). Some live in fish eggs where they do not seem to affect early development seriously—perhaps there is plenty of food for both—although the young fish seem to suffer and die soon after hatching.

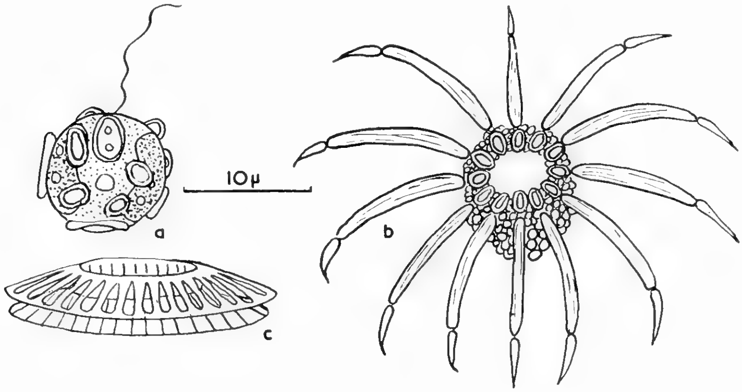


FIG. 11. Coccolithophores. (*a*) *Coccolithus* (*Pontosphaera*) *huxleyi*, (*b*) *Michaelsarsia aranea*, (*c*) a single coccolith from 'a' as reconstructed from photographs by an electron microscope. As reproduced here it represents a magnification of 17,000 diameters.

Minute plants, usually considered part of the nanoplankton, are the coccolithophores. These form a rather specialized group as each cell produces a layer of minute calcareous plates round it, often of fantastic shapes (Fig. 11). The cells themselves are so very small, mostly only 15 μ, that it is difficult or even impossible to see the structure of the plates—called coccoliths—even with a first-class high-power microscope. Only with the invention of the electron microscope have the details been resolved. Coccolithophores being plants need the sun's energy, but seem to require only the very minimum of light and live most abundantly at about 300 metres depth in the clear blue oceanic waters. Here they serve as a much needed food supply for other deep dwelling organisms in the plankton. Sometimes they are abundant quite near the surface and in inshore as well as oceanic waters. The minute calcareous plates catch the sunlight and make the water just a trace milky—a kind of duck-egg blue, as if a few drops of milk had been mixed with each gallon of sea water. Fishermen call this 'white water' and consider it a good omen for herring fishing (p. 133). We do not yet know enough about this group, and it may be that some we call separate species are phases in the life history of the same organism, or even phases in the life of something quite different.

CHAPTER 4

The animals—the zooplankton I

BIOLOGISTS CLASSIFY the plant and animal kingdoms into a number of major groups called 'Phyla', each of which is divided into 'Sub-Phyla', then into 'Classes', 'Orders', 'Families', 'Genera' and 'Species', with sub-divisions as necessary. For example: Man belongs to the phylum 'Chordata' as do also some very peculiar small planktonic creatures, to the sub-phylum 'Vertebrata' as also do the fishes and frogs, and to the class 'Mammalia' as do the mice and seals. Such divisions are recognized throughout the animal kingdom and it is but few of them that are not represented in the sea, although the marine plants, except for the eel grass, all belong to one phylum. There are no marine amphibians (frogs, newts etc.), but there are marine reptiles (some turtles, sea-snakes, and the marine lizards of the Galapagos Islands), and mammals (seals, dolphins, whales). All the invertebrate sub-phyla are represented, though there are extremely few insects, millipedes or spiders compared with the crustacea. Some phyla are totally marine, notably the Echinodermata (starfishes and sea-urchins) and the Chaetognatha (arrow-worms). Not all of these marine forms are planktonic of course, but it is remarkable how many are planktonic at some stage in their life history, and Chapter 6 will be devoted to the planktonic larvae of bottom-dwelling species. It should be noted that the odd turtle that is carried away from his normal habitat in Mexico and eventually stranded on the coasts of Ireland or Scotland has drifted across in spite of his ability to swim, and may thus be considered as aberrantly planktonic. These, however, are the exceptions and of passing interest (Chapter 11).

Many, very many, of the smaller marine creatures are planktonic all their lives; the scientist calls them 'holoplanktonic' as against 'meroplanktonic', a term that includes organisms that are only planktonic during part of their lives. The abundance of small creatures has given rise to the impression that the study of plankton is essentially a microscopist's calling; though in general true, this is not completely so, and quite a lot can be done by the naked eye or with a lens of only small magnification. Some of the largest jellyfish can be a yard or more across.

This and the next chapter will describe a selection of the commonest and most characteristic types in the classified order, but dealing only with the holoplanktonic species, and this will be very far indeed from an exhaustive survey.

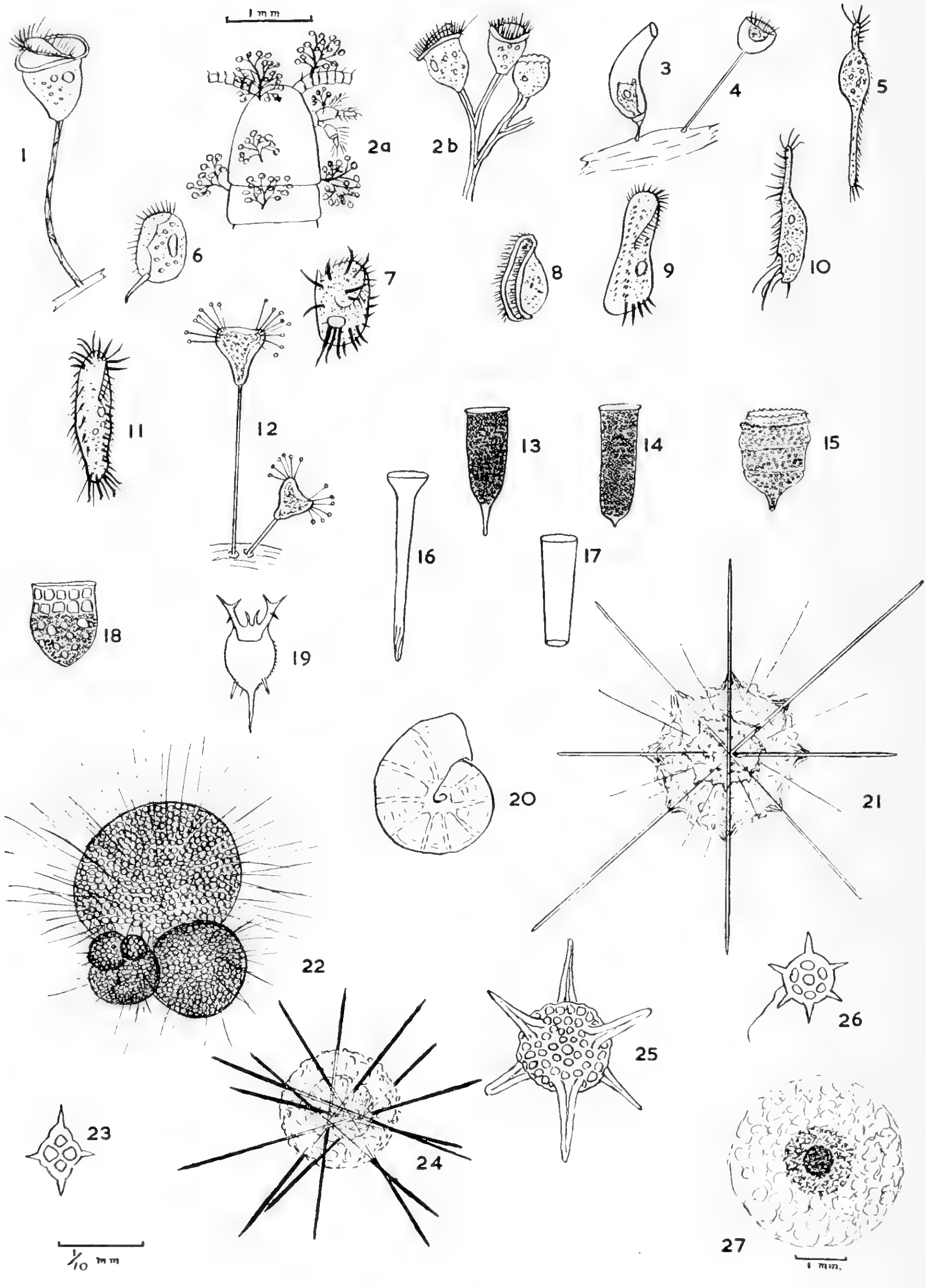


FIG. 12. Protozoa.

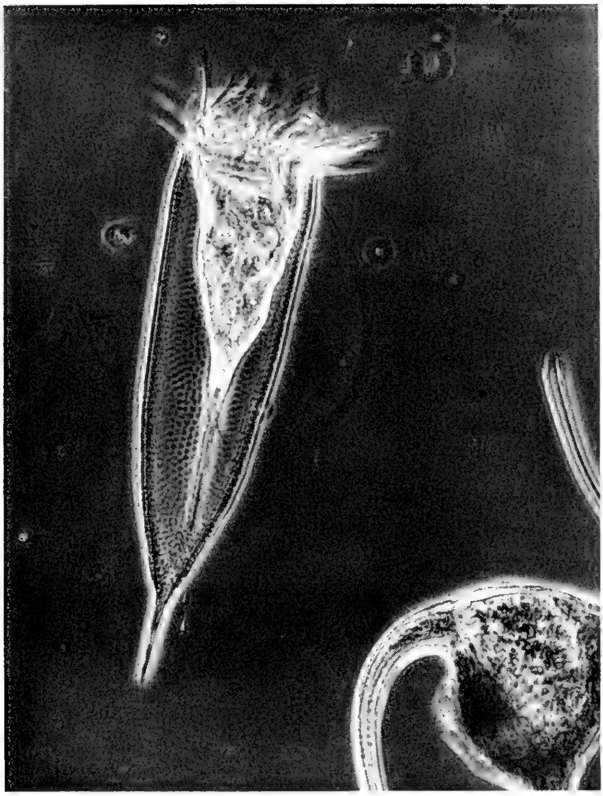
1, *Vorticella marina;* 2, *Zoothamnion marinum;* (2*a*, at a reduced scale showing colonies on the copepod *Eurytemora hirundoides*); 3, *Cothurnia gracilis;* 4, *Cothurnia havniensis;* 5, *Epiclintes retractilis;* 6, *Aegyria monostyla;* 7, *Euplotes harpa;* 8, *Aegyria oliva;* 9, *Amphisia pernix;* 10, *Stichochaeta pediculiformis;* 11, *Oxytricha pellionella;* 12, *Acineta tuberosa;* 13, *Parafavella elegans;* 14, *Parafavella edentata;* 15, *Ptychocylis minor;* 16, *Salpingella ricta;* 17, *Tintinnus tubulosus;* 18, *Dictyocysta magna;* 19, *Challengeron neptuni;* 20, *Nonion pompilioides;* 21, *Acathometron pellucidum;* 22, *Globigerina bulloides;* 23, *Dictyocha fibula;* 24, *Achanthochiasma fusiforme;* 25, *Hexalonche philosophica;* 26, *Distephanus speculum;* 27, *Thalassicolla nucleata.*

[1–11, Ciliata. 12, Suctoria. 13–18, Tintinnoidea. 20, 22, Foramenifera. 19, 21, 24, 25, 27, Radiolaria. 23, 26, Silicoflagellata. All to the same scale except 2*a* and 27.]

1. *Protozoa*

Protozoa are single-celled—or if you prefer it, acellular—animals and almost all are microscopic creatures. They occur in marine and fresh water, in the damp soil and as parasites of almost every living thing. In the plankton they may live freely, or attached to larger planktonic creatures and there are also many protozoan parasites of plankton. The free protozoa feed on bacteria and small particles of detritus which occur as particles either from land drainage or from the disintegration of marine creatures and they thus serve a useful role in the food cycle in the sea. Some, highly magnified, are illustrated in Fig. 12. Although many swim about as naked forms, others build shells of minute sand grains or secrete their own shells of very delicate and sometimes extremely intricate design. The tintinnids have fairly simple bell-shaped shells as shown in Plate X and Fig. 12; 13–17. Two most important groups of planktonic protozoa are the Foraminifera and the Radiolaria. The Foraminifera secrete calcareous shells, often resembling minute molluscan shells (Fig. 12; 20) punctured with many small holes, called foramina, hence the name. On death these shells sink to the bottom, sometimes in sufficiently vast numbers to form an ooze there. The most prolific of these is called *Globigerina* (Fig. 12; 22); Globigerina ooze covers the greater part of the Atlantic sea bed and most of the floor of the Pacific ocean south of the equator. Although the planktonic Foraminifera are extremely numerous individually, the number of species is small, in double figures only, but there are some 1,200 known species living on the bottom and about 18,000 fossil forms. These are important as the different species are known to have lived within certain temperature limits and examination of the Foraminifera from 'core samples' of mud and ooze from the sea bed can reveal the climatic conditions at the time the deposit was formed. A similar technique is used in dating sedimentary rocks.

The Radiolaria do not secrete external calcareous shells like the Foraminifera but an internal siliceous skeleton, sometimes fantastically delicate and precise, and often in a radial form (Fig. 12; 21) from which the name is derived. These, too, have been sufficiently numerous in the plankton for their deposited skeletons to form an ooze—the Radiolarian ooze—which is found most characteristically as a band across the Pacific from Panama to about 160° W lying to the north of the Globigerina ooze. Radiolaria are abundant in the north Atlantic today, especially in the warmer water and are carried by it to the North Sea, Faroe and Icelandic areas. One species of Radiolaria, *Thalassicolla* (Fig 12; 27), is relatively huge for a protozoan, and has a large central zone of about a millimetre in diameter surrounded by a foam of protoplasm up to about 5 millimetres, making it look very like



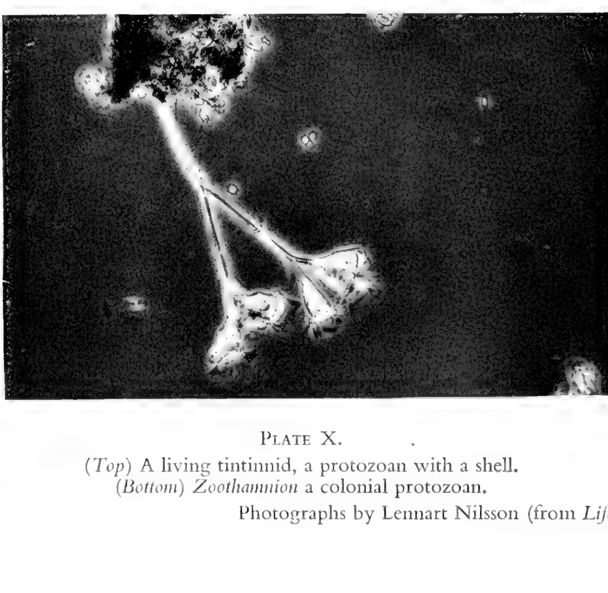


PLATE X.

(*Top*) A living tintinnid, a protozoan with a shell.
(*Bottom*) *Zoothamnion* a colonial protozoan.

Photographs by Lennart Nilsson (from *Life in the Sea*)

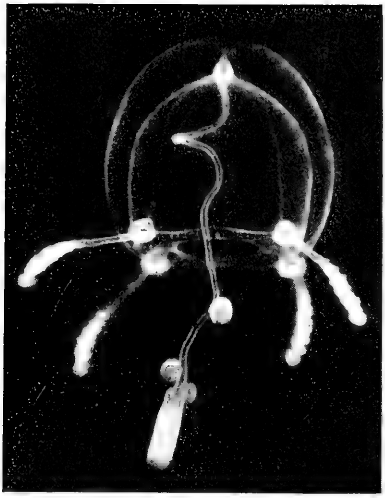
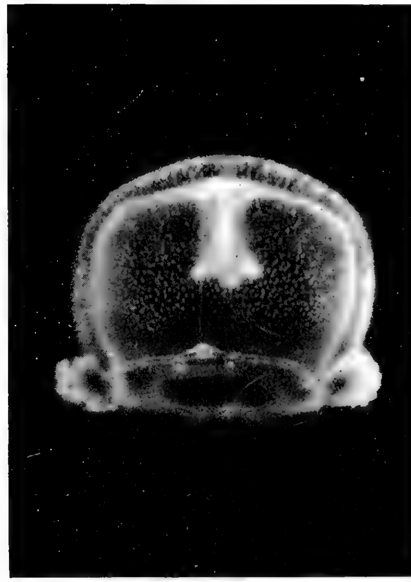
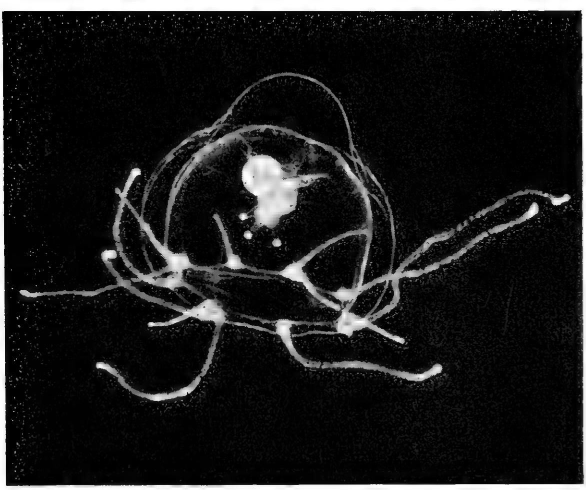
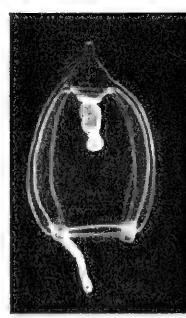





PLATE XI. Small jellyfish.
(*Top left*) *Sarsia gemmifera.*
(*Top right*) A young *Aequorea* just liberated from the hydroid.
(*Bottom left*) *Lizzia blondina.*
(*Bottom right*) *Steenstrupia nutans.*
All photographed from life by D. P. Wilson

a single blob of frog spawn. It can, indeed, be parasitized by some of the dinoflagellates (p. 41).

Also important are those protozoa attached to larger planktonic animals (Fig. 12; 2*a* and *b*: Plate X). As these feed on bacteria and detritus they are particularly abundant in estuaries which are polluted by untreated sewage and here they have a particularly useful function in the destruction of sewage bacteria. Their attachment to relatively active creatures ensures a continual change of water which thus provides an ample supply of their food, and in turn they are fed on by other animals, often by those which have carried them about. In a polluted estuary, e.g. the Mersey, Humber, Thames, and even places like the Oslo fjord, these abundant protozoa form the food of small crustacea, which are in turn fed on by the larger creatures. The local plankton is thus not so dependent upon the growth of plant life as it would be in a non-polluted area, and a good rich growth can exist even in winter conditions when the light is poor.

Coelenterata (Jellyfish, sea anemones, corals etc.)

Coelenterates are all aquatic, and with only a few exceptions are marine. Although a large proportion of coelenterates are attached at some part of their life history, some of the most characteristic are always free-swimming. The planktonic stage of jellyfish is so typical of the plankton that it should be considered here rather than in Chapter 6 which deals with the meroplanktonic forms. The feathery hydroids common in pools and on shore seaweeds produce small medusae (jellyfish) which are then part of the plankton. These small jellies, some of which are illustrated in Figs. 13 and 14, and in Plate XI, are vastly more abundant than the large conspicuous ones that annoy the bathers and fishermen so much. All are carnivorous, feeding on other planktonic creatures including small fish (Plate XIV). These they capture by paralysing them with their stings which are usually prolific, especially on their tentacles and round the mouth region, though they are usually absent from the upper side of the 'bell'. Each stinging cell is called a 'nematocyst' and there are quite a variety of types. Basically each is a sac of poison with an invaginated barb—like the inside-out finger of a glove, though much elongated (Fig. 15). When touched the sac is compressed, out shoots the barb, penetrating the skin of the unfortunate creature, and acting as a tube through which the poison is injected. The paralysed prey is then easily eaten. Jellyfish have small 'statocysts', little balancing organs with which they can not only sense which way up they are but can feel vibrations in the water caused by the turbulence of other moving creatures. So accurately can they sense these vibrations that, although quite unable to see, they can stretch out their mouths

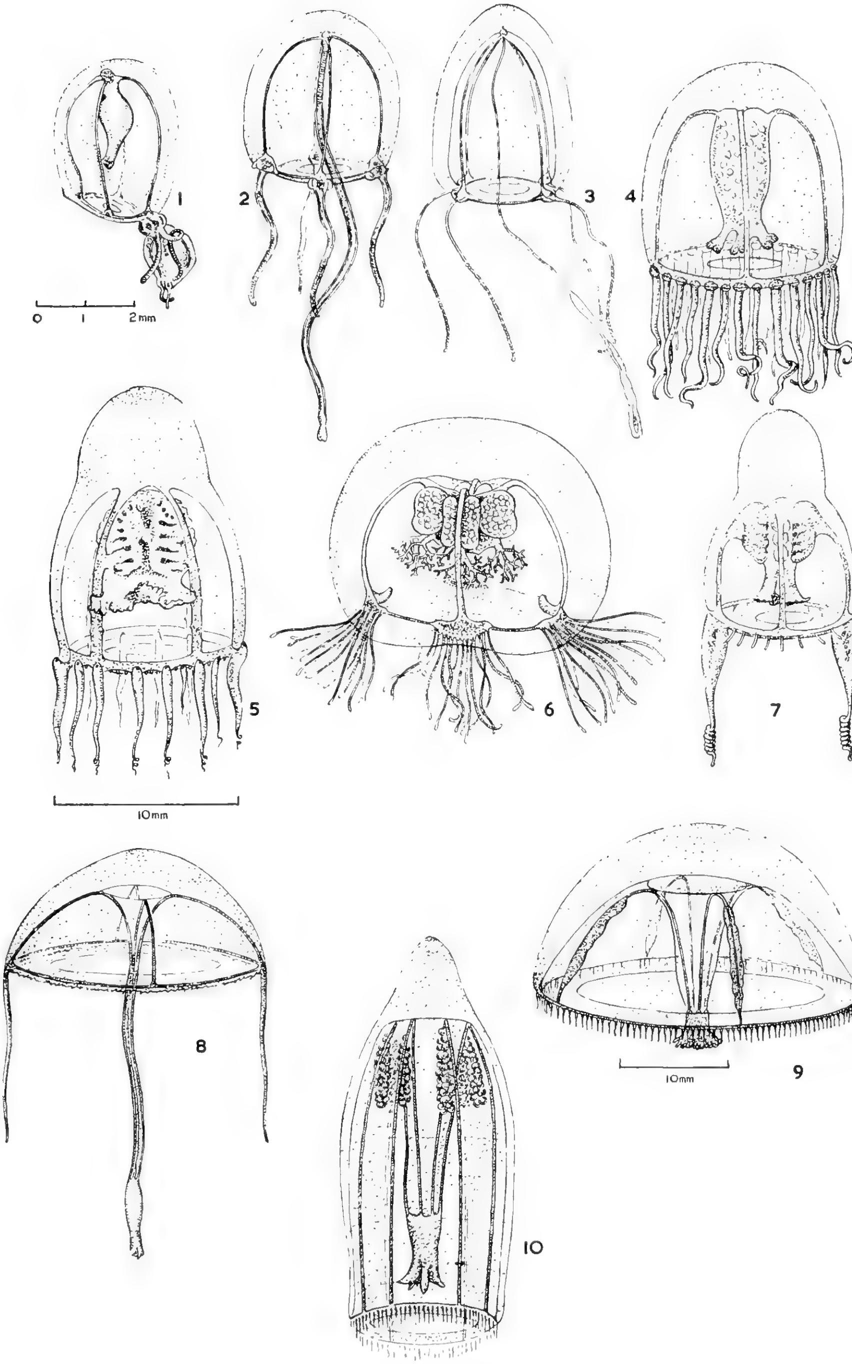


FIG. 13. Small jellyfish.

1, *Hybocodon prolifer;* 2, *Sarsia tubulosa;* 3, *Dipurena ophiogaster;* 4, *Podocoryne borealis;* 5, *Leuckartiara octona;* 6, *Bougainvillia principis;* 7, *Amphinema rugosum;* 8, *Eutima gracilis;* 9, *Eutonina indicans;* 10, *Aglantha digitale.*

2, 3, 4, 6 and 7 to same scale as Fig. 1; Figs. 8 and 10 to same scale as Fig. 5.

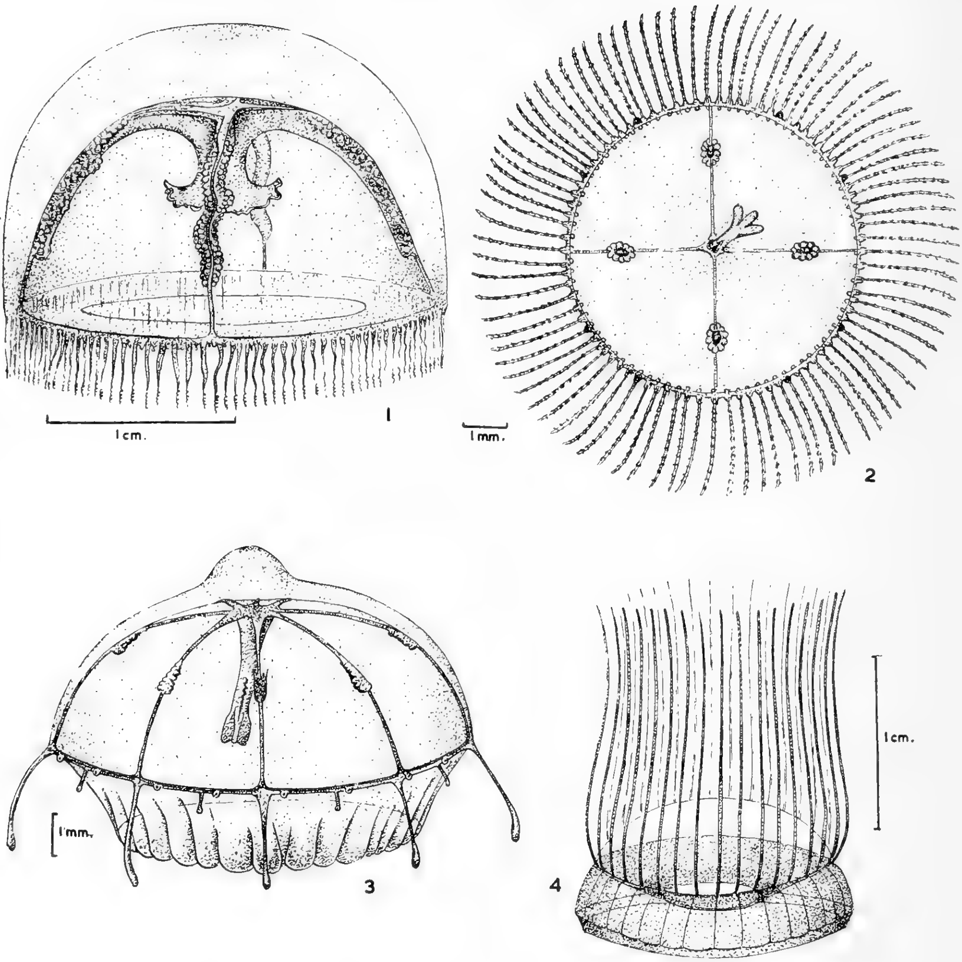


FIG. 14. More small jellyfish.
1, *Laodicea undulata;* 2, *Obelia* (see also Plate XII); 3, *Rhopalonema velatum;* 4, *Solmaris corona.*

with the stinging cells to capture unerringly a passing small fish or crustacean. They are sensitive to light and the shallow water species will sink deeper into the water in bright sunshine, returning towards the surface when a cloud covers the sun, or as evening approaches. They swim by a gentle pulsation of the bell and control their direction by inclining the bell in the direction they want to go; they sink by just ceasing to pulsate. The larger jellyfish (Fig. 16) have a special interest because their size makes them so familiar. There are large numbers of tropical species but not so many in temperate waters. The oceanic species may be carried into the shallower seas by ocean currents but do not usually survive long and rarely, if ever, breed far out of their normal habitat. The largest and best known are local species which live and breed in shallow water. Of these the commonest is the moon jelly,

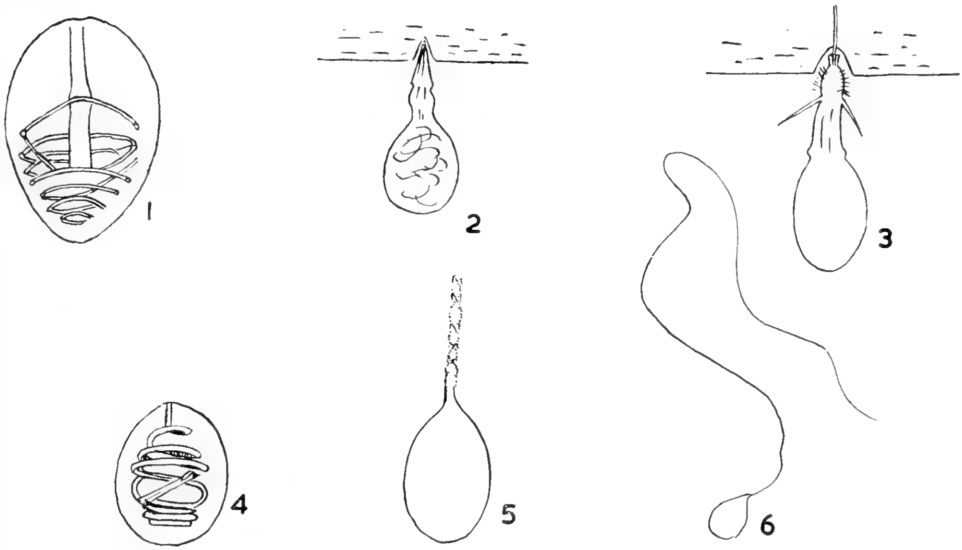


FIG. 15. Nematocysts, the stinging cells of jellyfish.
1–3 from the small jellyfish *Sarsia;* 1, undischarged; 2 and 3, two stages of penetration; 4–6 from the large stinging jellyfish *Cyanea;* 4, undischarged; 5, discharged; 6, as 5 but at a reduced scale to show the length of the thread. All after Russell, partly from the *Journal of Marine Biological Association*, and partly from *The School Science Review*.

Aurelia (Plate XIII and Fig. 16) sometimes called '88' because of the four horseshoe shaped gonads so readily visible in its very transparent jelly. It has four 'arms' hanging from the centre of the disc—the umbrella as it is called. This is not a stinging jellyfish to the bather as its stinging cells are not powerful enough to penetrate the skin of even a 'fair blonde' though it does live by paralysing its prey. Strangely enough when quite small, about an inch across, it can paralyse and eat small fish almost its own size, but as it grows its mouth capacity shrinks so that as a full grown jelly of 6 inches or 1 foot in diameter it feeds entirely on small planktonic animals.

The big stinger *Cyanea* (Fig 16. and Plate II)—which may be a yellow-brown, *C. capillata*, or a blue colour, *C. lamarcki*—is usually much bigger, often 2 feet and occasionally nearly 3 feet. It has a thick set of very long trailing tentacles which can extend in the water as much as 30 feet. These are liberally provided with powerful stinging cells which can indeed be unpleasant, not only to the tender skin of a bather but to the horny hands of a fisherman, and extremely nasty if the eyes are affected. Big stinging jellyfish nevertheless do form a protective umbrella to schools of small fish about 1 to 2 inches long, especially young whiting and rockling. They do not seem to suffer from the jellyfish and use the umbrella for a sunshade on bright days; no doubt they are safer there from some of their own predators and they may be feeding to some extent on 'crumbs from the jelly's table', or on crustacean parasites of the jellyfish.

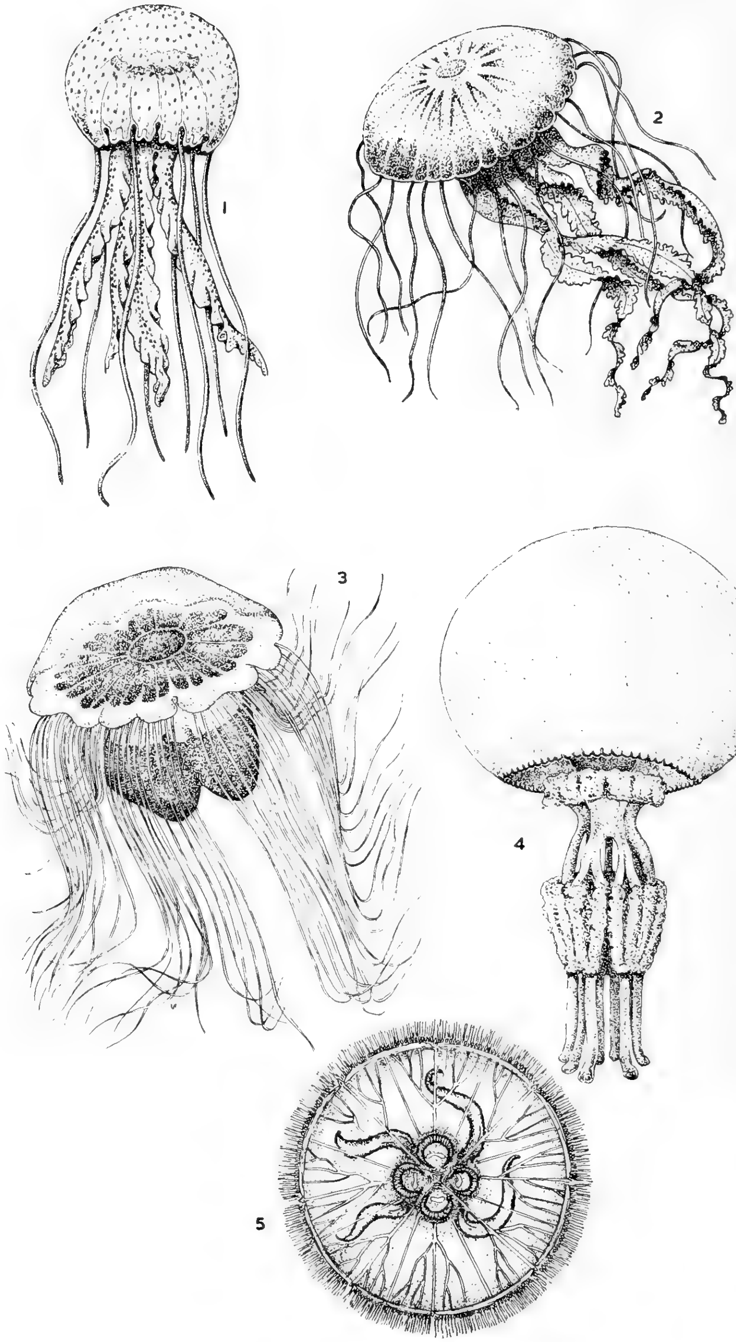


FIG. 16. Large jellyfish.

1, The pearl jelly, *Pelagia noctiluca;* 2, *Chrysaora hyoscella;* 3, The big stinger or lion's mane; *Cyanea,* see also Plate II; 4, The cauliflower jelly *Rhizostoma octopus;* 5, The moon jelly, *Aurelia aurita.*

1, rarely exceeds 3 inches; 5, reaches about 1 foot, but the others may occasionally be up to 3 feet across.

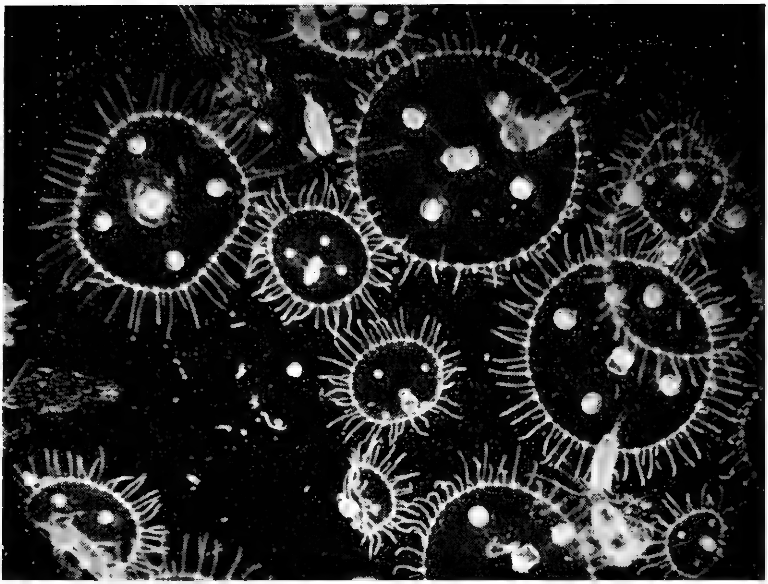


PLATE XII.

(*Top*) Medusae of *Obelia*.

Photograph from life by D. P. Wilson

(*Bottom*) *Chysaora* stranded on the Welsh coast.

Photograph by Margaret Nyblad

The big jellyfish spawn in the autumn before being killed off during the winter and the young larvae settle on rocks and stones, especially near the coasts, where they remain attached as elongated blobs of jelly called '*scyphistoma*' (Plate XIII). In the spring each divides like a pile of saucers, each saucer splitting off, turning upside down and swimming away as an 'ephyra' which grows into a new jellyfish. Not until the summer, however, when they have grown big are they generally noticed. A big outbreak, such as occurred in 1959, is thus the result of a good brood of young ones followed by conditions that enable more than usual to survive. Although this would produce a lot of eggs, the crop the following year would depend much more on the winter conditions and the plankton available as food during the following spring and summer.

Another large jellyfish that is native to the waters round the British Isles, and north-east Atlantic coasts generally, is the cauliflower jelly, *Rhizostoma octopus* (Fig. 16; 4). This, too, can reach a yard across. The upper side of the umbrella is a rather dirty white in colour and unmarked except for a bright purple fringe round the edge, and below it are four large holes leading to the reproductive organs. Hanging down is the 'cauliflower' part which is the stomach branched and rebranched until it ends in thousands of mouths—the name *Rhizostoma* means root like mouths—which filter off the plankton on which it feeds. It therefore does not need to paralyse its prey and in spite of its formidable look it is not a stinger. The 'cauliflower' ends in eight distinct arms and hence the specific name 'octopus'.

Chrysaora (Fig. 16; 2) is another large jellyfish which, although not so common as *Aurelia* or *Cyanea* is often stranded on our shores (Plate XII). It can be recognized by its chocolate-coloured wedge-shaped markings. The pearl jelly *Pelagia*, Fig. 16; 1, is an Atlantic form sometimes brought in by the ocean currents in quite large numbers.

Another 'Order' of Coelenterata occurring in the plankton is the Siphonophora, a wholly planktonic group. They are colonial forms, i.e. each is a colony of a number of individuals each with its own job to do, the whole acting as one animal. Some are simple transparent bells, or double bells with only small trailing tentacles (Fig. 17; 1). Others are more complicated, some of the individuals acting as floats, some as swimming bells, others as food catchers and yet others solely engaged in reproduction (Fig. 17; 2 and 3). Like the stinging jellyfish, they catch and paralyse their prey with trailing tentacles armed with stinging cells.

Although most of them are so delicate that they are difficult to capture whole and are quite harmless to us, one of them—*Physalia*, the Portuguese Man o' War—is a really nasty creature in spite of its pleasant colours (Fig. 17; 4: Plate II). Found in most of the warmer waters of the North

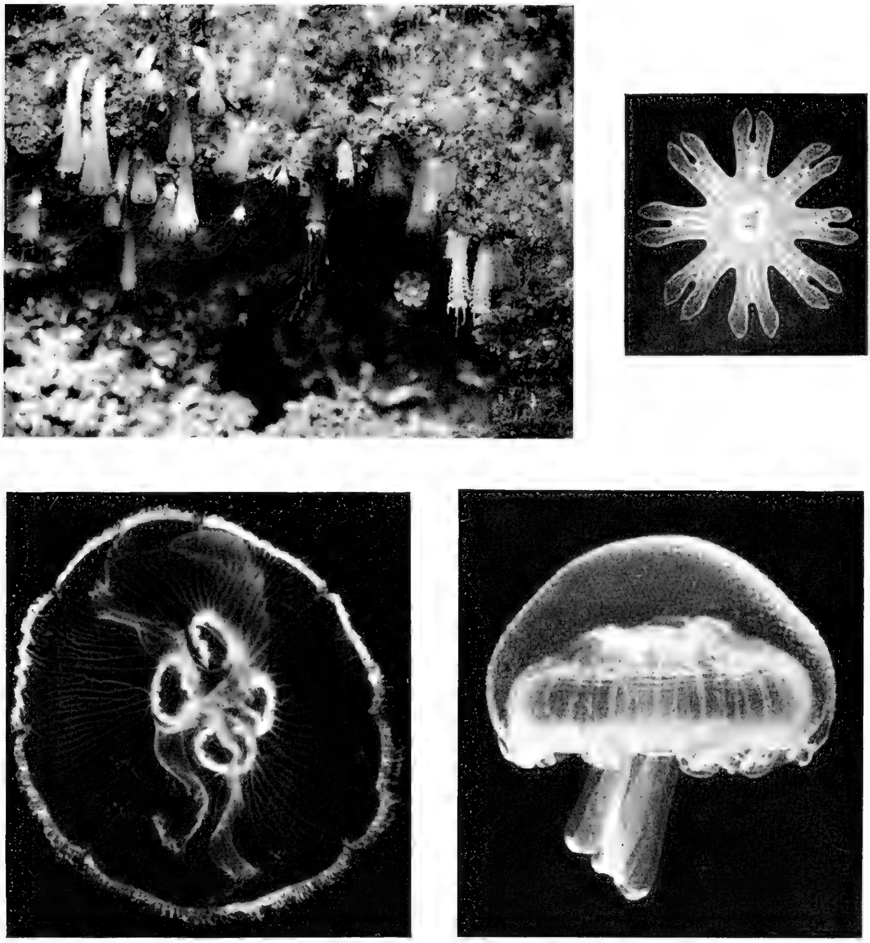


PLATE XIII. The life history of *Aurelia*.
(*Top left*) Scyphistoma hanging from rocks, one ephyra is seen having been just budded off.
(*Top right*) A single ephyra.
(*Bottom left*) A later stage of young jellyfish.
(*Bottom right*) The adult with the four horse-shoe shaped gonads.
All photographs from life by D. P. Wilson

Atlantic it is common in the Biscay area and from there invades the English Channel from time to time, in recent years notably in 1954 and 1957. It occasionally becomes carried farther north but records north of the Bristol Channel are extremely rare and it has not been found in the North Sea. Its virulent stinging powers make it a real nuisance to bathers and the 1957 strandings in particular caused quite a commotion in the British press. In medical terms it causes 'vasomotor dysfunction and collapse', i.e. the nerves just will not work. Local application of alcohol is effective if applied to the skin quickly as it reduces the toxicity and destroys any nematocysts still

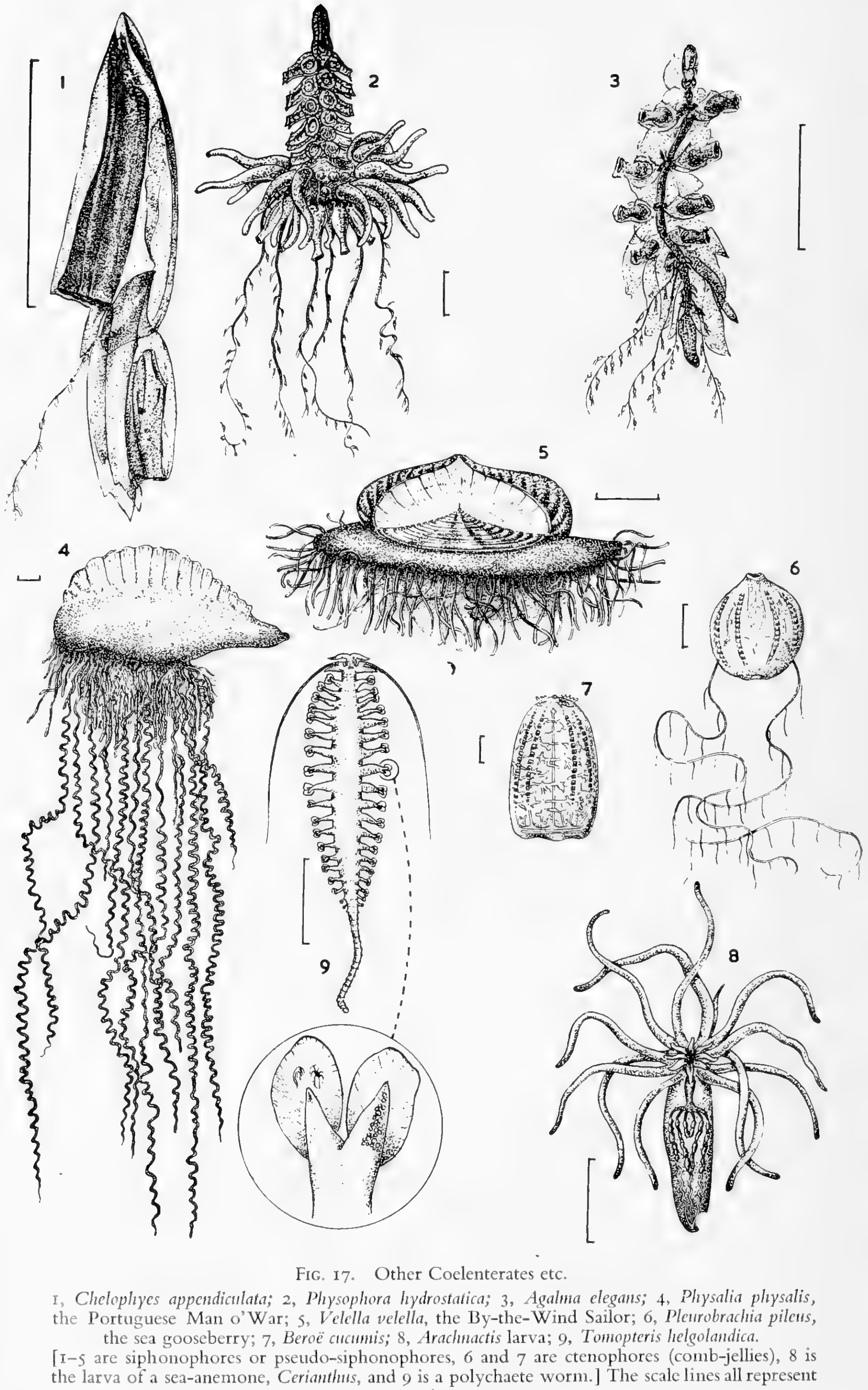


FIG. 17. Other Coelenterates etc.

1, *Chelophyes appendiculata;* 2, *Physophora hydrostatica;* 3, *Agalma elegans;* 4, *Physalia physalis,* the Portuguese Man o'War; 5, *Velella velella,* the By-the-Wind Sailor; 6, *Pleurobrachia pileus,* the sea gooseberry; 7, *Beroë cucumis;* 8, *Arachnactis* larva; 9, *Tomopteris helgolandica.*
[1–5 are siphonophores or pseudo-siphonophores, 6 and 7 are ctenophores (comb-jellies), 8 is the larva of a sea-anemone, *Cerianthus,* and 9 is a polychaete worm.] The scale lines all represent 1 centimetre.

adhering to the skin but not yet exploded. Fortunately, it is easily recognized by its large bluish or greenish float some 6 inches or so in length. This float, which also acts as a sail, is set at an angle to the rest of the body, sometimes to the left, sometimes to the right, with the result that they are differently affected by the wind and a shoal consists only of those with the same set of the sail. Because the dominant winds in an area are usually constant we are not sure if the two types are produced in equal numbers and separated at an early stage by the wind, one type tending to come ashore on the European coast and the other going out to sea. It may be that the different angles are associated with the two hemispheres, and those stranded in the southern hemisphere usually have their sails set in the opposite direction from those stranded in the northern hemisphere.

A small harmless siphonophore, *Physophora* (Fig. 17; 2), is found in boreal waters and is common in the northern North Sea, Norwegian Sea and Icelandic waters, though it also penetrates much farther south, even into the Mediterranean. A surface floating warm-water pseudo-siphonophore or chondrophore is *Velella*, also known as the 'By-the-wind sailor' or 'sallee man' (Fig. 17; 5). It is oval in shape, purple or blue and about 1 or 2 inches in length. This species has a stiff sail set at an angle across the disc and this may be set to the left or to the right as in *Physalia* with the result that almost all those stranded on the west coast of the British Isles have their sails set to the left. When they strand and so die their horny skeletons complete with sail are blown up on the beaches. Common off the south-west coasts of Britain, it is also found off the Hebrides, occasionally off Faroe and very rarely to the south of Iceland.

Another important and almost wholly planktonic phylum is the Ctenophora, which in older classifications was often placed in the Coelenterata. A number of species are known but only two are of sufficient abundance to merit description here.

The first is the sea gooseberry, *Pleurobrachia pileus* (Plate XVI), which although quite widespread in its occurrence is especially abundant in coastal waters, though strangely enough it is absent from the Icelandic shelf. Its name is appropriate because it does look just like a transparent gooseberry and the jelly is stiff enough for it to keep its shape when stranded on the beach. These gooseberries swim by the beating, to and fro, of rows of cilia—whip-like hairs—arranged in eight series of combs (Fig. 17; 6) and hence the name comb-jelly. They seem perfectly at ease any way up. They have a pair of retractile tentacles which they can tuck away in pockets (the name *Pleurobrachia* means 'folded arms') or extend to some ten times the body length when capturing food. Unlike the true jellyfish they have no stinging cells but capture their prey by entanglement in these rather sticky

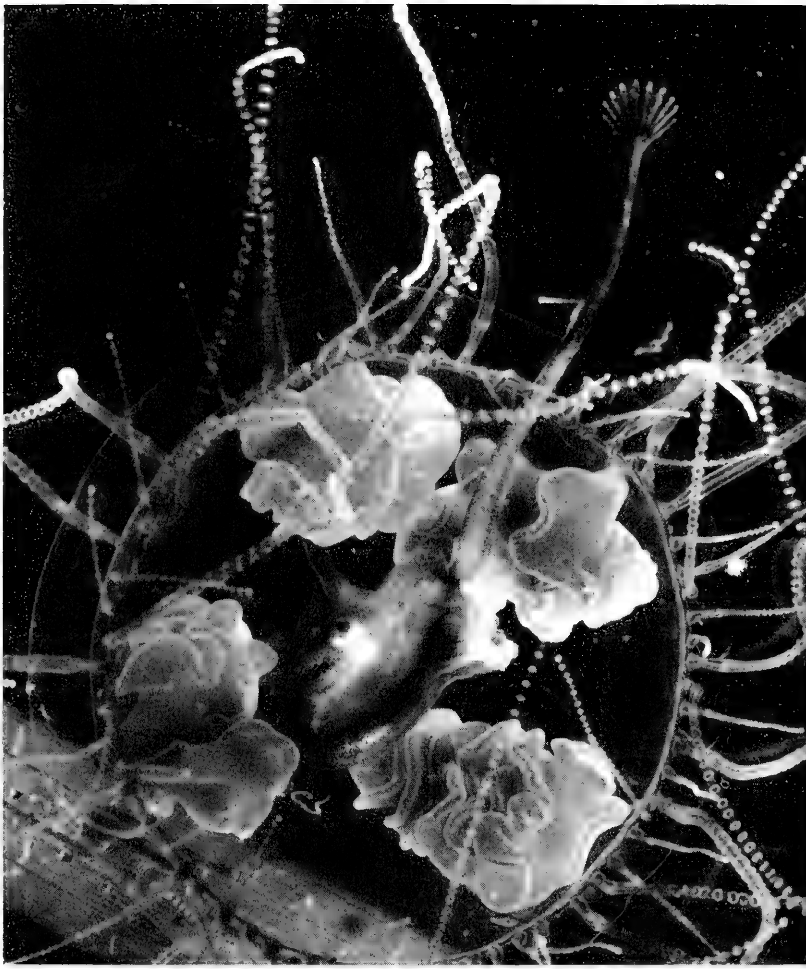


Plate XIV.
The small jellyfish *Gonionemus* feeding on a pipe fish.
Photograph by Lennart Nilsson (from *Life in the Sea*)

tentacles. They feed on other creatures in the plankton, especially young fish.

The other common ctenophore is *Beroë cucumis* (Fig. 17; 7) which is larger and flabbier than the gooseberry, and thimble shaped; as it may be 3 or 4 inches long it is big enough to be seen from the deck of a ship if the sea surface is quite calm. It is oceanic and rarely stranded in a recognizable form, belonging essentially to the arctic and boreal regions where it is abundant from Greenland to Spitzbergen, extending southwards to the North Sea, west Baltic and to the west of the British Isles. It is often rather pink in colour, the pinkness increasing with colder conditions. Unlike the gooseberry, *Beroë* has no retractile tentacles but the mouth is large—the

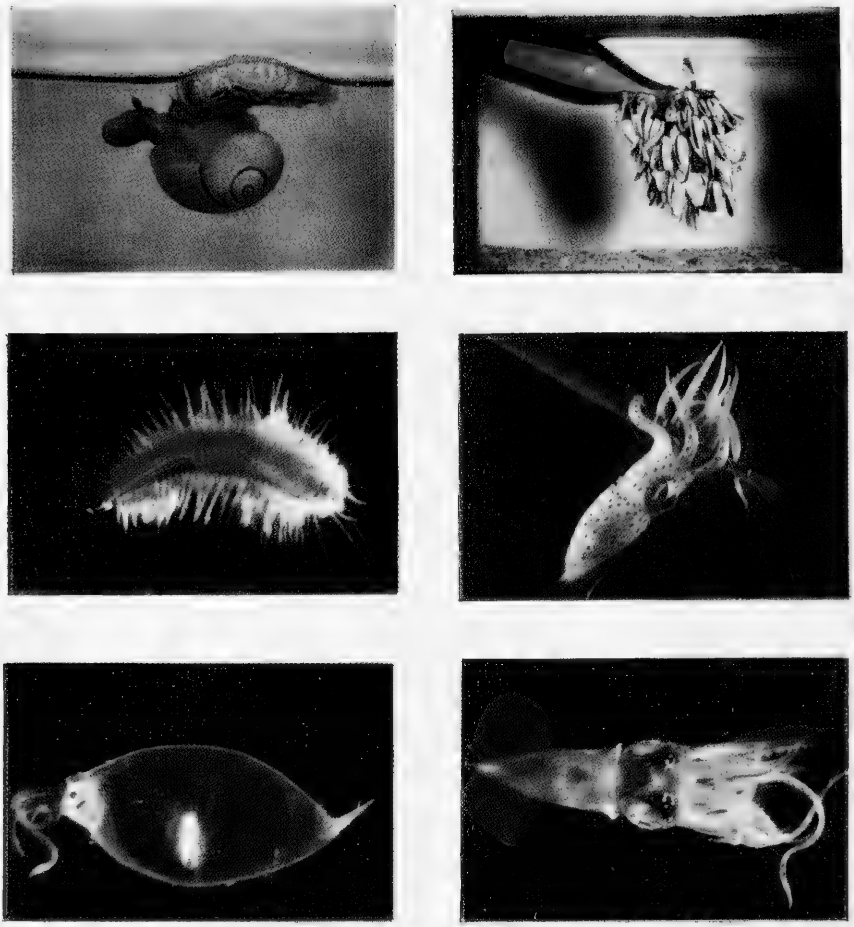


PLATE XV.

(*Top left*) The pelagic mollusc *Ianthina* with its gas bubble float.

Photograph by D. P. Wilson

(*Top right*) Goose barnacles, *Lepas*, attached to a floating bottle.

Photograph by D. P. Wilson

(*Centre left*) An oceanic polychaete worm *Lagisca*.

Photograph by Peter David

Three photographs of deep-sea squids by Peter David

(*Centre right*) *Calliteuthis*.
(*Bottom left*) *Lirocranchia*.
(*Bottom right*) *Pyroteuthis?*

opening of the thimble—and it not only feeds mostly on other ctenophores but is a voracious cannibal.

Worms

A wide range of really very different kinds of animals are loosely grouped together as 'worms'. Although the term is convenient enough for a popular book like this, they are so unrelated that such a grouping is a zoological miscellany. Only a few of them are truly planktonic although there are vast numbers of marine worms, free living, tube dwelling, internal and external parasites. The true worms in the plankton are mostly warm-water oceanic species that occasionally get drifted into the more temperate areas as exotics, for example *Lagisca hubrechti* (Plate XV). Only one need be further mentioned here as it is frequently found in the mixed oceanic and coastal waters of the North Atlantic. This is *Tomopteris helgolandica*, illustrated in Fig. 17; 9. It has a series of bi-lobed paddles on each side with which it can swim energetically but nevertheless it is difficult to see in life as it is so transparent.

The arrow-worms or glass-worms (Fig. 18; 5) need a more detailed description. They form the phylum 'Chaetognatha' and apart from one species that lives amongst the grains of sand and broken shell on the bottom they are all planktonic. They are extremely transparent in life, swimming with a shimmering movement or by quick darts and they are very voracious carnivores. Each is provided with a series of powerful hooks, and one or more (usually two) double sets of small teeth, and a distendible pharynx through which it can push creatures almost as big as itself.

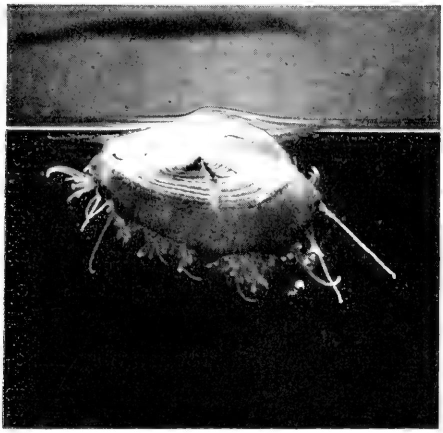
Over forty species are known and of these there are about a dozen in the North Atlantic but only two are common in inshore waters, *Sagitta setosa*, and *Sagitta elegans* (Plate XXXVI). *Sagitta setosa* is found in the southern North Sea, English Channel, Clyde and Irish Sea, and in other temperate places of relatively low salinity such as the Black Sea, parts of the Adriatic, estuaries like the Gironde; there is a record also from near Labrador. It is not found in the very low salinities of the Baltic nor in the arctic or boreal regions, nor in the tropics. The other common species, *Sagitta elegans*, is found in the rather higher salinities where oceanic and coastal waters mix such as the northern North Sea, western English Channel, Irish Sea, and around Faroe, Iceland and near the North American coast. The other ten species of the North Atlantic are all oceanic, some warm- and some cold-water inhabitants, some belonging to the surface layers and others to the deep or very deep waters. Thus each has a habitat of its own but can be carried into other environments by the currents; the value of these arrow-worms and other plankton animals as indicators of water movements will be dealt with in Chapter 11.

Molluscs

Familiar to everyone are the mussels, cockles and winkles of the sea shores. These and many more marine molluscs live on or in the sea floor or attached to rocks, and quite a large number of them have young planktonic larvae which will be mentioned in Chapter 6. However, there are some that are truly planktonic, even as adults, and thus belong to this chapter. The most abundant, and the most important in the food chains of the sea, is a small sea-snail now called *Spiratella retroversa* but which has usually been called *Limacina retroversa.*

This changing of scientific names deserves a paragraph of explanation. The use of the binomial system—a generic name and a specific name—was first started by Linnaeus and is the basis of all biological nomenclature. It is designed to prevent the misunderstanding that can arise with the use of popular names that so often mean different things in different localities and dialects even in the same language. Any system that is to be internationally rigid must be governed by equally rigid rules and one of these is that the earliest name given in a proper description is the one to be used unless this name has previously been used for something else. In this example the name 'les Limacines' was given to it by Cuvier in 1817 as a popular term, and Blainville also in 1817 gave it the name *Spiratella* in a proper description. However, in 1819 Lamarck *properly* described it under the name *Limacina* as distinct from the popular term 'les Limacines' as he presumably was unaware of Blainville's work. Most biologists followed Lamarck as his work was very widely known, but those in authority rightly decided that under the rules Blainville's name must stand.

Spiratella (Plate XVI and Fig. 18; 7) is only about 1/10 inch and grey to black in colour. It often occurs in dense shoals where oceanic and coastal waters mix and herring will then feed on it to the exclusion of their normal food. As *Spiratella* gives out a dark sepia-coloured stain the herring insides become stained; they have what it known to the herring trade as 'black gut'. This is accompanied by a rather foetid smell and the fish do not preserve well. Plankton containing a lot of *Spiratella* will also become stained in the jar and the inside label will turn a dark plum colour. In life they swim with a dancing movement using two extensions of their bodies as wings or paddles, and together with the other planktonic molluscs in the order Pteropoda, they have thus earned the name of sea butterflies. It is interesting to note that while most of the winkles and snails have shells that are right-hand spirals *Spiratella* is left handed.



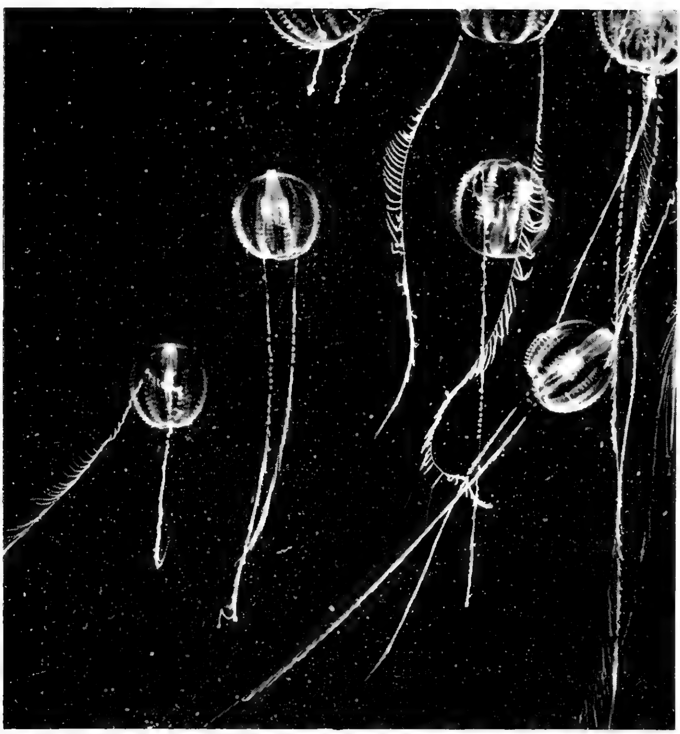


PLATE XVI.

(*Top left*) By-the-wind sailor, *Velella*.

Photograph by D. P. Wilson

(*Top right*) The sea butterfly, *Spiratella*.

Photograph by D. P. Wilson

(*Bottom*) Comb-jellies, *Pleurobrachia pileus*.

Photograph by Lennart Nilsson (from *Life in the Sea*)

There are a number of more oceanic species of pteropods which range from arctic to tropical seas, and some of these, like the arrow-worms are carried by currents to more inshore or mixed waters. They do not all have twisted shells (Fig. 18; 6) and some have no shell at all. typical of the unshelled pteropods is *Clione* (Fig. 18; 9) which, like *Spiratella*, is found quite commonly in inshore areas if there is a good admixture of oceanic water. Only small ones, about $\frac{1}{8}$ to $\frac{1}{4}$ inch long are usually found in the North Sea, but farther north and in the open ocean they are much bigger and reach almost an inch off Iceland and in Greenland waters. Pteropods feed by filtering the phytoplankton and other small particles out of the water.

Another planktonic group of molluscs is the Heteropoda, very transparent rather slug-shaped animals which swim upside down with the mere remnant of a shell hanging below them and acting as a keel. They are all warm-water creatures but, carried by the currents, do occasionally reach the temperate zones such as west of the British Isles. They are carnivorous, feeding on fish and other quite rapidly moving creatures.

Although it is not always appreciated, the squids and octopuses—the Cephalopoda—are also molluscs and they are most interesting animals. Some of course are bottom dwellers, others like the big squids are powerful swimmers and not therefore planktonic, but there are a host of small ones that are. They belong to both types—the octopuses which have eight arms and the squids which have ten, eight short and two long (Fig. 18; 10 and 11). Both kinds swim moderately slowly forwards by the use of their fin-like extensions of skin or can shoot rapidly backwards by jet propulsion. To do this they fill the cavity between the body organs and the outer skin or mantle with water, and then powerfully eject it through a nozzle at the base of the neck. As this nozzle is movable they can control the direction of movement. Like the larger and better known cephalopods they produce ink—sepia—and when escaping from an enemy they pour a cloud of it into the water, like a smoke screen, and then dart away in what must to the predator be an unpredictable and unseen direction. This can be further complicated by a simultaneous change of colour in the animal, while the cloud left behind is often shaped like the animal. There is such a size range that it is impossible to make a dividing line between those that are planktonic and those that can swim well enough to be called 'nekton'. Certainly many of those big enough normally to be considered nekton are occasionally drifted in shoals and stranded on the beaches, and included in this list could be the common cuttlefish *Sepia officinalis* and the common squid *Loligo forbesii*. The quick dart of some oceanic species is sufficient to make them shoot into the air and glide along like flying fish, often for 50 feet or more and up to 12 or even 20 feet above the sea surface. Carnivores themselves, they are preyed upon by many other creatures from the big toothed whales down. Squid indeed is one of the best foods for animals kept in marine aquaria and is good crab bait. Few indeed are the animals in the sea that eat animal tissue, alive or dead, that do not take it, or even prefer it to their normal food. Squid, and octopus too, are of course a popular food in the Mediterranean countries and boxes of squid are now landed at the British fish markets for overland transport across the continent, thus bringing in a cash return for something that was previously dumped. One of these days the British housewife and her family will realize its excellent taste and its value as food and prices will go up as the demand increases.

One of the interesting features of these cephalopods, big or small, is their ability to change colour very rapidly indeed. This they do by the expansion and contraction of pigment spots. When fully contracted the spots are minute and far between so that the animal is almost pure white, or the smaller ones very nearly transparent. As the spots expand their colour shows and the animal becomes at first speckled and then completely coloured, usually a brownish-red. Not all the pigment spots need expand at the same time, and as the expansion need take only seconds, waves of colour come and go in different directions, making it very difficult for a predator to be precisely sure where his prey is. Many are brightly luminescent at night with rows of light-producing photophores arranged in characteristic patterns. Some are illustrated in colour in Plate XV.

Squid and octopus are particularly fond of crab and other crustacean food, and to aid the capture of these active and well-armoured animals the salivary glands of cephalopods produce a crab-paralysing agent called cephalotoxin.

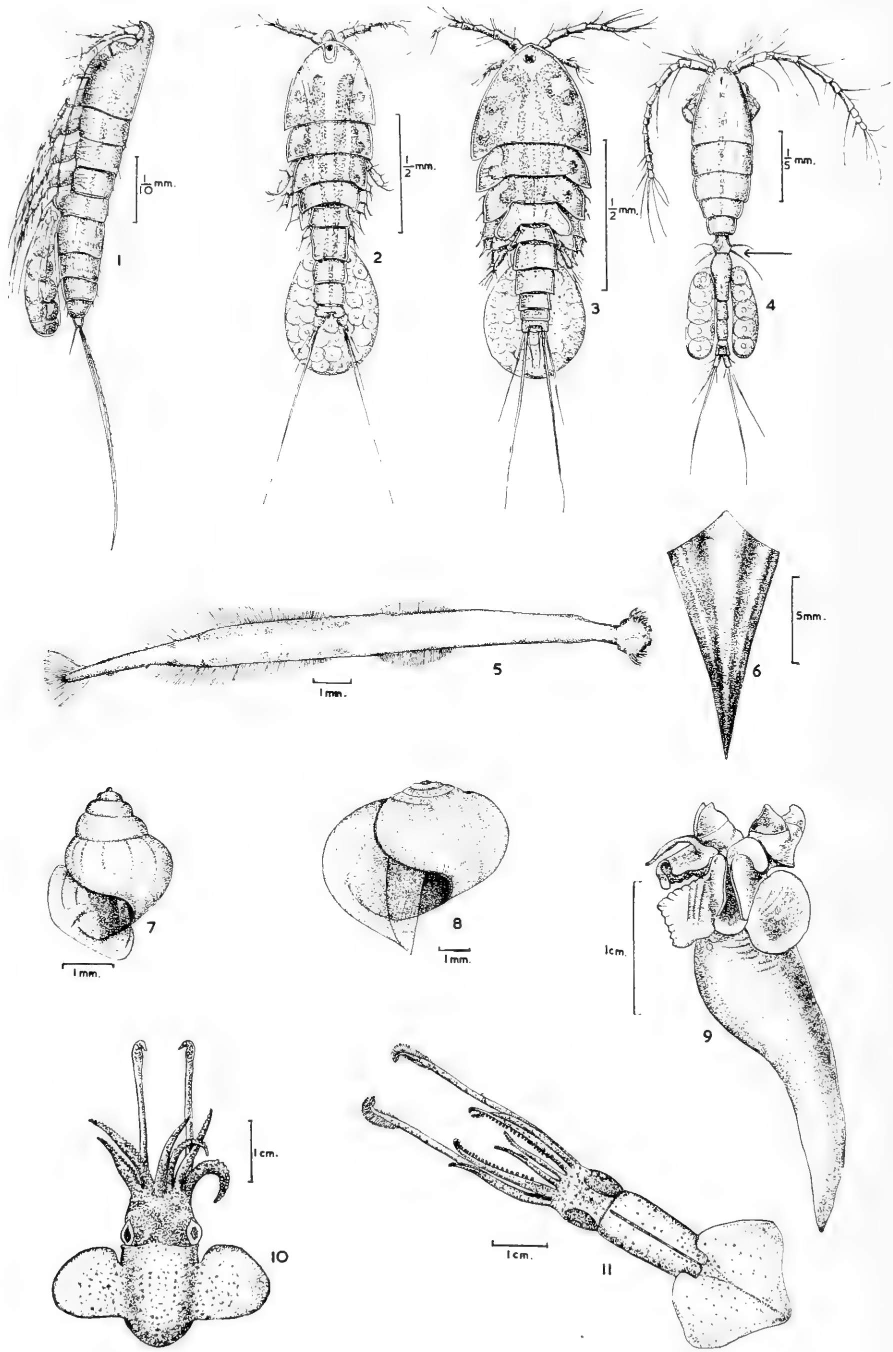


Fig. 18. Various kinds of zooplankton.

1, *Microsetella norvegica;* 2, *Tigriopus fulvus;* 3, *Idya furcata;* 4, *Oithona similis;* 5, *Sagitta elegans;* 6, Shell of *Clio pyramidata;* 7, Shell of *Spiratella* (= *Limacina*) *retroversa;* 8, Shell of *Spiratella helicina;* 9, *Clione limacina;* 10, *Sepiola;* 11, *Brachioteuthis.*

[The arrow in 4 indicates the joint between the cephalosome and abdomen, see text p. 65.]

CHAPTER 5

The animals—the zooplankton II

CONTINUING THE brief description of some of the commonest and most interesting species of plankton animals we come to perhaps the most important phylum of all—the Arthropoda, creatures with jointed legs, and the most important marine sub-phylum, the Crustacea. Included in the Crustacea are the crabs, lobsters and shrimps which crawl about the sea floor, the attached barnacles, freshwater shrimps and creatures like the garden woodlouse. There are, also, hosts of truly planktonic crustaceans, in fresh water as well as in the sea, and they form one of the vital links between the plants of the phytoplankton and the fish, or those creatures that so often form the food of the fish.

Belonging to one of the simplest types of the Crustacea, the sub-order Cladocera, are *Podon* and *Evadne* which are frequently abundant and are easily recognized from Fig. 19; 1, 2, and Plate XVII. Small crustaceans with a bivalve shell reminiscent of molluscs, in the class Ostracoda are very common living in or near the bottom in both fresh and salt water, but some are planktonic, particularly in oceanic waters (Fig. 19; 3).

The most prolific and most important class is, however, the Copepoda—oar-footed—and most of these are planktonic. Some are parasitic and are quite unlike the free-living forms and are not the concern of this book, others live closely attached to the surface of fronds of weed but they are usually easily enough identified as copepods. The free-living ones have a well-defined head-plus-body called a 'cephalosome' with antennae, mouth parts and swimming feet, and a tail region or abdomen called a 'urosome' which has no appendages except a bifurcated tip provided with hairs (setae). Both cephalosome and urosome are jointed, but one special joint is used in classification. In most of the truly planktonic marine species it is between the cephalosome and the abdomen so that there are no appendages behind this joint (Fig. 20); in most of the rock-pool and freshwater species it is in front of the last segment of the cephalosome so that the 'tail' has an extra joint which carries a pair of reduced swimming feet (Fig. 18; 1—4). Both kinds are found in the marine plankton, in rock pools and in fresh water. Planktonic copepods vary in size from very tiny, about $\frac{1}{2}$ millimetre or $\frac{1}{50}$ inch, to quite large, about 12 millimetres or $\frac{1}{2}$ inch, but the largest you are likely to find without an ocean-going vessel equipped to sample deep water will be about the size of a grain of rice. Some deep-water forms are quite big, for example, *Pareuchaeta* *barbata* is 8 millimetres long, and *Megacalanus princeps* is 12 millimetres and *Bathycalanus rigidus* shown in Plate XVIII is 11 millimetres.

The most important and the most studied of the truly planktonic marine copepods is called *Calanus* (Fig. 20; 6: Plate XVII) and a whole book has been written about it alone.* This species is one of the dominant food organisms of plankton-feeding fish like herring. Although most prolific in northern waters it is common, even abundant, in the North Sea, English Channel, Mediterranean, Black Sea, Red Sea, Indian and Pacific Oceans, Malaya, Australia etc., and is thus quite cosmopolitan. It feeds directly on the phytoplankton as do many other species living in the upper water layers, but some other copepods, for example, *Anomalocera* (Plate XVIII: Fig. 20; 10–11) and *Candacia* (Fig. 20; 8), are carnivorous. The deep-water forms, living below the level of plant growth, are either carnivorous or feed on particles of detritus which they filter from the water.

Most copepods have 'eyes' which are sensitive to light, but they cannot see in the accepted detailed sense, although some of the more developed eyes like those of the male *Anomalocera* might be able to detect movement but not shape. The planktonic species are usually very transparent, some like *Anomalocera* are very blue; some like *Calanus* are reddish due to a reddish oil in the body, and several of the deep sea species are truly red (e.g. *Bathycalanus rigidus*, Plate XVIII). *Anomalocera* deserves special mention because it is a real surface form, dancing about at the actual surface, jumping out and in, and causing a shimmer like rain on very calm water. It is more abundant in oceanic water than inshore but is often brought into the North Sea and Norwegian coastal waters where it is called 'blue bait'. One that the keen naturalist may find most convenient to obtain is *Eurytemora hirundoides* (Fig. 20; 5) because it inhabits estuaries; here it feeds on the protozoa which in turn have fed on the bacteria (p. 48). There are many hundreds of species of copepods and only a small selection are illustrated here. They also probably form the largest proportion, by volume, of most plankton collections and their total numbers in the sea must indeed reach astronomical figures. They are excellent food value being rich in proteins and oils and are the natural food of almost all the small fish (including the young stages of the big fish). No wonder they are so important in the economy of the sea. Rock-pool copepods like those in Fig. 18; 2 and 3, are very easy to catch alive (p. 14) and most delightful to watch. One of them *Tigriopus* (Plate XVII) is about 1/20 inch, bright orange and lives in those pools near the high-water mark where the green filamentous weed *Enteromorpha* lives and decays. It can reach fantastic

* *The Biology of a Marine Copepod*, by S. M. Marshall and A. P. Orr, Oliver & Boyd, 1955, 21s.

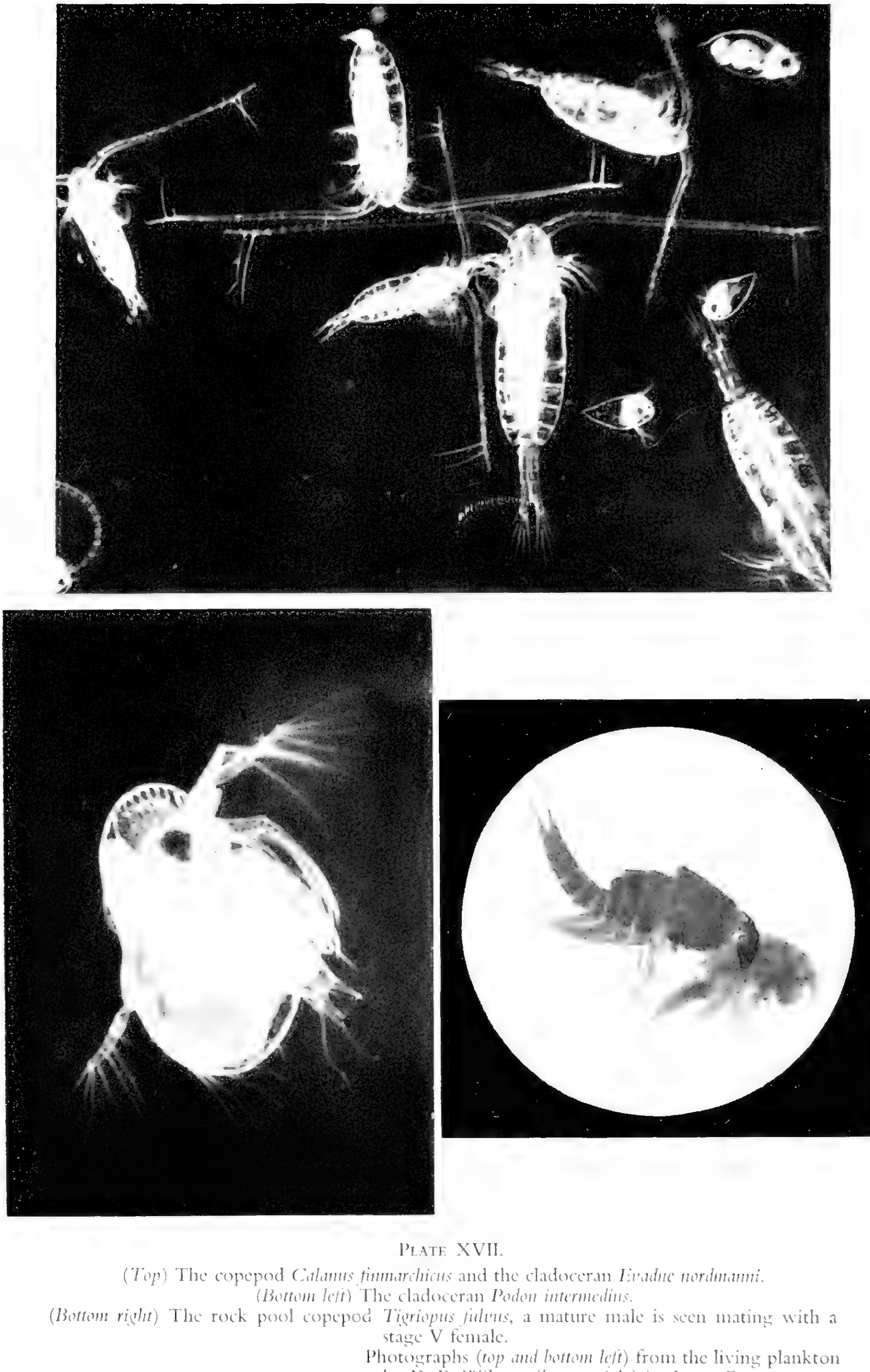


PLATE XVII.

(*Top*) The copepod *Calanus finmarchicus* and the cladoceran *Evadne nordmanni*.
(*Bottom left*) The cladoceran *Podon intermedius*.
(*Bottom right*) The rock pool copepod *Tigriopus fulvus*, a mature male is seen mating with a stage V female.

Photographs (*top and bottom left*) from the living plankton by D. P. Wilson; (*bottom right*) by James Fraser numbers, 9 to a cubic centimetre or 140 to the cubic inch of water, and because of its position on the shore it can be flooded with rain, dried out to a salt cake, frozen, or warmed to 100°F by the sun. Few living creatures are so resistant, and because of this they are often used for physiological experiments—the guinea-pigs of the sea!

The sexes are separate in copepods and after mating the females produce their eggs. These are sometimes just liberated freely into the water or carried about by the female in egg-sacs. Most of the rock-pool females carry their eggs and in *Tigriopus*, for example, the unripe eggs are dark green but turn orange, just before they are ready to hatch One mating can last for several batches of eggs in this species and, if this is general, it may help to account for the fact that, although mature males of *Calanus* are scarce compared with females, there never seems to be a scarcity of fertilized females. This lack of males is probably due to quicker development and a shorter life and not to a difference between the numbers hatched.

The young larvae that hatch out of the eggs are called nauplii (Fig. 21), and have at this stage three pairs of 'legs'. Though used for swimming at this stage they are the beginnings of what will later be the antennae and mouth-parts. This first nauplius soon casts its skin—a feature of all the Arthropoda—and the second nauplius is slightly bigger. This procedure continues until the fifth or sixth stage according to the kind of copepod, but the number never varies—e.g. always five in *Tigriopus*, always six in *Calanus*, extra appendages being formed stage by stage. The last nauplius then moults into something much more like the parent, and is called a copepodite. Again after successive moults, with the appendages better formed at each stage, the adult is reached as the mature sixth copepodite, and so the story is repeated. The number of generations per year varies according to species and locality. Many rock-pool copepods have several generations in a season, the colder water planktonic forms have usually only one a year. When there is only one, the eggs are laid in the spring when there is phytoplankton present for the young nauplius to feed on; they continue to grow and moult during the season spending the winter as the fifth copepodite and finally maturing in the early spring in time to mate and reproduce.

Whilst it is generally true to say that most parasitic copepods live attached to their hosts there are a few which can be caught in the plankton. These are 'sea lice', external rather than internal parasites of fish, which are either washed off or voluntarily leave their hosts, perhaps to find a new one. The commonest of these is *Caligus* (Fig. 19; 9).

The next class of Crustacea to consider here is the barnacles, the Cirripedia. Barnacles are of two main types the 'acorn' type attached to rocks, which have a planktonic life history and so are due to be dealt with in the next chapter,

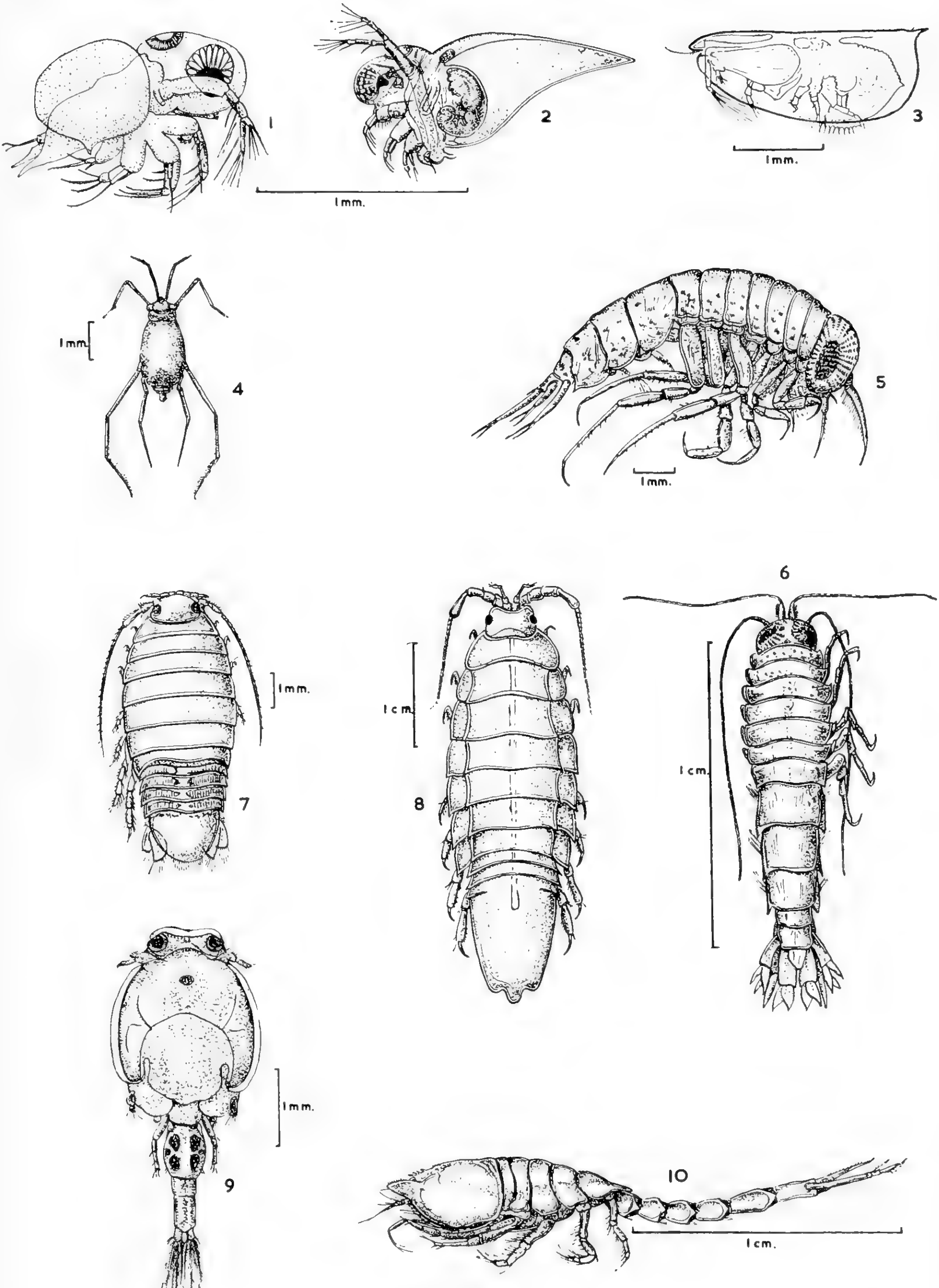


FIG. 19. Various planktonic crustacea etc.

1, *Podon leuckarti* 2, *Evadne nordmanni*. 3, *Conchoecia elegans*. 4, *Halobates micans*. 5, *Themisto abyssorum*. 6, *Hyperia galba* male (the female is much broader). 7, *Eurydice pulchra*. 8, *Idothea balthica*. 9, *Caligus rapax* male. 10, *Diastylis rathkei*.

[1 and 2, cladocerans; 3, ostracod; 4, insect; 5 and 6, amphipods; 7 and 8 isopods; 9, sea louse; a semi-parasitic copepod; 10, cumacean.]

and the stalked barnacles (Plate XV and Fig. 21; 7). These are, of course, attached, but almost always to floating objects, pieces of wood, bottles, ships' bottoms and particularly to pieces of floating weed. They are thus carried about and, except for those attached to ships, are at the mercy of the currents and they can thus be regarded as planktonic. They are mostly warm-water forms but they are often stranded on the seashore still attached to their floating object. One species *Lepas fasicularis* grows a spongelike float of its own.

These stalked barnacles, often called goose barnacles, are associated with a most extraordinary legend, once widely believed though we can now hardly credit it. The legend, judging from designs on Mycenaean pottery, dates back to the nebulous past of some three thousand years ago, and it spread from Troy to Britain and Ireland, and by the Caucasus to India and Japan. Wood, floating at sea becomes infested with barnacles and the rotting tree trunks and timbers from wrecked ships become washed ashore, sometimes to places where geese are feeding. It was thought that the shelled barnacles, with their long 'neck', somewhat goose-shaped shells and feathery feeding appendages turned into young goslings. Embellishments arose and it was sometimes stated that barnacles grew on the living trees near the water's edge and they fell off into the water to grow into geese. This origin of 'barnacle geese' was accepted as authoritative from the eleventh to the end of the sixteenth century. As late as 1597 the English observer John Gerard described in detail how he 'saw' the whole process himself at a place on the Lancashire coast called the 'Pile of Foulders'. Since then belief in the story gradually died but the name of the 'barnacle goose' remains and the barnacle is called *Lepas anatifera*, meaning 'goose barnacle'. According to the legend, the barnacles grow as part of the timber and must thus be of vegetable origin; therefore the geese must also be of vegetable origin. This remarkable piece of logic led to the barnacle goose being considered in all good faith as acceptable lenten fare by Roman Catholics, this in spite of a Papal Bull issued by Pope Innocent III in 1215 forbidding the eating of barnacle geese in Lent. The somewhat rubbery stalks of these barnacles are included in various sea-food recipes particularly in Spain, Portugal and Mediterranean countries.

Next in the list of planktonic crustaceans is the class Malacostraea, the 'top' class, which includes a number of orders containing the larger and more familiar crustaceans. One of the lesser known of these is the Cumacea, which are here only mentioned in passing. They are all small (Fig. 19; 10) and inhabit the sandy or muddy sea floor or live amongst the weeds in rock pools, but sometimes swim sufficiently far off the bottom to be caught by a plankton net near the bottom or in inshore waters.

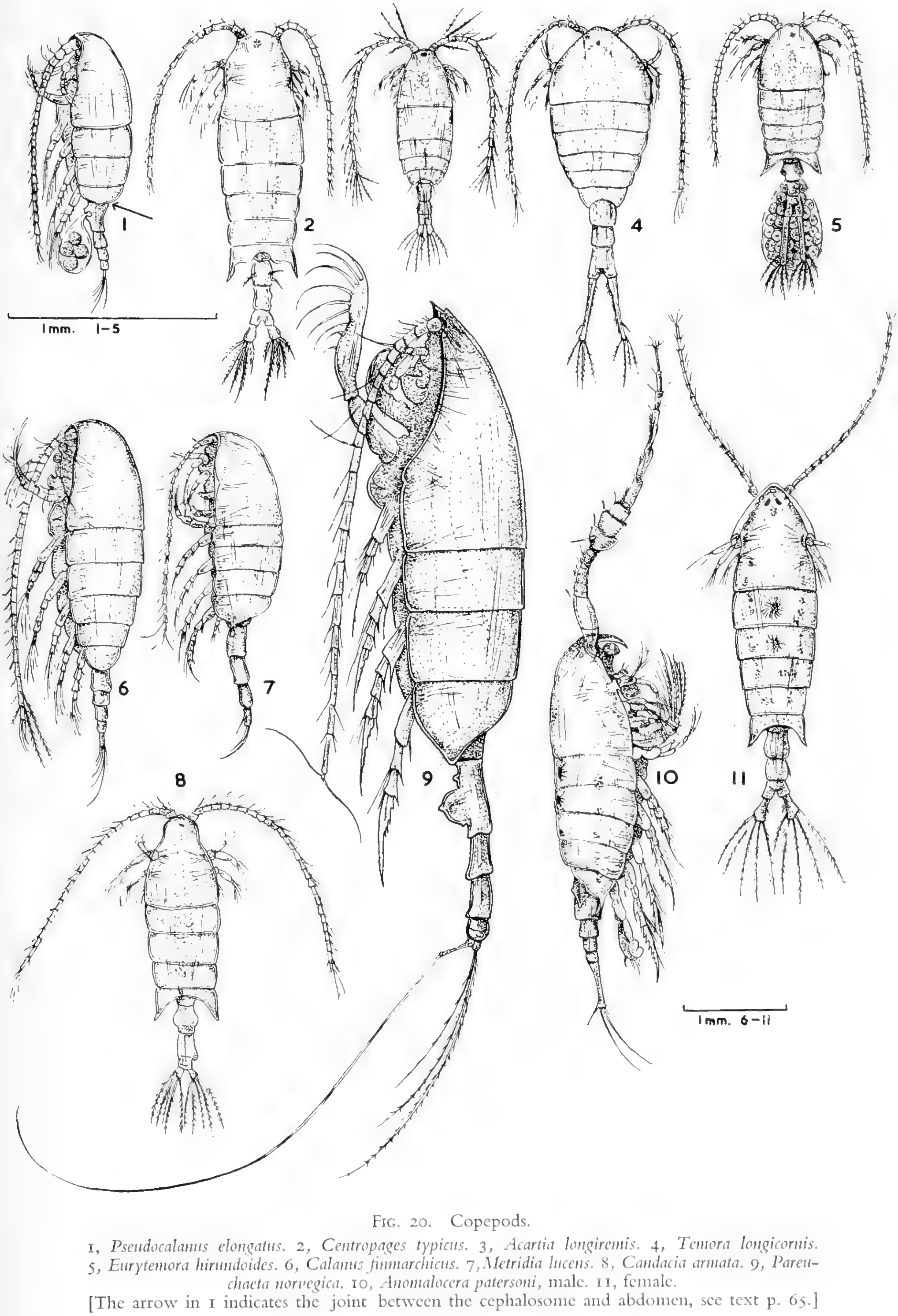


FIG. 20. Copepods.

1, *Pseudocalanus elongatus*. 2, *Centropages typicus*. 3, *Acartia longiremis*. 4, *Temora longicornis*. 5, *Eurytemora hirundoides*. 6, *Calanus finmarchicus*. 7, *Metridia lucens*. 8, *Candacia armata*. 9, *Pareuchaeta norvegica*. 10, *Anomalocera patersoni*, male. 11, female.

[The arrow in 1 indicates the joint between the cephalosome and abdomen, see text p. 65.]

The next order is the Amphipoda, probably more familiarly represented by the freshwater 'shrimps' and the sand hoppers often so abundant amongst rotting seaweed stranded on the seashore. They will be commonly found, too, in the rock pool fauna but are less typical of the plankton of the open sea. There are some grotesque planktonic amphipods from deep water but only a few species are to be found in the surface or inshore waters. Strangely enough, when they do occur they can be very abundant indeed. *Themisto*, for example (Fig. 19; 5), is another truly surface form, and like the copepod *Anomalocera* frequently causes a 'rain' on the surface of calm water by jumping up and down, but is rarely taken in large numbers in sub-surface nets. Its outer surface has the property—surprising for a marine creature—of being unwettable so that if any part of it comes above the water the effect of the surface tension brings the whole of the rest out to float, quite dry. Unless it is pushed or wriggles completely below the surface, out it comes again, a most disconcerting habit when one is trying to look at it through a microscope. Another amphipod, closely allied to *Themisto*, is called *Hyperia* (Fig. 19; 6) and is found most commonly in the plankton close to the larger jellyfish as it is an ectoparasite on them, feeding on the jelly itself.

As in other groups, there are many exotic kinds of deep-water amphipods, some brightly coloured, some very swollen and transparent such as *Mimonectes* (Fig. 22; 3).

The Isopoda are typically represented by the familiar garden wood louse, but there are also freshwater and marine species, including one, *Ligia oceanica*, that runs round the rocks of the seashore at or above high-water mark just as the wood louse does on land. Structurally they rather resemble the amphipods but are usually flattened dorso-ventrally (like a wood louse) instead of from side to side as in the amphipods, and their legs are of almost equal length—hence the name. Some quite big ones, *Idothea* is about $\frac{3}{4}$–1 inch long, live in the rock pools (Fig. 19; 8). Planktonic *Idothea* are almost always associated with floating weeds and can be carried hundreds of miles by the currents, crawling about the fronds, occasionally swimming a little, and several generations can live in their little drifting patch, perhaps only a foot across. *Eurydice* (Fig. 19; 7), is a truly planktonic isopod; there are also some planktonic deep-sea isopods and a whole book could be written about those peculiar isopods which are parasites of other crustaceans.

Further up the crustacean series of orders there are the Mysidacea, the fairy shrimps (Fig. 22; 2) rather shrimp-like in shape, usually extremely transparent except for their eyes which are usually very dark but in some species are bright red, orange or opaque white. They have a short carapace which encloses the thoracic region of the body but is only fixed at the front,

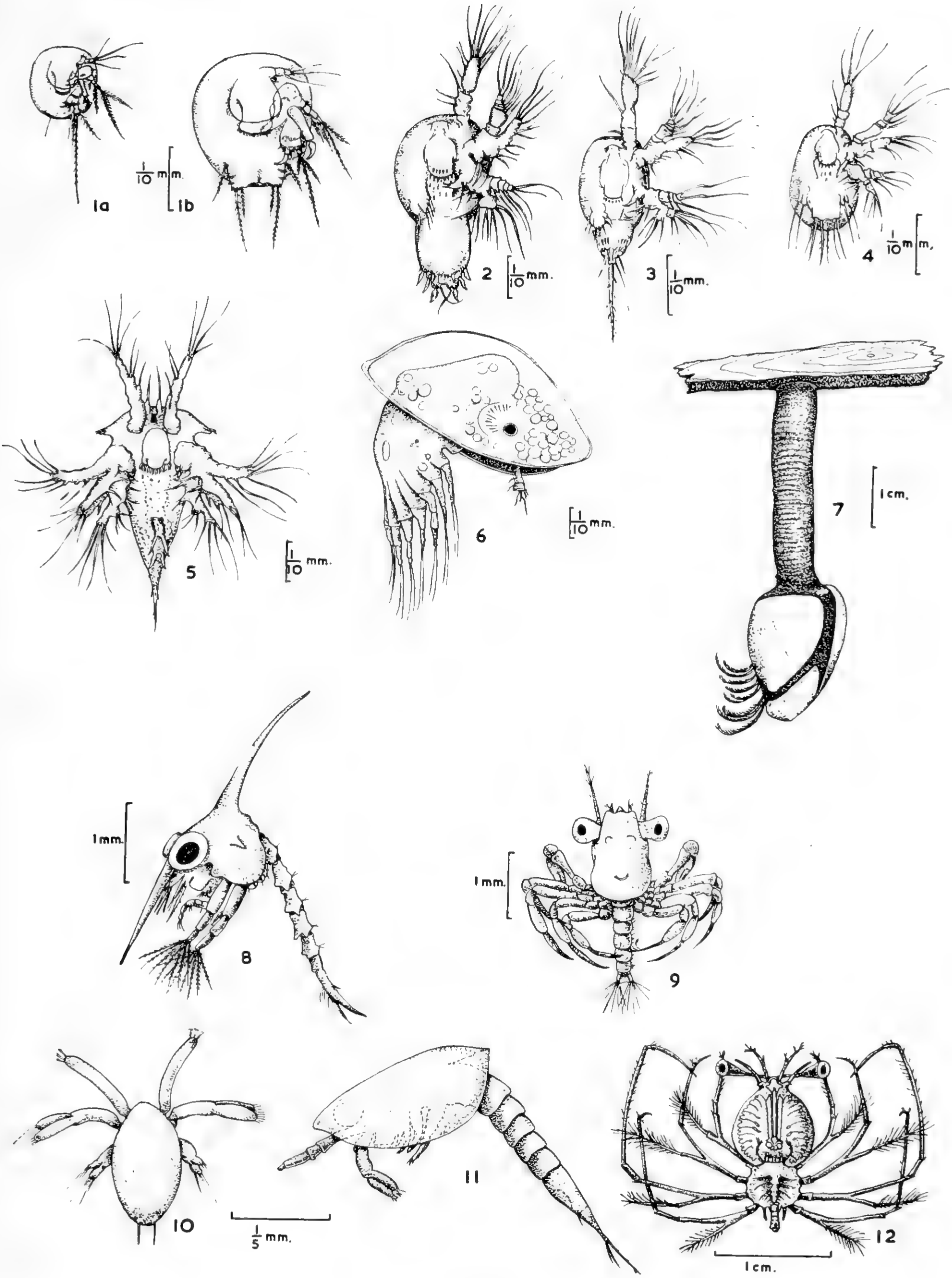


FIG. 21. Crustacean larvae etc.

1*a* and *b*, 1st and 3rd stages of the nauplius of *Tigriopus*. 2, 4th nauplius of *Calanus*. 3, 5th nauplius of *Centropages*. 4, 5th nauplius of *Oithona*. 5, 2nd nauplius of acorn barnacle, *Balanus*. 6, Cypris stage of same. 7, Adult goose barnacle, *Lepas*. 8, 3rd zoea of crab, *Portunus puber*. 9, Megalopa of same. 10, 2nd nauplius of euphausid, *Thysanoessa inermis*. 11, 2nd calyptopis of euphausid, *Thysanoessa longicaudata*. 12, phyllosoma of spiny lobster, *Palinurus*.

fused to, at most, the first three segments. The abdomen has a series of swimmerets and the tip has a distinct fan tail the inner vanes of which usually contain statocysts or balancing organs. In these a small stone-like concretion or otocyst is free to move about in a sensitive spherical container, and the position of this otocyst lets the mysid know which way up it is.

Mysids are very common in inshore waters along the sandy coastlines, and especially in estuaries where they move up and down with the tide thus keeping in water of more or less constant salinity. There are oceanic mysids also, mostly in deep water and some of these are bright red in colour; one species *Gnathophausia* (Fig. 22; 1) reaches about 3 inches in length.

Somewhat similar in shape to the mysids are the *Euphausiacea*, which after the copepods are the next most important crustaceans in the plankton. Euphausids (Fig. 22; 4, 5) differ from mysids in the carapace which is fused to the whole thorax but leaves the gills exposed below it. They have no statocysts in the tail fan and they usually have quite prominent luminescent photophores under the abdomen between the well-grown pairs of swimmerets. Whilst as a rule not so abundant as the mysids in closely inshore waters they are often extremely common offshore, in the northern half of the North Sea and the Clyde estuary for example, as well as in the open ocean. One species, *Euphausia superba*, or krill, is by far the most important food for the plankton-eating whales of the Antarctic, while a similar species, *Meganyctiphanes*, the northern krill, forms the chief food of the arctic and boreal whales as well as of basking sharks and indeed forms an important part of the food of herring. There are several warm water species that are drifted into temperate waters, some that live naturally in temperate waters, for example *Thysanoessa inermis* and *Nyctiphanes couchii*, and some such as *Thysanoessa longicaudata* prefer colder water, and even the northern krill, *Meganyctiphanes*, although common in places like the Clyde estuary in Scotland, is fundamentally a cool water species.

The highest order of the Crustacea is the Decapoda. Decapods are mostly bottom-living species, usually with planktonic larvae which will be considered in the next chapter, but the occasional shrimp or prawn is found in the plankton especially near the coasts. A truly planktonic adult is the ghost shrimp *Pasiphaea*, which sometimes occurs in isolated and local shoals quite near the shore. There are also a number of deep sea planktonic decapods most of which are bright red in life, such as *Acanthephyra*, or other bright colour such as *Eryoneicus* (Plate XVIII).

The other classes of the Arthropoda, represented by the centipedes, insects, spiders and mites, all have a few marine forms but none are planktonic except for one insect called *Halobates*, a warm water species allied

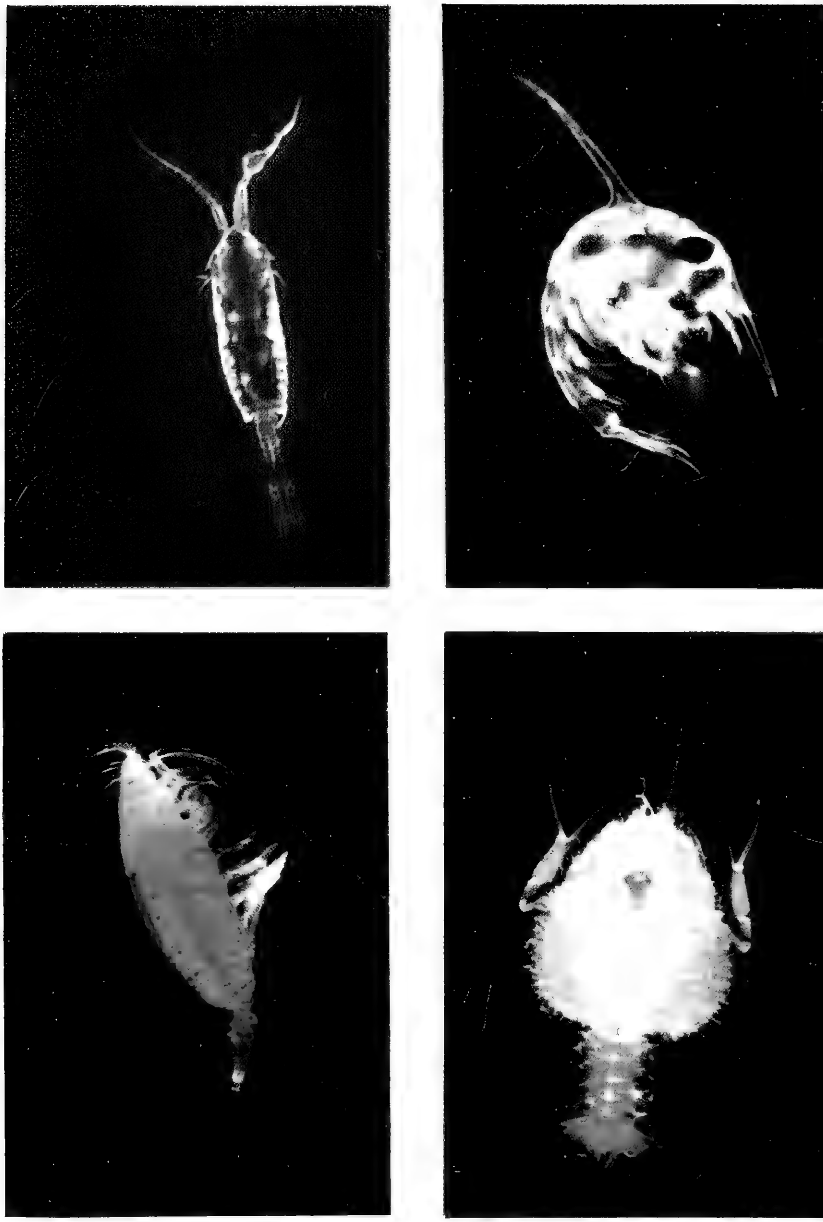


PLATE XVIII. Crustacea.
(*Top left*) The copepod *Anomalocera* (male).
(*Top right*) Zoea larva of crab.
(*Bottom left*) The deep-water copepod *Bathycalanus rigidus*.
(*Bottom right*) The deep-water decapod *Eryoneicus puritani*.

Upper photographs by D. P. Wilson,
lower by Peter David

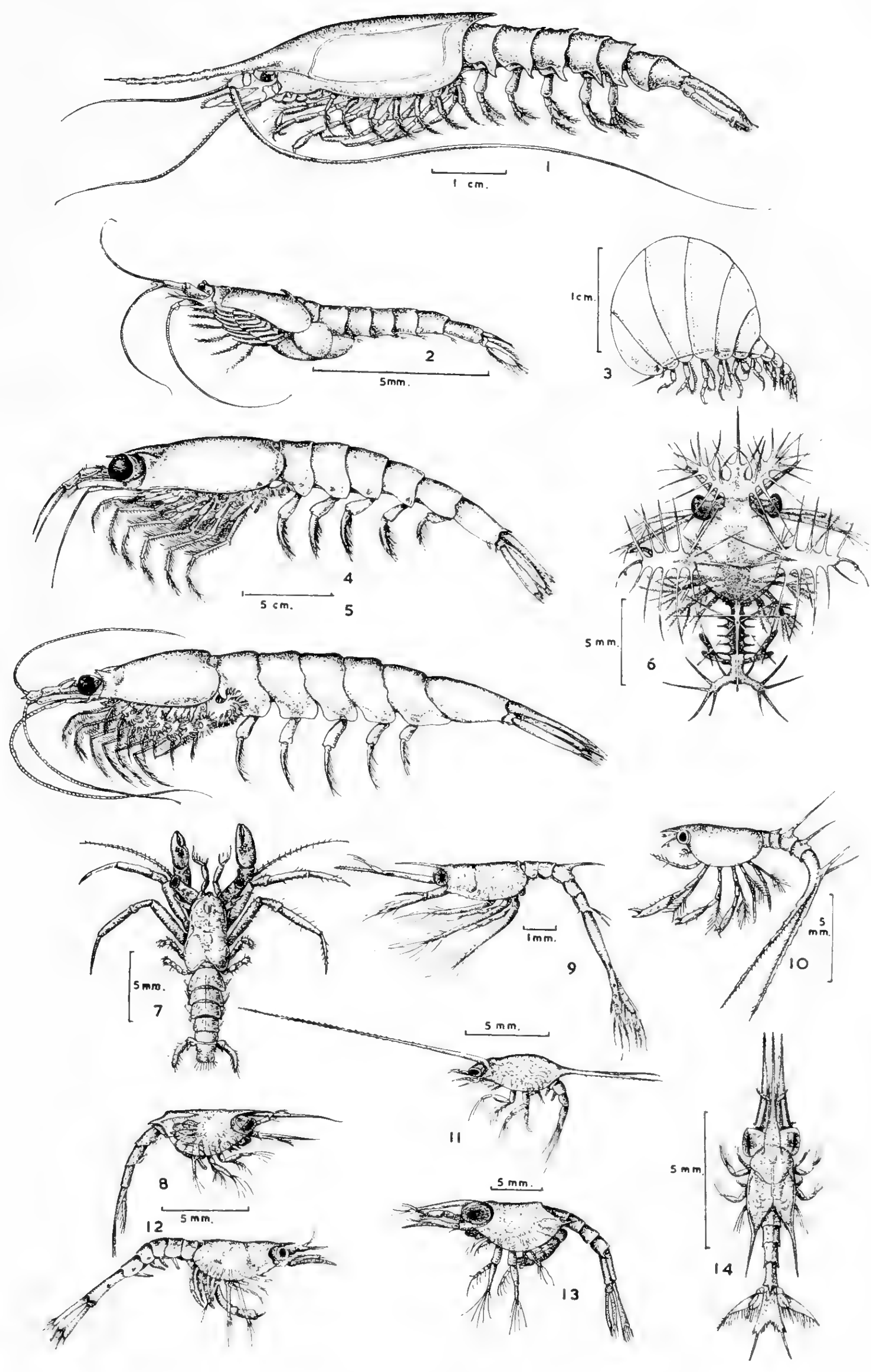


Fig. 22. Crustaceans.

1, *Gnathophausia zoea* (mysid). 2, *Gasterosaccus sanctus* (mysid). 3, *Mimonectes loverni* (Exotic amphipod). 4, *Thysanoessa inermis* (euphausid). 5, *Meganyctiphanes norvegica* (euphausid). 6–14, Larvae of various decapod crustacea. 6, *Sergestes* (an oceanic prawn). 7 and 8, *Eupagurus* (hermit-crab). 9, *Pontophilus*. 10, *Nephrops* (Norway lobster). 11, *Porcellana* (pea-crab). 12, *Crangon* (shrimp). 13, *Galathea*. 14, *Munida* (squat lobsters).

to the pond skaters. Several species are found in the Pacific and Indian Oceans but only one, *H. micans* (Fig. 19; 4), is found in the tropical Atlantic. It is most unlikely to be found in the temperate seas round Europe and is merely mentioned here as of passing interest.

Although the Echinodermata (starfishes and sea urchins etc.) are an entirely marine phylum, only one, *Pelagothuria*, is planktonic though they have planktonic larvae (p. 90).

The next group to consider is the Tunicata; a sub-phylum of the Chordata to which the fish and mammals also belong. They are rather jelly-like creatures that look too simple to be placed so high in order, but which are not so simple as they look. They possess internal gill slits, an endostyle and an epipharygeal groove which morphologically bears a resemblance to the primitive notochord or first rudiments of what grows into the backbone of the vertebrates. Some are attached to rocks—the sea squirts—but others are planktonic and fall into two distinct orders, the Appendiculata (or Larvacea) and the Thaliacea. The Appendiculata (Plate XIX: Fig. 23; 1 and 2) are all very small creatures, with a blob of a body and a muscular tail which is often brightly irridescent. By means of glands called 'oikoplasts' they secrete a relatively enormous balloon of jelly called their 'house' and in which they live. This house is delicately punctured in definite patterns and the animal inside lives by filtering off only the minutest cells of the plankton, the nanoplankton, which pass through the pores of the house and become stuck to a rather sticky band which in turn passes them on to the stomach. The commonest species in the British area are the *Oikopleura dioica*, which has separate individuals of each sex; *Oikopleura labradoriensis*, a more oceanic species in which both sexes are in the same animal (hermaphrodite); and a third smaller and hammer-headed species called *Fritillaria borealis*.

There are three main families in the Thaliacea each having points of special interest. All are truly oceanic and are therefore useful indicators of the ocean currents (Chapter 11) and are rarely found in places like the Irish Sea or southern North Sea. One of these families is the Salpidae. Salps are cylindrical or spindle shaped blobs or barrels of jelly, usually between ½ inch and 2½ inches in length, that could easily be mistaken for jellyfish in a casual glance, but they contain a definite pattern of muscles and a distinct stomach which is usually a prominent dark green ball-shaped structure. There are many species of tropical and sub-tropical salps, but only one cosmopolitan species, *Salpa fusiformis* (Fig. 23; 5 and 6), is found in the north-temperate Atlantic areas, and even as far north as Norway and Iceland. *Ihlea asymmetrica* is also fairly common in the open ocean but is so delicate that it rarely reaches our shores in recognizable shape. The other species are warm water invaders. One of these *Iasis zonaria* (Plate XXXIX)

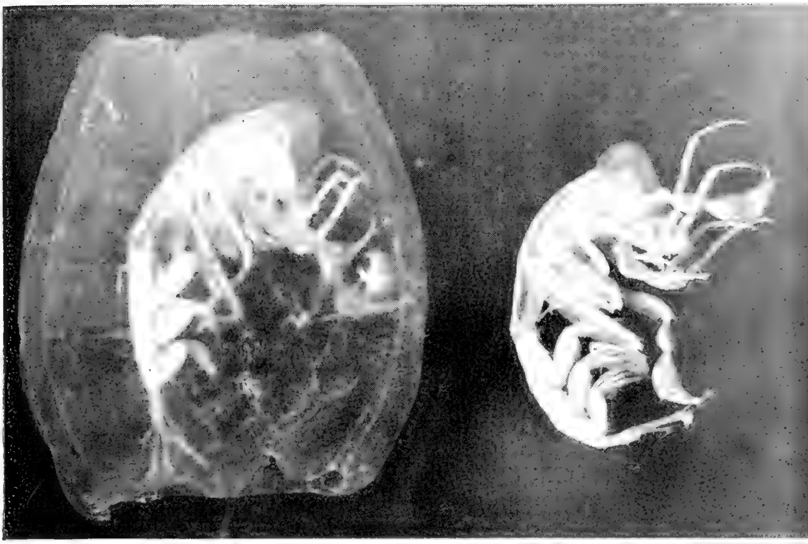


PLATE XIX.

(*Top*) The amphipod *Phronima*, one is inside the gelatinous case made from the salp *Iasis*, and one has been taken out to show it more clearly.

Photograph by James Fraser

(*Bottom*) *Oikopleura*.

Photographed from life by D. P. Wilson

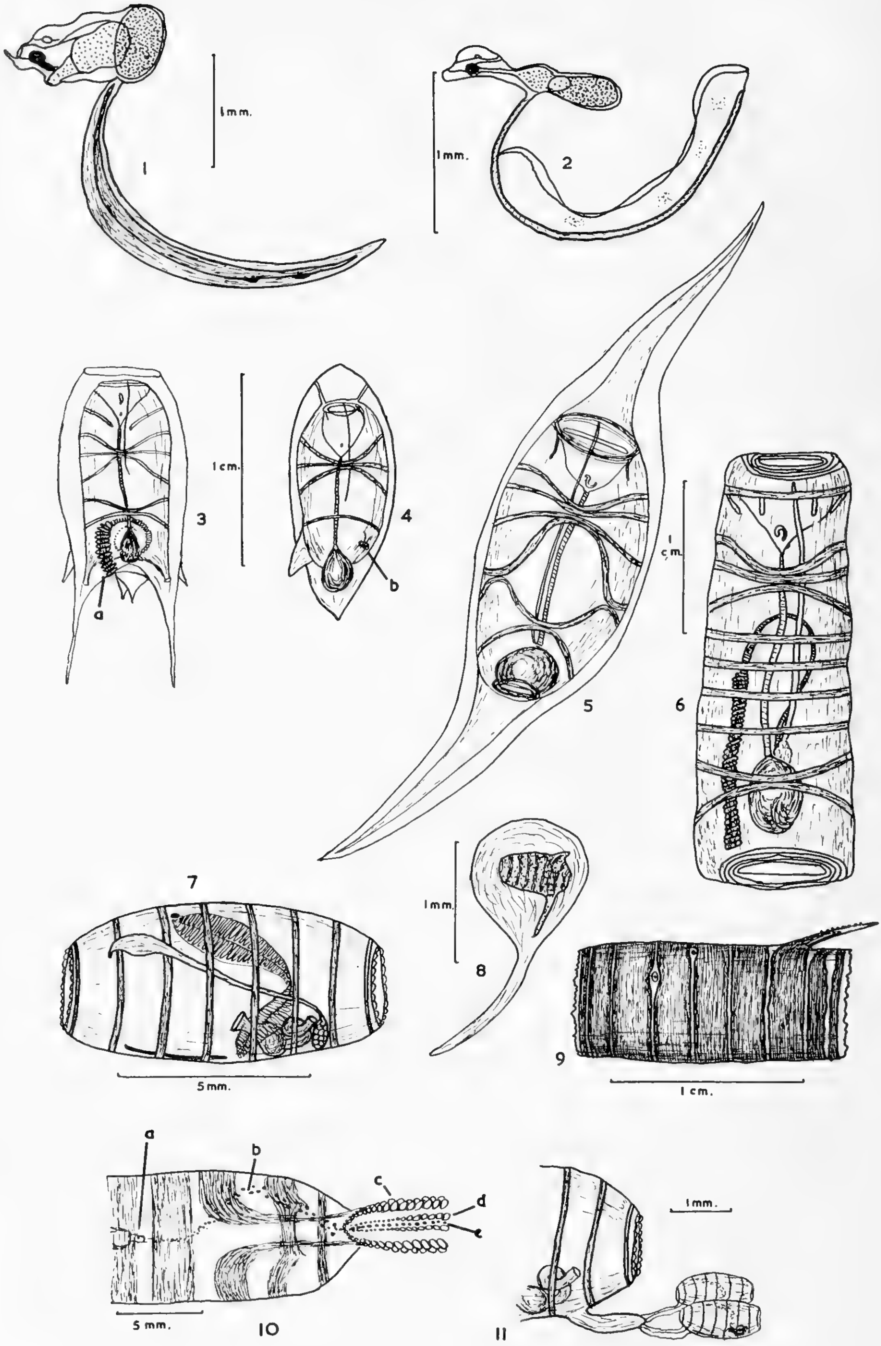


FIG. 23. Planktonic Tunicata.

1–2, Appendiculata. 3–6, Salps. 7–11, Doliolids (*Dolioletta gegenbauri*) showing the life history.

1. *Oikopleura dioica.*
2. *Fritillaria borealis.*
3. *Thalia democratica*; solitary stage showing the budding stolon (*a*) which gives rise to a chain of aggregate stages.

continued opposite

has a very tough jelly which is not easily disintegrated and thus in spite of its warm habitat it too can reach Norway. Its tough jelly is taken advantage of by an amphipod called *Phronima* which eats its way into the salp, leaving nothing but an empty barrel of jelly in which it continues to live as a protective house (Plate XIX). Salps feed only on phytoplankton which they filter off from a stream of water they pass through their insides as they swim by the rhythmic contraction of their muscle bands. They have an interesting life history with an 'alternation of generations'. Single individuals, the solitary generation, produce a stolon or ribbon of buds in a long 'chain' which may give rise to several thousands of chain forms, the aggregate generation. The growth and release of the chains in *Thalia* take only ten days. The aggregate salps stay together in this loosely attached chain until broken off by waves or other disturbances in the water. Each individual is a sexual form and after fertilization one or more 'buds' inside the body grow to form little embryos of the solitary generation, to be released on the death of the mother (Plate XXI). Thus a few of the solitary salps transported by the currents can give rise to great numbers of aggregate salps if the conditions are suitable. The solitary and aggregate individuals look so different that at first they were given separate names but it was soon realized that they were different forms of the same species, and the two names were then hyphenated. This clumsy terminology was later dropped but some of the older books still read today use names like *Salpa runcinata-fusiformis* and *Salpa mucronata-democratica*. This latter species, now called *Thalia democratica* (Fig. 23; 3 and 4) is probably the most abundant salp in the world, but only now and then are conditions suitable for it to reach the British Isles. It occurred in numbers in Plymouth Sound in 1893 and off the Hebrides in 1886, 1904 and 1958 but has not yet been found farther north. Occasionally a specimen of the larger tropical form is found

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4. *Thalia democratica*; aggregate stage with a single embryo (*b*) which will eventually become a free solitary stage.
5. *Salpa fusiformis*; aggregate stage.
6. *Salpa fusiformis*; solitary stage, with stolon.
7. *Dolioletta gegenbauri*; gonozoid, complete with sexual organs. The eggs from this stage hatch into 'tadpoles' (cf. Plate XX).
8. A later stage of the 'tadpole' showing the remains of the outer capsule and the oozoid developing inside.
9. The late oozoid or 'old nurse' now devoid of almost all its internal organs, but with broad muscle bands and balancing organ (statocyst), a nerve centre and the remains of the dorsal process.
10. A view from above of the oozoid at its functional stage with a prominent dorsal process. (*a*) the buds developing on the stolon (*b*) the buds migrating to the dorsal process, (*c*) double rows of lateral zooids, the trophozoids which serve only to catch food for the whole, (*d*) median rows of phorozoids, and (*e*) the youngest migrating buds which will become new gonozoids.
11. A later stage of a phorozoid, now broken free from the dorsal process of the oozoid and acting as a bearer for two developing gonozoids. These will eventually become the free living sexual forms figured in 7.

and one, *Thetys*, about 6 inches long was caught in a herring net in the northern North Sea near Wick in 1929.

The second family is the Doliolidae. Doliolids are usually smaller, and more delicate than salps and rarely reach an inch in length. They are barrel-shaped and their eight or nine muscle bands encircle the body like the hoops of the barrel. These also feed only on phytoplankton. Their life history is more complicated than in the salps (Fig. 23; 7–11). Starting with what corresponds to the aggregate individual in the salps is the sexual doliolid called a gonozoid which has eight muscle bands. The fertilized eggs do not grow in the body of the mother as do the salps but are shed into the water to grow into small 'tadpoles' (p. 91), which become oozoids with nine muscle bands. These reproduce asexually by the development of buds which then migrate along the body of the oozoid to congregate on a specially grown dorsal 'tail'. These buds are of three kinds, the trophozoids which are specialized only to catch food and remain attached to the oozoid; phorozoids which are free swimming but sexless, and the gonozoids which in their earliest stages are carried about attached to the phorozoids. The disintegrating remains of the oozoid often persists as an 'old nurse' with nothing left but its muscular structure and so it is unable to feed. Only one species is found in the northern part of the north-east Atlantic, *Dolioletta gegenbauri* (= *D. tritonis*) (Plate XXXIX) but there are several in or near the Mediterranean which can be drifted towards the area south-west of Ireland and into the English Channel, one is *Doliolum nationalis* (Plate XX).

The third family of the Thalicaea is the Pyrosomidae. Pyrosomes are colonial forms in which many hundreds of very small individuals remain attached together to form thimble-shaped colonies, the ones mostly found are 3 or 4 inches in length but really big ones can reach 2 feet. They are only found in warm water and very rarely reach the British Isles. As their name implies pyrosomes (fire bodies) are brilliantly phosphorescent, looking like an old-fashioned long incandescent gas mantle.

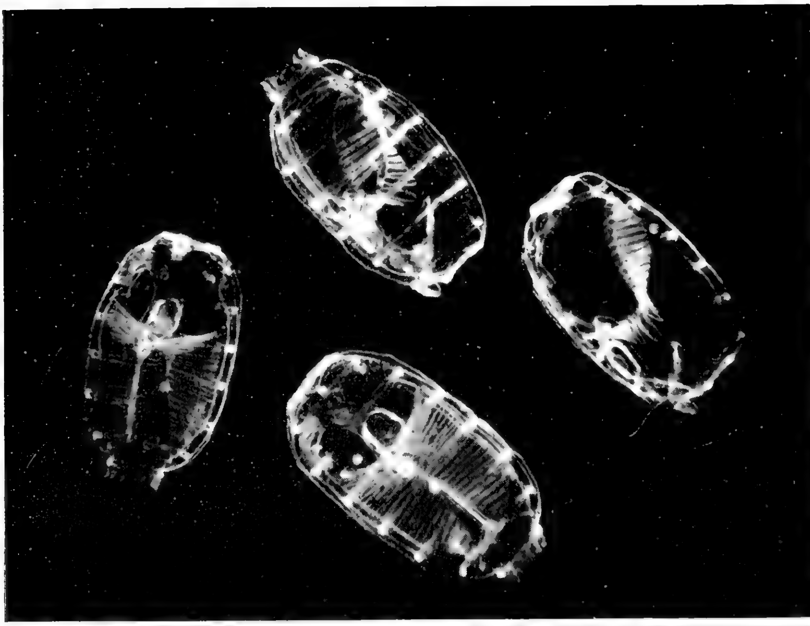


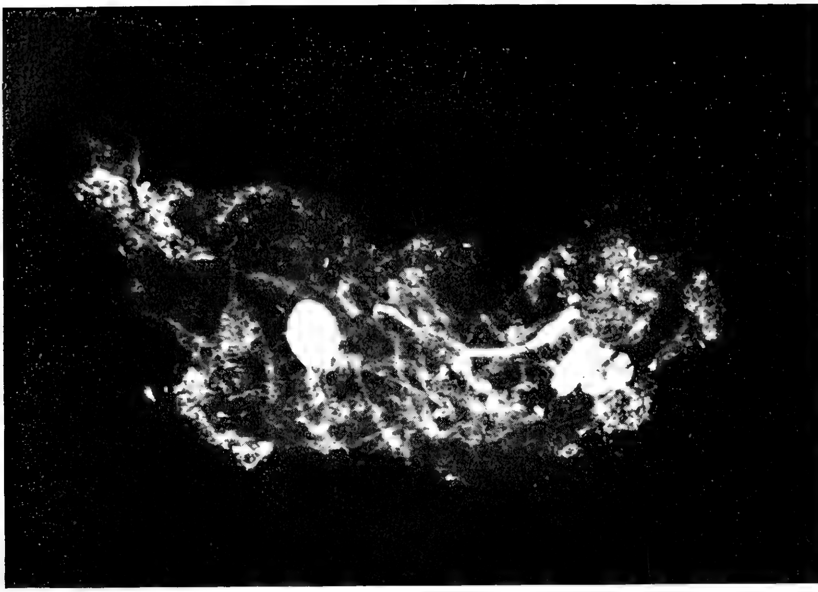
PLATE XX.

(*Top*) *Doliolum nationalis.*

Photographed from life by D. P. Wilson

(*Lower*) The 'tadpole' of the ascidian *Clavelina lepadiformis.*

Photograph by Lennart Nilsson (from *Life in the Sea*)



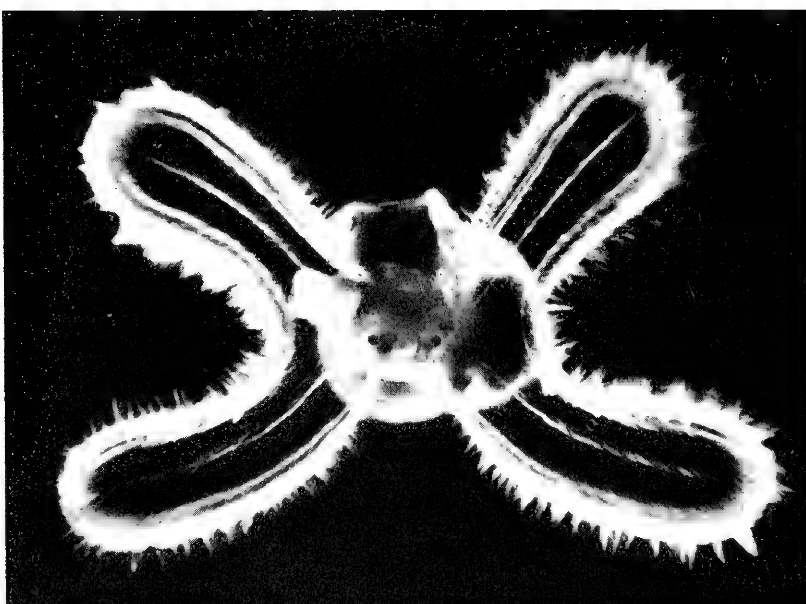


PLATE XXI.

(Top) A disintegrating 'aggregate' salp with a young embryo 'solitary' salp ready to be liberated.
Photograph by James Fraser

(Bottom) The living 'veliger' larva of the mollusc *Nassarius incrassatus*.
Photograph by D. P. Wilson

CHAPTER 6

The planktonic larvae

THE SURVIVAL of the results of reproduction, whether they are seeds, eggs or youngsters is all important in maintaining the species, and the dispersal of large numbers in the hopes that at least some will find favourable conditions is one of the ways of ensuring this. In the sea what better means of dispersal are there than the movements of the water itself, especially as life there can be a prolonged one because the environment is already adequately provided with a good food supply? A planktonic stage in the life history of so many marine organisms is thus to be expected and indeed is found over a wide range, from the spores of the attached seaweeds to the eggs and larvae of the fish themselves. In this chapter some of this great variety of forms will be considered, but the fish will be dealt with in Chapter 7.

The spores of the major seaweeds are liberated into the sea and form, for the time being, part of the nanoplankton (p. 30) and would be assessed as such in any estimation of productivity. They would, of course, be far more abundant in inshore than in offshore waters but only their life history would readily separate them from the true planktonic flagellates, because they settle down to grow into seaweeds whereas the true flagellates continue to reproduce as such.

There are marine representatives of almost every class of invertebrate living attached or freely moving on the bottom. To describe all their planktonic larvae is far beyond the scope of this book, and indeed as yet beyond the scope of any marine biologist for the details of so many of them are still unknown. We can, within limits, make sensible comparisons and so make guesses about the kind of larvae some adults will have; we find larvae of these kinds in the plankton which we cannot yet link with certainty to an adult. Sometimes because of times of spawning and the localities in which they are found we can guess which are which, but often the overlap is too big. It is only a question of time until someone has the opportunity to breed them in aquaria and publish the results, and indeed it is amazing how many thousands of species have already been associated with their larvae—but there are plenty of others yet to be done.

A glance through the figures illustrating this chapter will give an idea of the range of forms found, and an idea of the types of larvae belonging to the different classes. The text will merely be devoted to certain aspects of interest and will not attempt any descriptions aimed at specific separations.

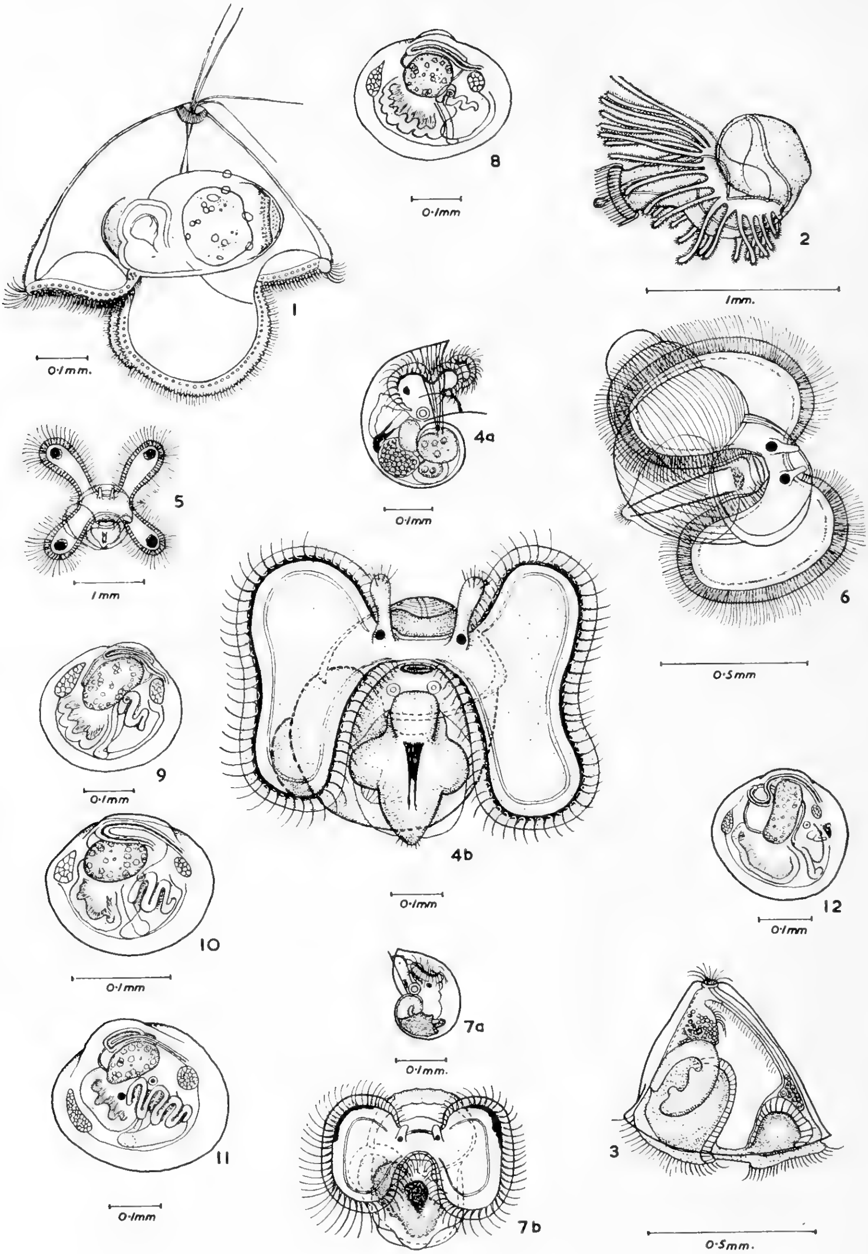


FIG. 24. Planktonic larvae of various invertebrates.

1. Pilidium larva of nemertine worm.
2. Actinotrocha larva of *Phoronis*.
3. Cyphonautes larva of a sea moss, *Membranipora*.

4–7. Gasteropoda (univalve molluscs):

4. *Nassarius reticulata* (*a*) larva just after hatching; (*b*) old larva with shell forming.
5. *Nassarius incrassata*, old larva.
6. *Actis minor*, old larva with shell forming.
7. *Littorina littorea* (periwinkle) (*a*) young larva; (*b*) later larva.

continued opposite

The planktonic medusoid stage of the attached hydroids has already been mentioned (p. 48), but although the medusa is the adult sexual stage it is the attached hydroids on the sea shore that will be most familiar to the readers of this book and so the medusae deserve this passing mention again in this chapter (Figs. 13 and 14). Most sea anemones attached to the rocks have a very short planktonic stage—the planula—which soon settles down, but one group, the family Cerianthidae, live offshore on the bottom usually in muddy sand, and their larvae have a prolonged planktonic stage called an arachnactis larva (Fig. 17; 8). These were at one time thought to be separate species of animals and had their own names such as *Arachnactis bournei* and *A. albida*. They are especially common in warm oceanic water, but are also found in inshore areas.

Each phylum of that miscellaneous group called 'worms' has its own characteristic type of larva but many species have not as yet been associated with their larvae. The nemertines—proboscis worms—have a pilidium larva (Fig. 24; 1) but the nematodes—round worms—have no planktonic stage. The larvae of the bristle-worms or Polychaeta are called trochophores which after a while begin to segment (Fig. 25). These larvae appear to have the ability to prolong their planktonic life considerably if the conditions (e.g. the texture of the bottom) are not suitable for their metamorphosis, and indeed recent work at the Plymouth laboratory indicates that their requirements are very finicky indeed. *Ophelia bicornis* larvae, for example, will only settle on clean loose sand of the right size and consistency. If the grains are too small the larvae cannot wriggle into the spaces, if the sand is not clean enough the spaces get choked with silt or finer particles, and yet there must also be enough food for them to live on. The sand must be roughly rounded and not sharply pointed; sand lying loosely in places where there are strong tidal currents has the right mixture of characters. A series of drawings of some of the types of polychaete larvae is given in Fig. 25 and photographs in Plates XXII and XXIII.

Other 'worms' which have characteristic larvae are *Phoronis* with its 'actinotrocha' (Fig. 24; 2 and Plate XXIII) and the sea mosses and sea mats, or Bryozoa with their 'cyphonautes' (Fig. 24; 3) which can often form an important fraction of the plankton in the spring before they settle down on the sea floor (sea mats—*Flustra*) or to encrust the seaweeds and rocks (sea mosses).

8–12. Lamellibranchiata (bivalve molluscs):
8. *Tellina* sp.
9. *Macoma baltica*.
10. *Cardium edule* (cockle).
11. *Mytilus edulis* (mussel).
12. *Pecten opercularis* (queen, or small scallop).
[1–7 from Thorson, 8–12 from Jørgensen.]

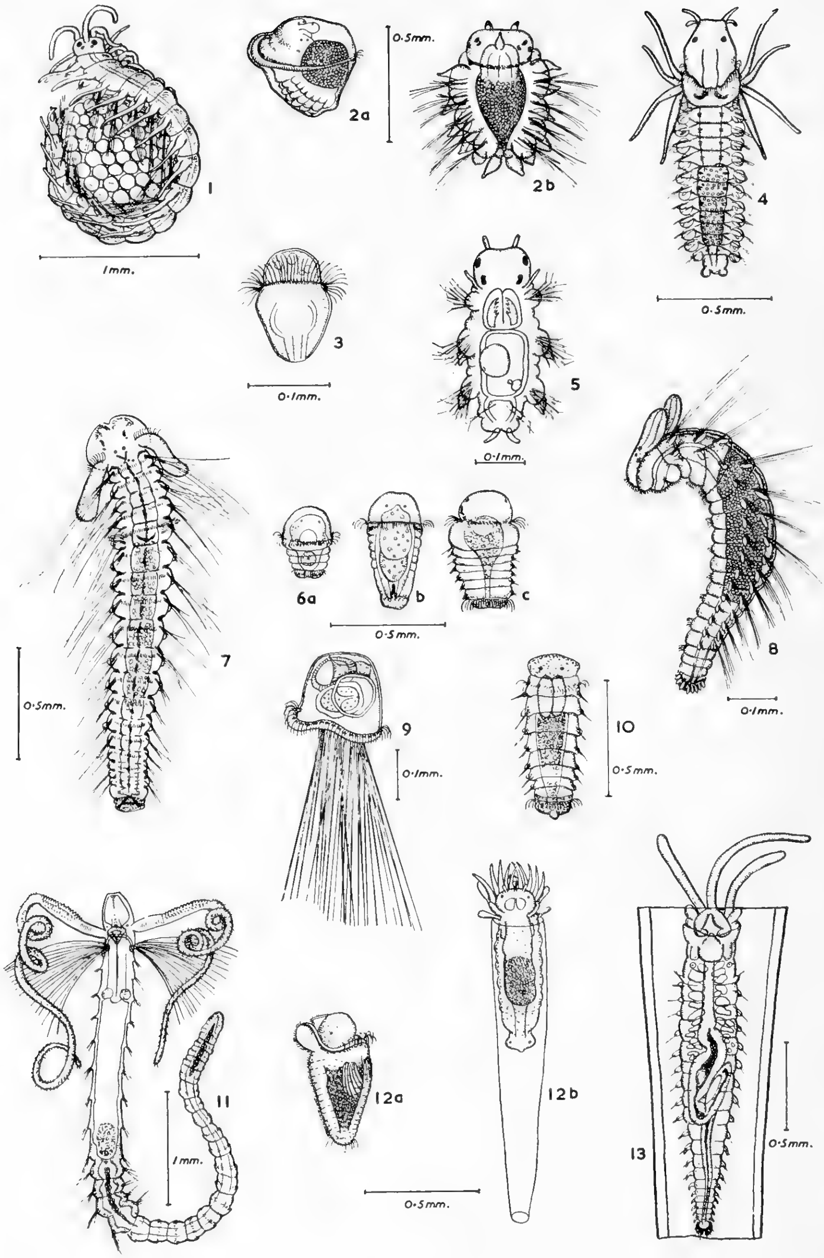


FIG. 25. Planktonic stages of polychaete worms.

1. *Autolutus prolifer,* with eggs.
2. *Harmathoë imbricata* (*a*) metatrochophore, (*b*) nectochaete stage.
3. *Phyllodoce groenlandica,* old trochophore.
4. *Phyllodoce maculata,* old larva.
5. *Nereis pelagica,* nectochaete stage.
6. *Nepthys ciliata* (*a*) young trochophore, (*b*) and (*c*) metatrochophores.
7. *Polydora coeca,* old larva.
8. *Pygospio elegans,* old larva.

continued opposite

Not all marine molluscs have a planktonic stage and indeed some quite closely related types differ, e.g. winkles have but whelks do not have them. The earliest planktonic stage of the univalves (Gasteropoda) is a 'trochophore' very like that of a polychaete worm but instead of segmenting it gives itself a peculiar twist in what is called the 'veliger' stage (Fig. 24 ; 4-7: Plate XXI) and it then develops its shell which is usually spiral. In some the trochophore stage lives inside the egg capsule and only the veliger is planktonic, and in some (e.g. the whelks) both trochophore and veliger live inside the egg and they emerge as tiny, shelled adults.

The bivalves (Lamellibranchiata or Pelecypoda) also have a trochophore and a veliger stage but after metamorphosis the little bivalves with shells already formed (Fig. 24; 8–12) sink only slowly to the bottom, often in immense numbers, and are thus frequently taken in the plankton.

Most of the more primitive types of marine crustacea are planktonic all their lives and so have been considered in the previous chapter, but this chapter must refer to the larvae of the attached barnacles and the bottom living shrimps, prawns, crabs and lobsters.

The attached acorn barnacles are not obviously related to the crabs, but any doubts about their relationships are at once settled by the planktonic larva, which is a typical nauplius (Fig. 21; 5: Plate XXIV) very like those of the copepods dealt with in Chapter 5 (Fig. 21; 1–4). This swims freely in the plankton, moulting and adding more and more appendages just as do the copepod nauplii, but after the final moult it develops simple bivalve shells reminiscent of the ostracods (p. 65) and it is then called a 'cypris' stage (Fig. 21; 6: Plate XXIV). This gradually sinks out of the plankton and if it lands in a suitable place it becomes attached and metamorphoses into the typical barnacle—though 'landing in a suitable place' could itself form a most interesting chapter in a book.

Euphausids (p. 74) also have a nauplius larva (Fig. 21; 10) but this gradually changes, via a long series of moults (Fig. 21; 11) which are named according to the development of the appendages, into the adult. All, including of course the adult, are planktonic.

The normal practice in the bottom-living decapods is for the female to carry her eggs, usually underneath the abdomen (e.g. the berried lobster) or under the carapace between the paired legs. The first stage of development —a nauplius—is often passed inside the egg shell although there is a free

9. *Myriochele danielsseni*, young larva.
10. *Nepthys coeca*, nectochaete stage.
11. *Magelona papillicornis*, old larva.
12. *Pectinaria auricoma*, (*a*) young larva; (*b*) old larva in a gelatinous tube.
13. *Lanice conchilega*, old larva in a gelatinous tube.

[All from Thorson.]

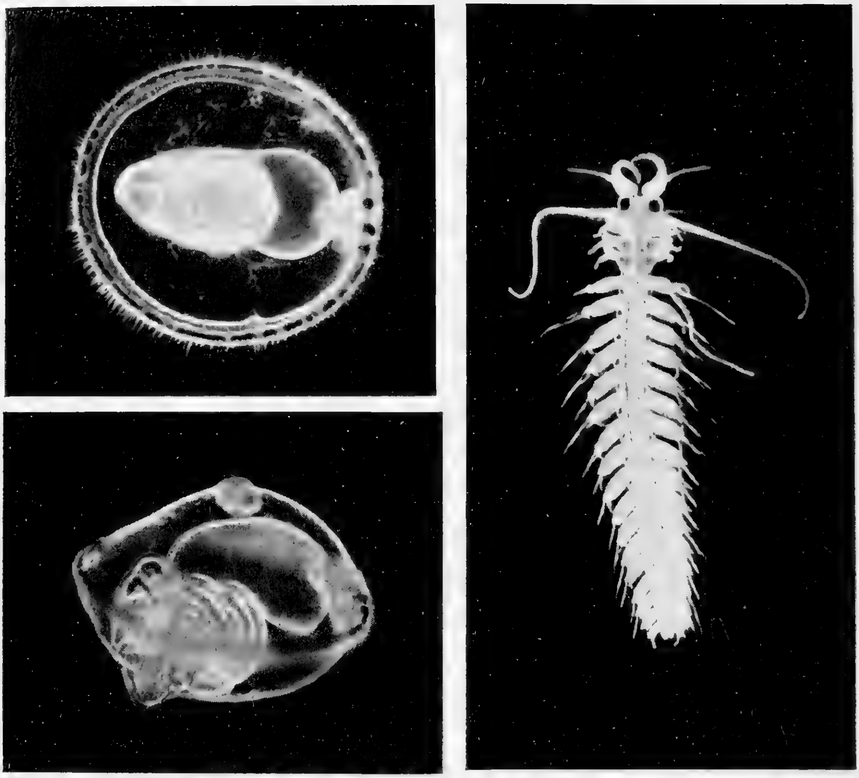


PLATE XXII.

(*Left*) Two views of the 'trochophore' of the worm *Polygordius lacteus*: top, from above; bottom, side view; the mouth in each is to the right.
(*Right*) Segmenting stage of the worm *Autolytus*.

Photographs by D. P. Wilson

swimming nauplius in some prawns (Penaeidea). The young decapod hatches at a later stage, typically a 'zoea' as in the crabs (Fig. 21; 8: Plates XVIII and XXIV). There then follows a series of moults, often a long series, each a little further advanced than the previous one, before the adult stage is reached. There may be quite distinct changes in form as in crabs, for example, where the zoea changes to a 'megalopa' (Fig. 21; 9: Plate XXIV), or the change may be much more gradual as in shrimps. A series of examples of decapod larvae is illustrated in the figure. Some are very exotic in style such as the spiny larva of the oceanic prawn *Sergestes* (Fig. 22; 6) and the flat 'phyllosoma' (Fig. 21; 12) of the spiny lobster which is the French 'langouste'. These queer transparent larvae can live in the plankton for some six months and be carried 1,000 miles before going to the bottom to become little spiny lobsters. It is this ability that is responsible for the French fishery for 'langouste' in the deep water west of the Hebrides and for the less abundant spiny lobster stocks in

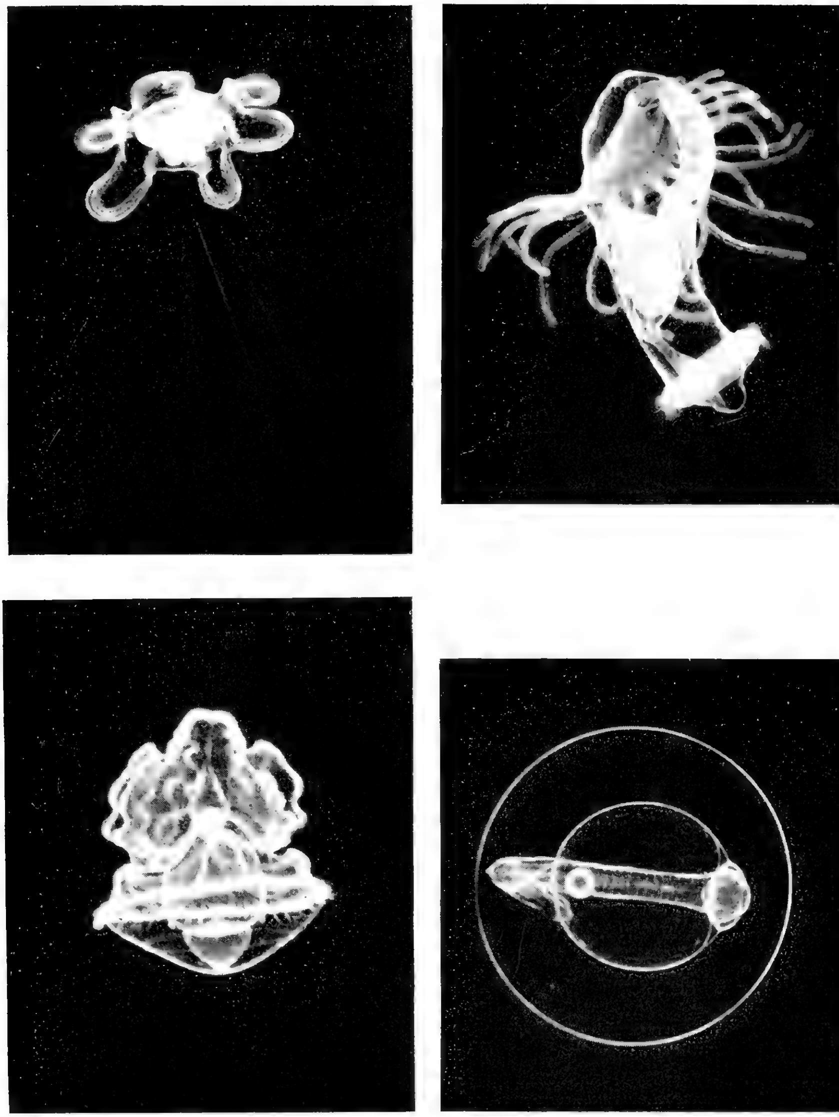


PLATE XXIII.

(*Top left*) The 'mitraria' larva of the worm *Owenia fusiformis*.
(*Top right*) The 'actinotrocha' larva of *Phoronis*.
(*Bottom left*) The 'tornaria' larva of *Balanoglossus*.
(*Bottom right*) A pilchard egg from the plankton.

Photographs by D. P. Wilson

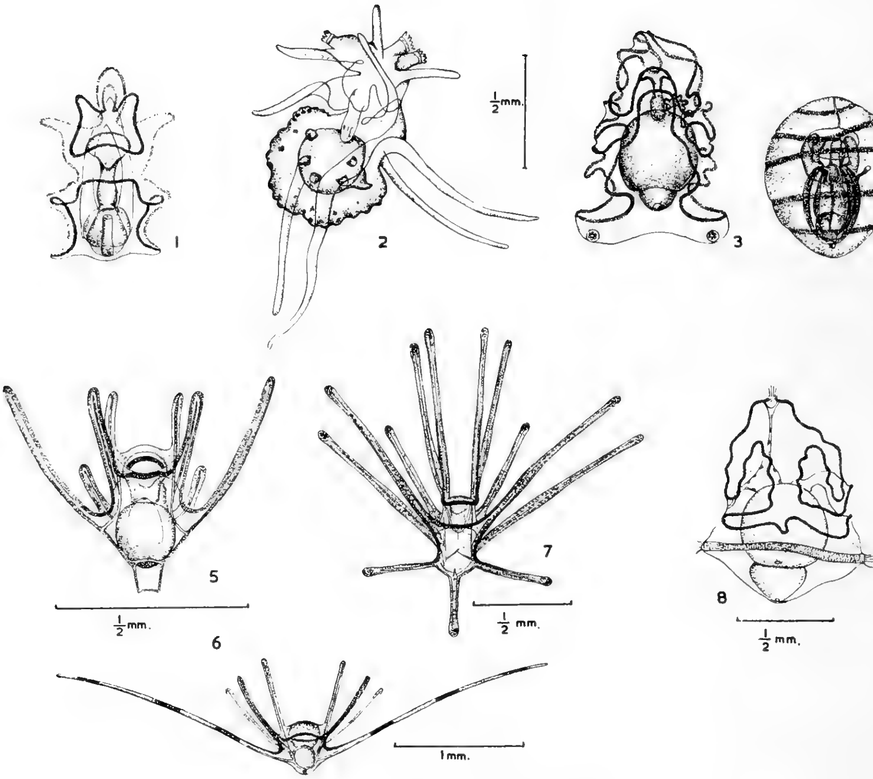


FIG. 26. Echinoderm larvae etc.

1. Bipinnaria larva of a starfish, *Asterias glacialis.*
2. Brachiolaria larva of *Asterias rubens.*
3. Auricularia larva of a sea cucumber, *Synapta digitata.*
4. Doliolaria larva, or pupa, of *Synapta.*
5. Pluteus larva of Brittle star, *Ophiura texturata.*
6. Pluteus larva of Brittle star, *Ophiothrix fragilis.*
7. Pluteus larva of sea urchin, *Echinocardium cordatum.*
8. Tornaria larva of the acorn-worm, *Balanoglossus* (a Hemichordate).

The first four are to the same scale.

Shetland and in Norwegian waters between 60° and 62° N. Berried females have never been found north of 57° N west of Scotland and only rarely north of about 54° N, whereas phyllosomas have been found frequently off the north-west of Scotland and even as far afield as Faroe.

The ordinary lobster has an ordinary and typical decapod life history and a young one from the plankton is shown in Plate XXV.

The Echinodermata—starfishes and sea urchins and sea cucumbers—have planktonic larvae, some of them of exotic shape (Fig. 26). The ordinary asteroid starfish (like the common starfish) have a larva called a bipinnaria, which is not unlike the 'auricularia' larva of the sea cucumber. This gradually changes to a 'brachiolaria' which metamorphoses into a tiny starfish (Plate XXVI). The larvae of the brittle stars and sea urchins are also similar to each

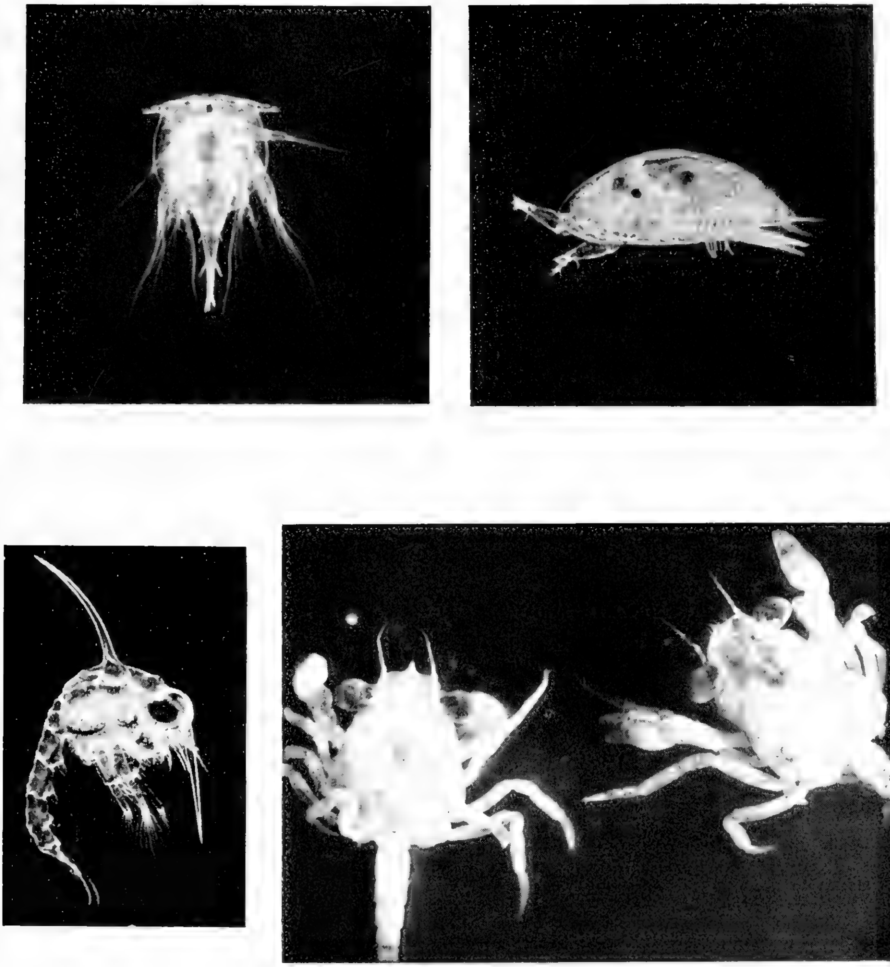


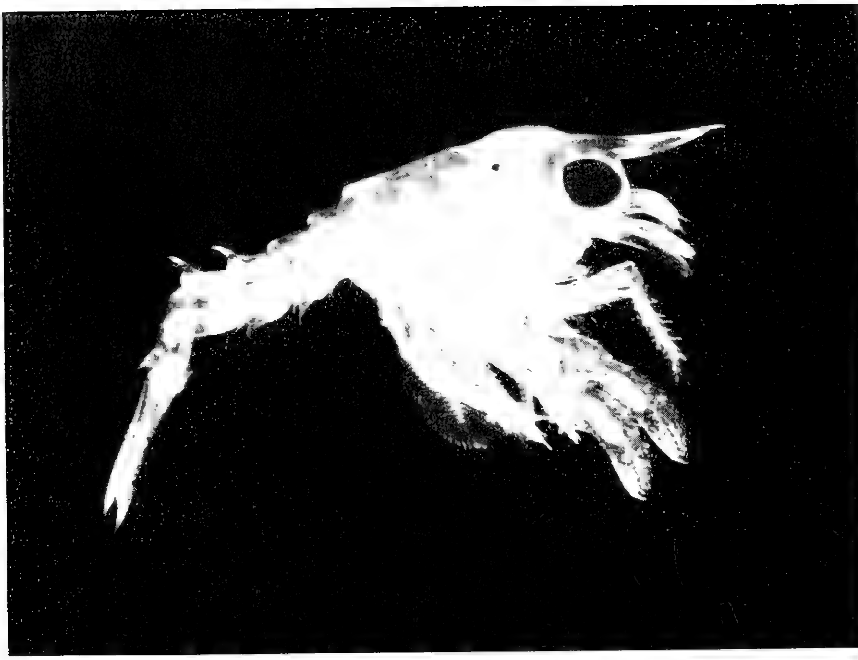
PLATE XXIV.

(*Top*) *Left*, the nauplius stage, and *right*, the cypris stage of the acorn barnacle, *Balanus balanoides*. (*Bottom*) *Left*, the zoea stage, and *right*, the megalopa stage of crabs.

Photographs: 3 by D. P. Wilson, megalopae by James Fraser

other and are called 'plutei'. These, too, gradually metamorphose (Plate XXVII). Fertilized sea urchin eggs, in particular, are easy to obtain by mixing the eggs and sperm in sea water and have been much used for physiological experiment.

To end this chapter mention should be made of the larvae of the bottom-living members of the Chordata, excluding fish. These are the worm-like Hemichordata such as *Balanoglossus* which has a 'tornaria' larva (Fig. 26; 8: Plate XXIII) and the attached Tunicata, the ascidians or sea squirts which have a 'tadpole' stage (Plate XX). These ascidian tadpoles (and those of the



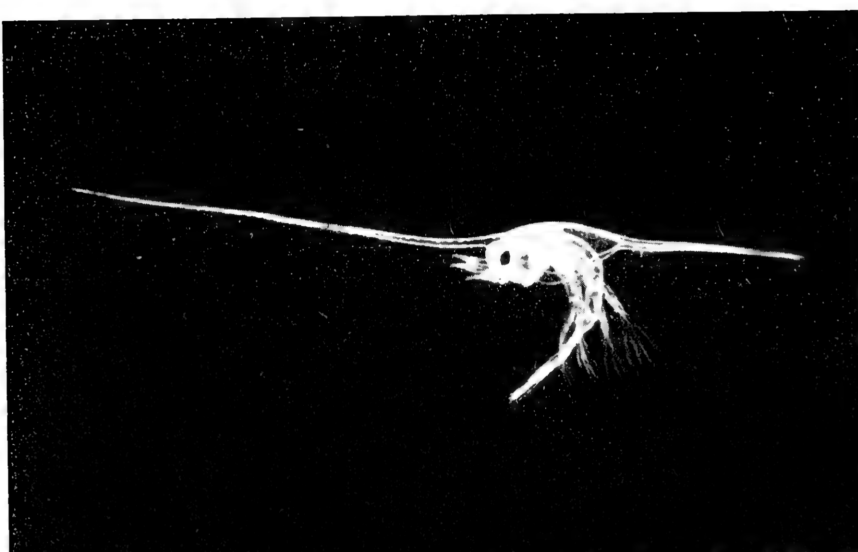


PLATE XXV.

(Top) The planktonic larva of the common lobster, *Homarus vulgaris.*
(Bottom) The first zoea of the pea-crab, *Porcellana longicornis.*

Photographs by D. P. Wilson

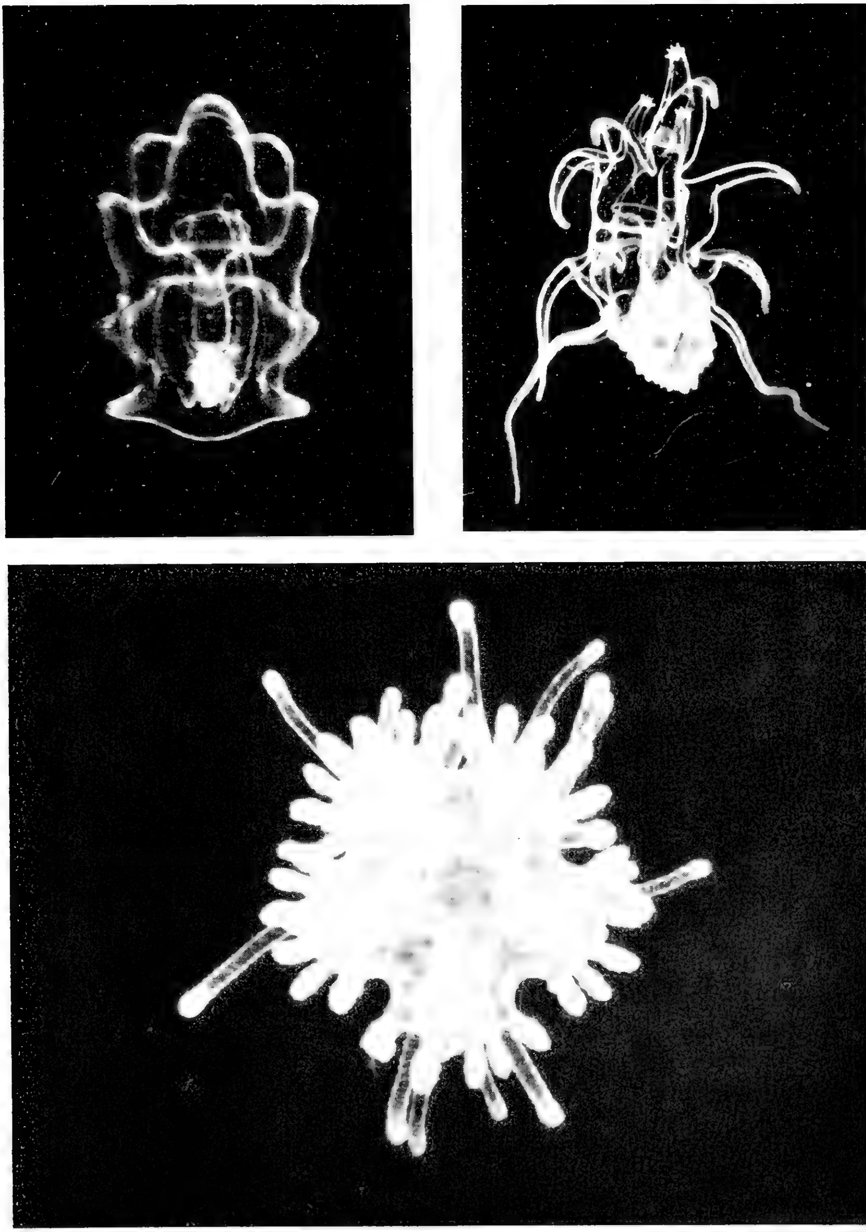


PLATE XXVI. Three stages in the life history of the starfish, *Asterias*. *Top left*, the bipinnaria, *top right*, the brachiolaria, and *bottom*, the early baby starfish.

Photographs by D. P. Wilson

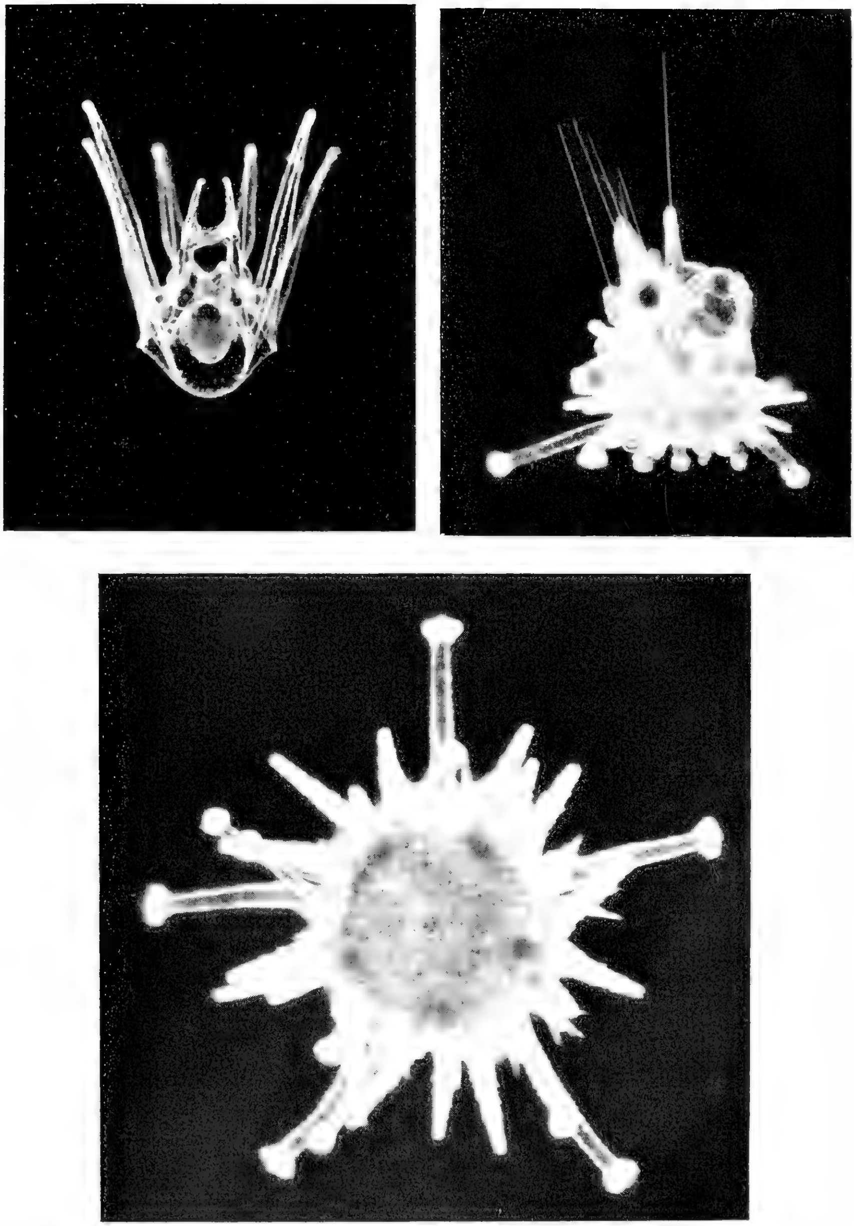


PLATE XXVII. Three stages in the life history of the sea-urchin, *Echinus esculentus*. *Top left*, the pluteus, *top right*, a later stage, and *bottom*, the early baby sea-urchin.
Photographs by D. P. Wilson

doliolids: see p. 80) are more than reminiscent of the tadpoles of frogs as they show, far more easily than the adults, their primitive Chordate affinities, with gill slits, endostyle and notochord. They are not very often taken in the plankton as their free life is very short, only six to twenty-four hours, but they can be found in collections made close to the rocky shore in middle or late summer.

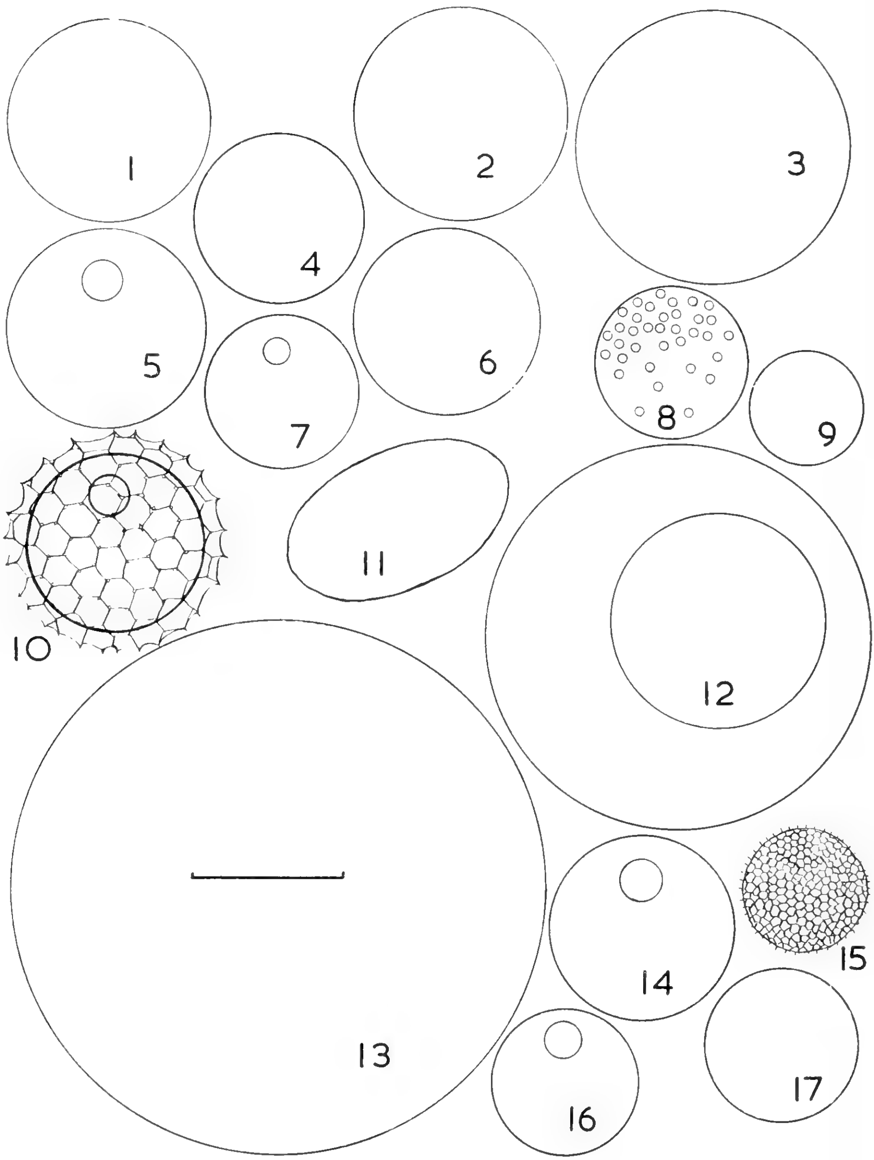


FIG. 27. Some fish eggs drawn to the same scale. Small circles inside represent oil globules and these, too, are drawn to scale.

1, cod; 2, haddock; 3, plaice; 4, whiting; 5, gurnard; 6, lemon sole; 7, turbot; 8, sole; 9, dab; 10, lantern fish (*Myctophum*); 11, anchovy; 12, long rough dab (with a large perivitelline space between the yolk and the shell); 13, halibut; 14, mackerel; 15, dragonet; 16, hake; 17, sprat. The line inside the halibut egg represents 1 millimetre

CHAPTER 7

The young fish

HERRING CONGREGATE in shoals for spawning and lay their eggs in a thick carpet, maybe a dozen eggs deep, glued to a stony area of the sea floor. Here incidentally they are a rich and easy source of food for other creatures, especially the haddock. Skates and some dogfish lay their eggs in 'mermaids purses', some shore fishes make 'nests' or lay their eggs in gelatinous masses, but the eggs of by far the majority of marine fishes are freely floating in the plankton. Mating takes place usually near the bottom and with a greater degree of intimacy than has usually been supposed, the male shedding the milt into the water in close proximity to the eggs as they are extruded. Fertilization occurs freely in the sea water and usually well over 90 per cent of the eggs are fertilized. They then float upwards as part of the plankton of the upper layers and are drifted about by the currents. The eggs (Fig. 27: Plates XXIII and XXXII) are usually spherical, but some—such as the anchovy—are oval. Some are characteristically sculptured, for example the lantern fish, *Myctophum*, and the dragonet, but most are just plain transparent spheres while alive and opaque white after death or preservation. (There is nothing peculiar about this change which is essentially the same as the white of a hen's egg changing from transparent to opaque white on cooking.) The egg is filled with a clear yolk which is the food supply of the developing young fish until after it hatches and can feed for itself. This yolk may look homogeneous or be broken up into globules—a 'segmented' yolk. There may or may not be an oil globule in the egg, but some, such as the eggs of the sole, have numerous tiny globules. Each species of fish lays its own type of egg within a fairly close size range, although the eggs get smaller as the spawning season progresses. Apart from the few sculptured or oval eggs, their identification depends on size, on whether the yolk is segmented or not, if there is an oil globule and, if so, its size in proportion to the total diameter of the egg. The sizes overlap considerably so it is not always possible to identify newly spawned fish eggs with certainty. As the embryo develops inside the egg its own characteristic pigment patterns gradually appear making identification much easier and more reliable. This takes about ten days in the cold waters of the North Sea in March. The rate of development is very largely dependent on temperature so that a fairly reliable indication of the age of an egg is obtained from the state of development if the temperature is known. The hatching time of plaice, for example, is roughly 120 'degree-days'; i.e.

twenty-four days at 5°C, twenty days at 6°C, twelve days at 10°C or ten days at 12°C. The smaller the eggs the quicker they develop and hatch.

The eggs hatch before the young fish have developed sufficiently to have a mouth so that for the first few days they continue to feed on the remnants of the yolk carried under the body in the 'yolk sac'. When the mouth has opened the young fish starts to feed, first on the phytoplankton and small zooplankton animals like the earliest nauplii of the smaller copepods (Fig. 21). As it gradually grows, larger and larger planktonic animals are taken. The food taken is partly dependent on what is available and partly on selection by the little fish themselves, which are sometimes quite choosy. Young plaice and lemon sole are particularly partial to *Oikopleura* (Plate XIX) which does not seem so attractive to young cod or haddock, although adult haddock have been known to eat them in large numbers on occasions. The young crustacea, copepods especially, and many of the larval invertebrates discussed in the preceding chapter, are widely acceptable.

For several weeks, and sometimes months, these little fish will be part of the plankton, feeding on it, being drifted by the water movements and being eaten by other predatory species in the plankton. The economic significance of this will be considered in Chapter 10, but it is obvious that there must be very great losses. To make up for this the numbers of eggs laid by each female fish at one spawning can be very large indeed, and vary with the amount of care taken and with the size of egg in relation to the size of the fish. Shore fishes with nests in which the eggs are guarded have comparatively few eggs, a herring which lays its eggs in a carpet on the sea floor unattended lays about 50,000. Fish with planktonic eggs lay greater numbers; plaice which have large eggs (1·8 millimetre in diameter) produce about $\frac{1}{4}$ million, haddock lay about $\frac{1}{2}$ million eggs about 1·4 millimetre in diameter, cod which are larger fish lay well over a million eggs about the same size as haddock eggs, and ling with small eggs of only 1 millimetre diameter produce over 2 million; even greater figures have been quoted. The eggs of the same species of fish tend to be smaller when the fish first spawns and increase in size as the fish grows older and bigger. Egg size will affect survival as bigger eggs have more yolk and give the young fish a better start in life.

As there are 'lots of good fish in the sea' the total egg production is enormous. Even in a relatively small area like the shelf water round the Faroe Islands the annual production of haddock eggs alone is about 6,000,000,000,000 The plaice egg production in the southern North Sea is about the same figure, more than half of which is in the Southern Bight. Pilchard eggs in the English Channel in 1950 were estimated at 400,000,000,000,000. The usual method of obtaining such estimates is by sampling the area with a series of vertical hauls with a Hensen net (Chapter 2: Plate IV) from the bottom to the

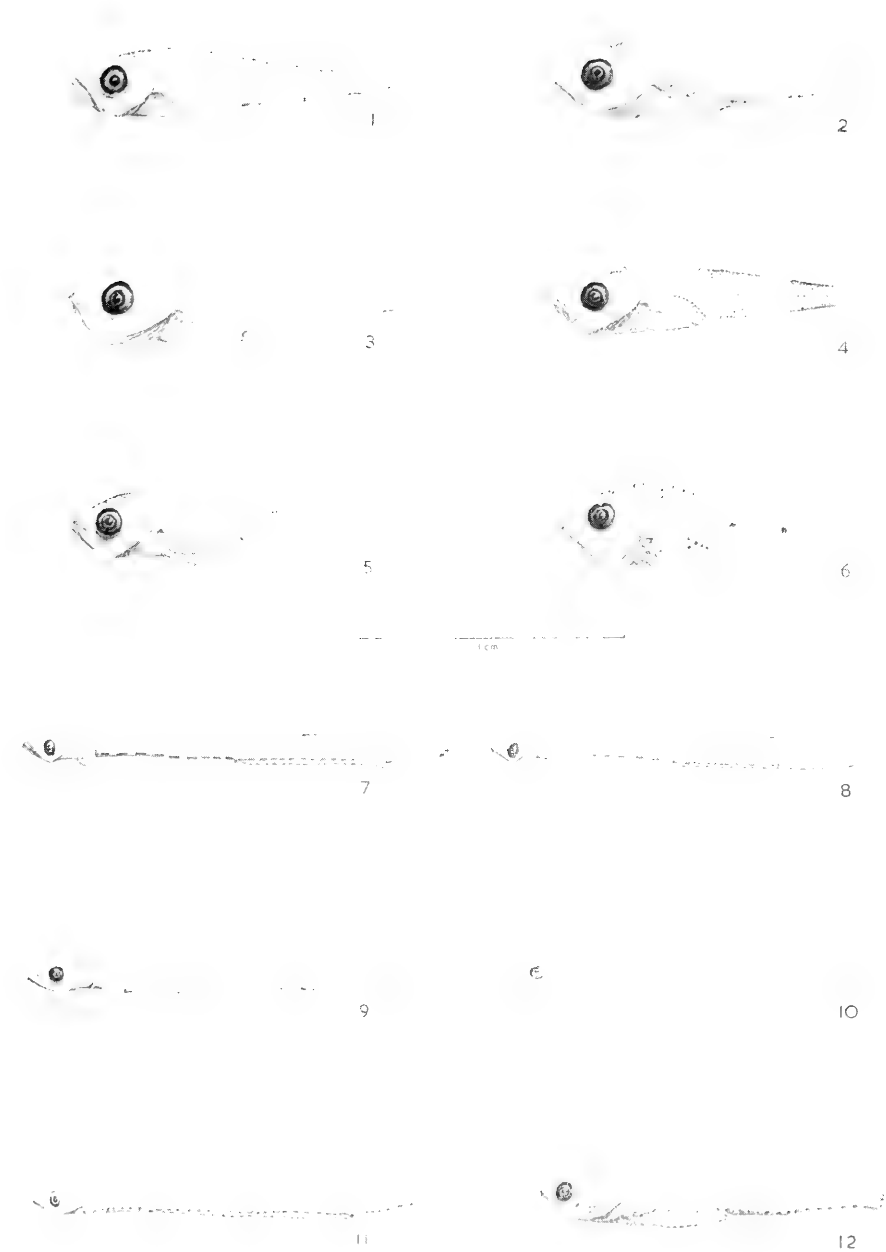


PLATE XXVIII. Planktonic stages of fish.

1, cod; 2, haddock; 3, whiting; 4, saithe; 5, ling; 6, hake; 7, herring; 8, sprat; 9, anchovy; 10, sandeel; 11, capelin; 12, goby. All to the same scale.

Drawings by N. T. Nicoll

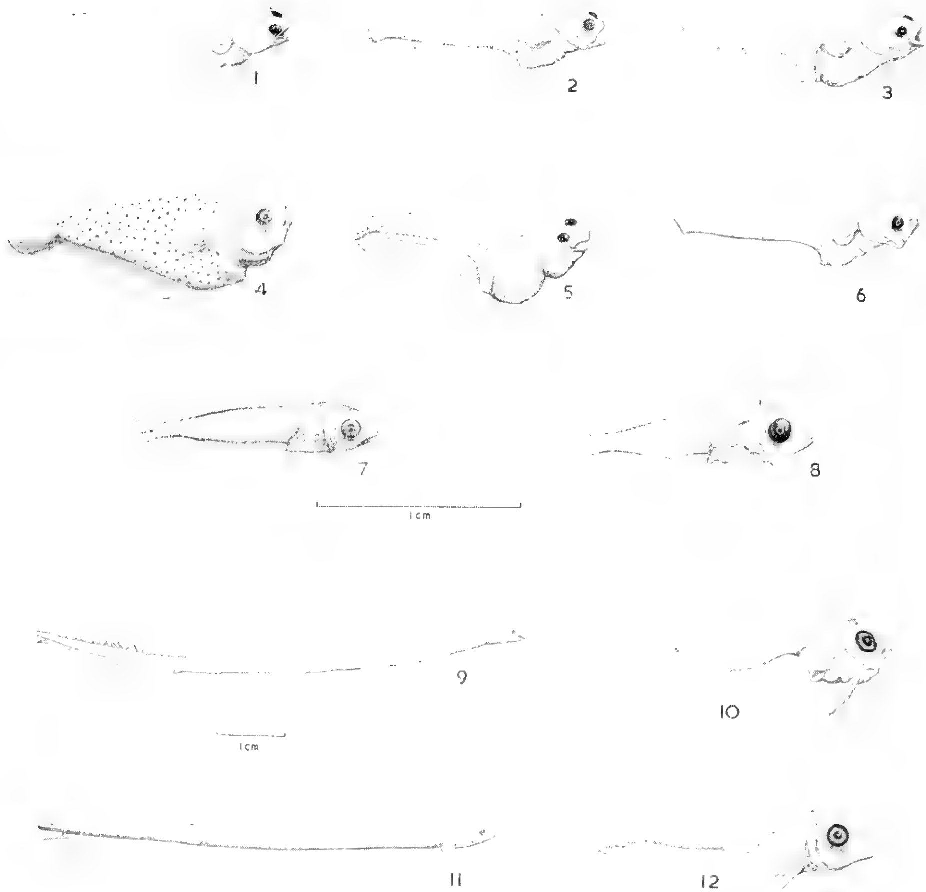


PLATE XXIX. Planktonic stages of fish (*continued*).

1, plaice; 2, dab; 3, lemon sole; 4, turbot; 5, sole; 6, halibut; 7, mackerel; 8, Sea bream (*Sebastes*); 9, leptocephalus stage of the eel; 10, angler (*Lophius*); 11, glass eel stage of the eel; 12, gurnard. 9 and 11 to smaller scale, all others to the same larger scale.

Drawings by N. T. Nicoll

surface. The eggs in each haul are counted and contours of the numbers drawn on a chart, interpolating mathematically when necessary. Knowing the surface area of the sea area under investigation and the number of eggs in the hauls, a total figure can be calculated.

The young planktonic fish usually bear little resemblance to the adults, but are nevertheless quite characteristically marked by pigment patterns which make identification fairly simple, though some of the rarer deep-sea fish larvae have not yet been identified. Drawings of the larvae of some well-known fish are given in Plates XXVIII and XXIX. In addition to the pigment patterns so useful for identifying the individual species there are more basic differences which help to separate the various families. Of these the most important are the shape of the gut, the position of the anus, the type of fin arrangement, and the number of muscle segments and developing vertebrae. This number is affected, within limits, by the temperature at the critical stage when the muscle segments and vertebrae are laid down. In colder regions the number tends to be larger than in warmer, and indeed this can be shown experimentally. Cold and warm treatment given to sea-trout eggs of the same parentage given at the sensitive period resulted in differences of as many as three vertebrae, sixty in cold and fifty-seven in warm treated eggs, and experiments with herring show very similar results.

Flat-fish start life bilaterally symmetrical just as the round fish, but as they gradually metamorphose into the adult shape one eye starts to move over the head (Plate XXX) and the fish then swims on its side. Nearly all the common flat-fish have both eyes on the right side, but turbot, brill, megrim and the topknots are left-sided. Every now and then, but remarkably infrequently, a left-sided plaice or flounder or a right-handed turbot is found.

Special mention must be made here of the common freshwater eel of which there are several kinds in the world. The European and the American eels come from spawning grounds in the Atlantic and these two eels are very alike, the main differences being in the number of vertebrae, 103–111 in the American and 110–119 in the European. Although the European eels are found from the Baltic and Iceland to the Mediterranean there is no evidence at all of racial differences as there are with so many fish and other animals in such a wide geographical range. The elucidation of their life history we owe mainly to the Danish oceanographer, Dr. Johannes Schmidt. The eggs are laid in deep water, 250 fathoms (500 metres) or more, in a fairly closely confined area in the region of the Sargasso Sea, 20°–30° N, 50°–60° W, and the eggs and the young larvae, at first only about $\frac{1}{4}$ inch long, gradually rise. Those of the European eel, hatched in the eastern part of the spawning area, are drifted across the Atlantic by the Gulf Stream. Those of the American eel, hatched in the western or south-western section are in a different part of the current system and are carried towards the American coast. The larva, in its oceanic form, is very transparent, thin and flattened like a willow leaf and is called a 'leptocephalus' (Plate XXIX). This reaches about 3 inches in length, swimming nearer and nearer the surface as it grows. On reaching the coastal water the larvae gradually shrink in size and at the same time become rounded instead of flat the glass eel stage; these swim with the flood tide but go to the bottom at the ebb tide. They approach the river mouths and swimming always against the current go up the rivers. The attraction of the fresh water,

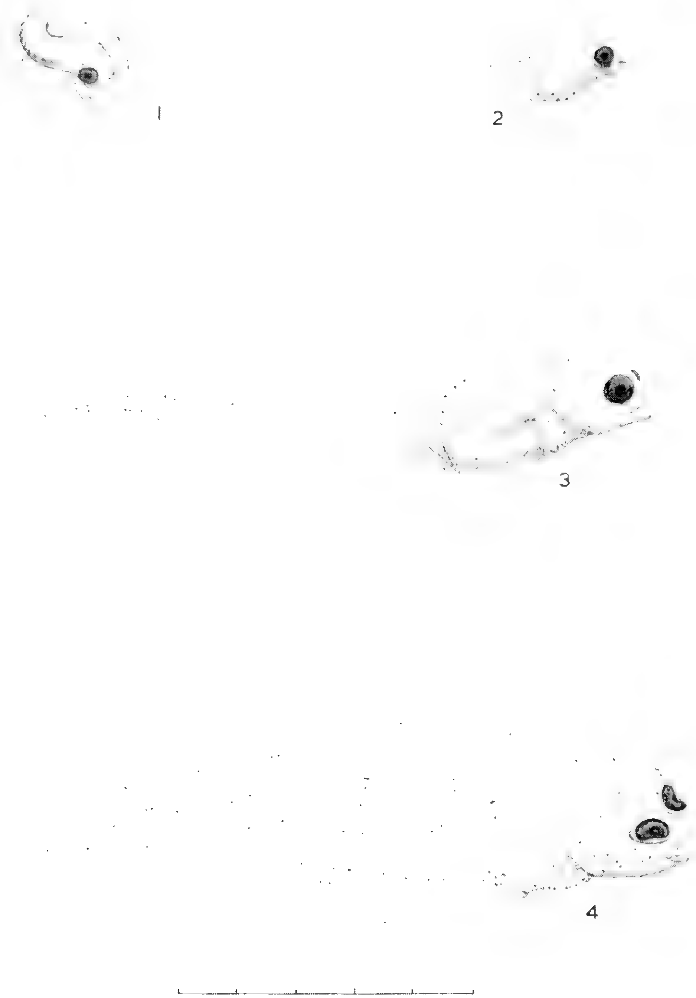


PLATE XXX. The development of the plaice.
1, egg with embryo developing inside; 2, the newly hatched larva with its yolk sac; 3, a later stage with the eye starting to come over; 4, a still later stage with the eye now almost in the adult position. All to same scale.

Drawings by N. T. Nicoll

which had been thought to be the reduced salinity, has recently been shown to be the 'smell' of the fresh water, and if the 'smell' is extracted by filtering through charcoal the young eels do not react to it. (The filtering through charcoal extracts dilute organic chemical substances, and is the same principle as used in the wartime gas mask.) Once in the vicinity of the rivers they

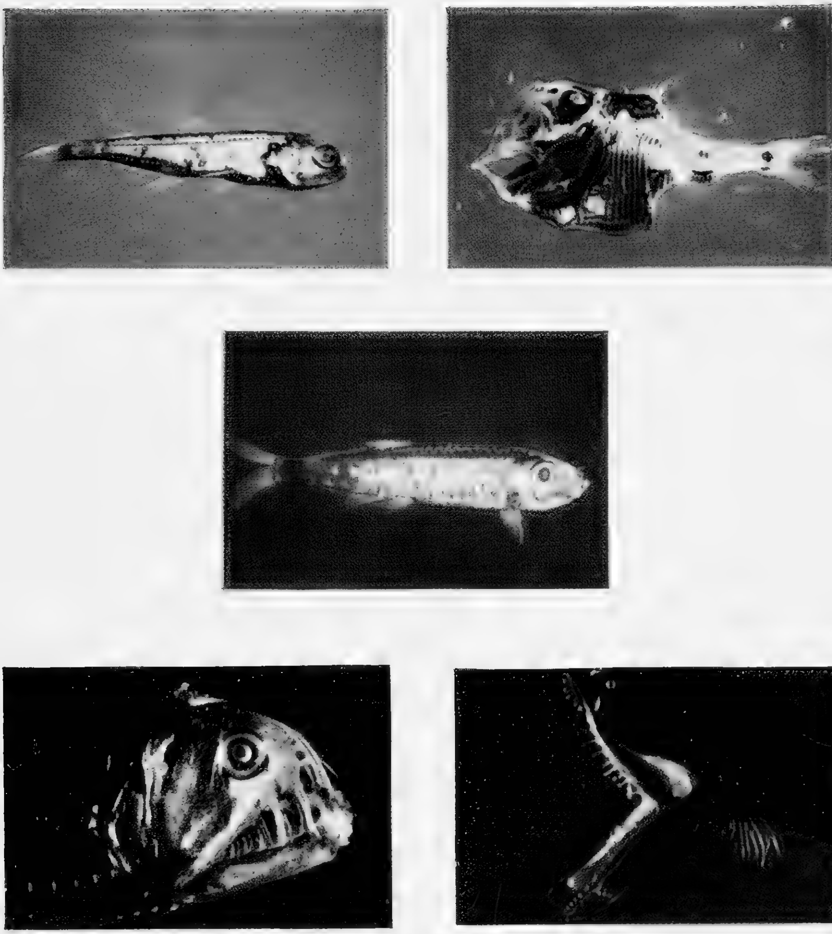


PLATE XXXI. Oceanic fish.

(*Top left*) *Myctophum punctatum.*
(*Top right*) *Argyropelecus hemigymnus.*
(*Centre*) *Maurolicus mulleri.*
(*Bottom left*) Head of *Chaulodius.*
(*Bottom right*) The wide open mouth of *Gonostoma bathyphilum.*

Upper three photographs by James Fraser,
lower two by Peter David

become more and more pigmented and are called 'elvers', and these migrate up river, even across damp grass etc., to ponds where they live until adult.

At the onset of maturity, they migrate downstream, becoming silvery in colour and with enlarging eyes, and so out to sea. The ovaries of the females at this stage are enlarging but are far from properly mature, and the males show little sign of development. They thus disappear into the sea, never to return, and the next we know is the young new generation from the Sargasso on its drifting passage back across the Atlantic. This raises interesting problems and theories. As there is a certain amount of overlap between the spawning grounds of both the European and the American eel, how do the larvae become so completely segregated? Never a European larva seems to go to America and never an American to Europe! An attempt has been made to explain this on the length of life of the leptocephalus stage which in the American eel is about one year but in the European three, corresponding to the time necessary to make their respective journeys. Thus, should an American type of leptocephalus be carried towards Europe it would never have time to make the journey. Should any European type be drifted to America it would arrive too soon in its development and would not react properly to the presence of the river water. Thus it would not migrate up the rivers but go on being carried about in the ocean currents and so become lost.

As recently as 1959 Dr. Tucker, lately of the British Museum, suggested a new hypothesis to account for this strange life history and migration. Briefly it is this. He considers that the European adult eel cannot reach the spawning grounds 3,500 miles away as the gut is rapidly disintegrating with the onset of maturity; they cannot feed and they could not cover such a distance and retain sufficient vitality to spawn even if they reached there—laying 10 million eggs is no small achievement. Their instinct is to attempt to do so, but they soon die. Only the American eels, which have so much less distance to travel and are larger and in better condition, reach the spawning ground. Eggs laid to the east of the Sargasso Sea, as they rise through the water layers, are thought to reach a lower temperature than those in the west and thus grow to be European eels with 110-119 vertebrae and are carried by the current system eastwards across the Atlantic. Eggs laid to the west may rise through a layer with a sudden temperature increase and grow to be American eels with 103–111 vertebrae and are carried to the American coast. We have already seen (p. 101) that this is not an improbable effect of temperature at just this critical period. The length of life of the leptocephalus is considered to be dependent upon the conditions of its environment and not a factor dependent upon heredity. Its metabolic rate will be higher in the warmer waters towards America and it will be ready to change to the glass eel stage as soon as the river water stimulus is felt. Those carried eastwards towards Europe will develop more slowly and so prolong their leptocephalus stage until the coastal region is reached after about three years. Those that for some reason do not conform to pattern will die. If this theory is correct all the European eels are dependent upon American stock.

So far neither theory has been proved, and the proof is eagerly awaited as at present it is one of the most interesting problems in marine biology. Both theories have one major assumption: the original Danish theory assumes that the adult European eel can actually make the journey to the spawning ground, though it should be mentioned here that the experiments showing that environmental differences could affect vertebral count were carried out after Schmidt's ideas were published. Tucker's theory assumes that the environment really does have this effect. Many do not accept Tucker's hypothesis because, they say, the difference in vertebral number—the average difference is eight—is too big to be only an environmental difference and that we would expect more evidence of dead eels washed ashore on the European coasts. They say the degeneration of the gut has been exaggerated and it is not always so far gone as Tucker states, and that some at least could be capable of making the 3,500 mile crossing of the Atlantic. If only some do, and lay 10 million eggs each, it would be sufficient. It is going to be interesting to see what the correct explanation is. The proof could lie either in finding an adult European eel in the Sargasso Sea area, or in experimental evidence that both kinds of larvae can come from the same parentage.

Although the leptocephali when they reach the European coasts are only some 3 inches in length, much bigger ones have been found. They are the larvae of different species, those of *Nemichthys scolopacus* are up to about 10 inches (25 centimetres), others have been found up to 20 inches (50 centimetres), and a leptocephalus has been found off New Zealand which was 34 inches (89 centimetres) in length. But the biggest of all was taken by Johannes Schmidt's ship, the *Dana*, on her expedition round the world in 1928–30, and this was 62½ inches long (184 centimetres).

We do not know to what species these giant eel-larvae belong, and various exciting visions can be conjured up. Do they grow up continuing the same proportions found in the common eel and so grow to become gigantic 'sea-serpent' eels of 70 feet in length, or do they metamorphose into an adult perhaps little or no bigger than the leptocephalus—or something in between? The adult *Nemichthys* are only three to five times as long as the larvae. Could they be 'lost' leptocephali that have never found the right conditions to metamorphose and yet have survived—though their vertebral number and other characters show they are not just overgrown specimens

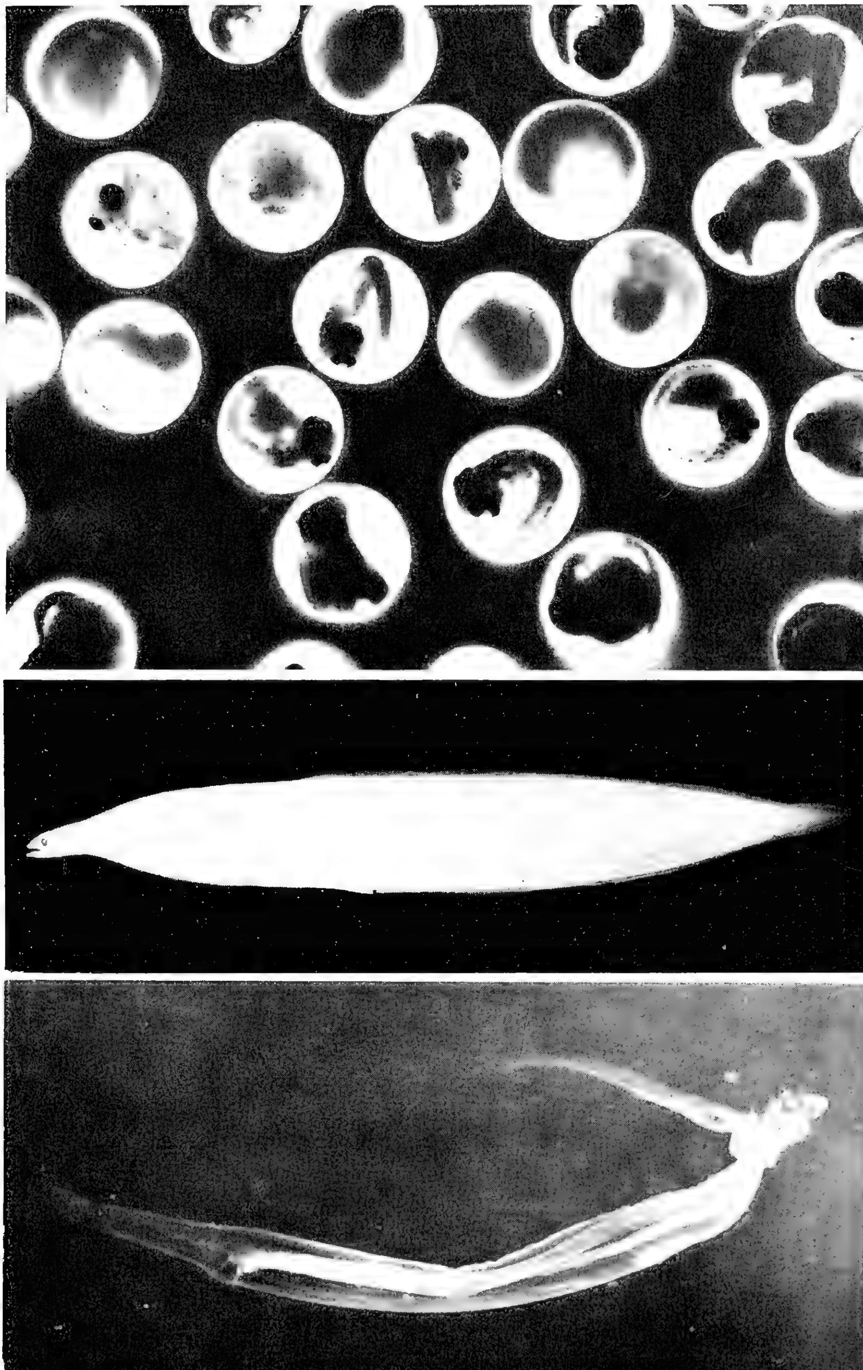


Plate XXXII.

(*Top*) Fish eggs.

(*Centre*) The 'leptocephalus' stage of the eel.

(*Bottom*) *Sagitta maxima* catching a small lantern fish (*Maurolicus*).

Photographs by James Fraser

of the known species. If this were so, will they ever metamorphose, and if not can they mature in the larval state? Such a feat is not unknown to zoologists as the larval stage of the Mexican salamander, if prevented from leaving the water, retains its tadpole-like larval form, the axolotl, and can become mature. We still have a lot to learn about the sea and the living things in it!

Conger eels do not migrate up rivers but remain as marine fish, but they, too, spawn in deep water never to return, though their spawning grounds are more widespread than those of the freshwater eel. They also have a leptocephalus larva.

This chapter must close with a brief reference to small but adult fish which are planktonic—this definition excludes of course any fish like herring which, although they live in the upper waters of the sea, are capable swimmers, i.e. pelagic and not planktonic. The planktonic fish are mostly small deep-water fish, certainly capable of swimming and chasing their prey, but generally staying within the same water mass, and being carried where its movements take them. They live amongst the other species of the oceanic plankton and often come to the surface at night but go down to deeper water during the daytime. Some of them are grotesque shapes, vicious carnivores sometimes able to eat whole fish bigger than themselves because of very distendible jaws and a stomach to correspond. Although they could look very frightful if they were large they are mostly measured only in centimetres or inches. Some are illustrated in Plate XXXI. They often have patterns of luminous organs (photophores), the pattern being very strictly specific (Chapter 12) and they live and feed in a world of everlasting twilight or utter darkness except for the light of their own luminous organs and those of other creatures.

And what about the sun-fish—that great but curiously abbreviated and often surface-living fish? Sun-fishes can grow up to some 8 feet in length and weigh about 8 cwt, they live in warm or temperate waters, and are often found right at the very surface lying on their sides. When living below the surface they will swim in an upright position, but why lie on their sides at the surface? One suggestion is that they like basking in the sun, but it seems more probable that they are feeding on the surface-floating crustaceans of the plankton like *Themisto* (p. 72), and lying on their sides is the only way of getting their mouths there. They are normally very sluggish indeed and are drifted by the Gulf Stream and other currents well into the North Atlantic to the west and north of the British Isles and occasionally even into the North Sea, Irish Sea, Baltic and Icelandic waters. They seem so lazy, and they most certainly drift, so perhaps they, too, can be called planktonic!

CHAPTER 8

Geographic and seasonal distribution

As PLANKTON is so dependent on the conditions of its environment—the weather above the sea, the temperature and the chemical content of the water itself, its biological history—it is only to be expected that there will be great geographic and seasonal variations. The most important physical factor is temperature and, because temperature has such profound effects, it would be worth-while giving a page or so to it. Temperature differences in the water are of course fundamentally dependent on the climate above and it is almost too obvious to mention that tropical seas will be warmer than polar seas, but this fact is of such major importance in so many ways that it just has to be stated. With the winds, particularly the fairly constant trade winds, temperature is one of the causes of the main current systems, the plankton distributions and the location of the world's dominant fisheries.

Warm water is lighter than cold, and where the tropical sun warms the seas the warm water stays on top and so gets warmer still. In cold areas the cold water sinks. A general circulation is thus set up, cold water sinking in the polar regions; this heavier cold water spreads along the ocean floor towards the tropics and is counterbalanced by the movement of warm water, northwards in the Northern Hemisphere and southwards in the Southern, to replace it. One might thus expect that the colder the air near the poles the more water would sink, and as more warm water would then replace it, the temperature near the poles would rise and conditions would be kept fairly stable. This is not so, however, due to freezing. Fresh water, when cooled, expands just before it freezes and continues to expand as ice forms (and bursts the unprotected water pipe or car radiator), and so it becomes lighter and stays on top to freeze solid and form a stable layer there. Sea water behaves differently and continues to contract as it cools to temperatures below the freezing point of fresh water. It thus sinks away from the atmospheric cold before it freezes and is absorbed into and warmed by the slightly warmer water below. If the water is deep there is a very great reserve of warmth, and deep sea water is thus very difficult to freeze. But if there is a less saline—and therefore lighter—layer overlying the deep water, the increased density due to cooling may not be enough to let it sink into the warmer saltier water below, and this stable surface layer can thus freeze. Ice crystals are made from more or less fresh water and are therefore light and float leaving even saltier water below. Less saline waters are, of course, formed when the ice melts in the summer and such conditions are often helped in winter by snow, or where there is excess cold and ice crystals can form before the water has time to sink. Shallow waters can freeze more easily as there is no mass of deep water below to absorb and warm the cold water as it sinks.

Really cold weather at the poles forms more and more ice, and there is less circulation than before. This behaviour of salt water on cooling also means that the coldest water in the deepest part of the sea is always nicely above its freezing point with no seasonal variation.

Both temperature and the amount of salt affect the density of the sea and dense water always tends to sink and to be replaced by inflow of less dense water whether the density is due to coldness, to salt content or to both, so that the current systems are more complex than if caused by temperature alone. Wind also has its effect. It blows surface water in front of it and water from sub-surface or deeper layers must upwell to replace it. This may be on a small local scale or the vast scale of the whole ocean system where the currents are thus due to a complex combination of winds, convection currents caused by temperature changes, and the rotation of the earth itself.

Relative to the size of the oceans these currents are slow moving, though they transport immense volumes of water. The Gulf Stream, east of Florida, sweeps across the Atlantic spreading out and slowing down in the process, so that although at first it is a narrow stream fast enough to be a nuisance to shipping making headway against it, it is hardly noticeable as a current a hundred miles across by the time it reaches Europe. The crossing takes about three years, and at such a speed it seems very slow compared, for example, with the mighty roar of Niagara, which copes with 200,000 cubic feet of water a second. Nevertheless it would take Niagara three years to deal with the amount of water carried by the Gulf Stream in a single day. Only part of this Gulf Stream reaches the northern part of Europe as most of it continues in its circular motion towards the African coast and south to the Equator again. The northern part, called the North Atlantic Drift sends its main branch to Europe affecting the area from the Bay of Biscay northwards west of the British Isles, round the north of Scotland, between the Faroe Islands and Shetland, and so towards Spitsbergen (Fig. 28). A minor branch of this turns into the North Sea. Another continues northwards well to the west of the British Isles towards the south and west of Iceland. The topography of the bottom has its effect, submarine ridges in particular causing big changes in what might otherwise be a fairly simple system. Of these the most important are the Iceland-Faroe Ridge and the Wyville Thomson Ridge from Faroe Bank to the Hebrides, which are approximately only 500 metres in depth. The North Atlantic Drift crosses the Wyville Thomson

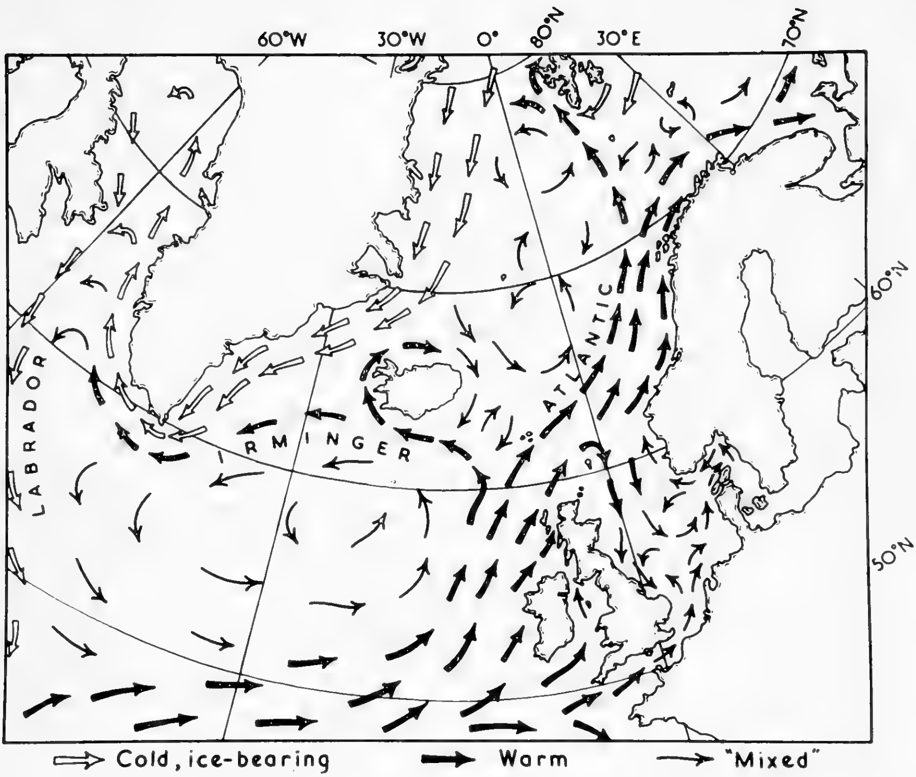


Fig. 28. The surface currents of the North Atlantic. Simplified diagram by A. J. Lee.

Ridge so that to the north-east of it the warm water is never deeper than the upper level of the Ridge and below this 500 metre level is cold arctic water, although relatively warm Atlantic water may be found at 2,000 metres on the south west side. The ridges between Iceland and Greenland, and between Faroe and Iceland, act as barriers to the flow of cold deep water into the Atlantic and the main outflow of cold water is forced to the surface well to the west as the Greenland current. This continues, by then somewhat mixed with water from west Greenland, as the Labrador Current passing close to Newfoundland and then affecting the Atlantic coast of the United States. It is the warmth of the North Atlantic Drift that keeps the seas of the North European areas ice-free when corresponding latitudes on the western side of the Atlantic are frozen. The Bear Island area, well into the Arctic Circle north of Norway, supports a great winter fishery for cod and is the same latitude as the north of Baffin Island; yet the flow through the Faroe-Shetland Channel is only one-fifteenth of the Gulf Stream. The St. Lawrence is about the same latitude as the Scilly Islands; west Iceland is ice-free but only 200 miles across the Denmark Strait is frozen Greenland. Why does the

Gulf Stream work its way eastwards right across the Atlantic instead of going due north? The answer is linked with the earth's motion, and currents in the Northern Hemisphere tend towards the right and in the Southern Hemisphere to the left; the oceanographers call this the 'Coriolis Force'. Thus in the northern hemisphere the north-going warm currents will tend further and further east and the south-going cold current further west.

These currents are mentioned in this chapter on plankton because they are responsible for carrying the plankton and they also provide the environmental conditions that enable some species to thrive and prevent others from doing so. Other currents of importance in plankton distribution along the Atlantic coasts of northern Europe are the low salinity outflow from the Baltic, and the mixed sub-arctic current east of Iceland and north of Faroe continuing towards the Norwegian Sea north and west of the warm water. There is a complex but, in general, anti-clockwise circulation in the southern North Sea.

Strangely enough the British area is also affected by outflow from the Mediterranean, which spreads out into the Atlantic at about 1,000 metres depth west of Gibraltar. Some of this goes northwards to the Biscayan area, to the English Channel and Celtic Sea, and west of Ireland. When it is particularly strong its presence can be detected, much diluted, at the edge of the continental shelf west of Scotland and even on occasion as far as the North Sea and in the vicinity of southern Iceland. The part played by plankton in the detection of these currents is dealt with in Chapter 11; here it is only necessary to emphasize that they are responsible for so much of the geographical distribution of plankton.

The ocean currents are, of course, very slow-moving. The sun maintains the warmth of the tropical surface waters, and also in the summer warms the surface layers of the temperate waters, which brings about a stability of the water mass with little or no mixing between the warm and cold layers. The junction may be very sharp indeed, and is then called a 'thermocline'. To the phytoplankton this stability means that there is little replenishment of nutrients in the illuminated surface waters where the plants utilize them until there is a scarcity of plant food; little plant-growth means a scarcity of food for the zooplankton so that plankton is poor, volume for volume, in the warm water. In the tropics this condition continues throughout the year (Fig. 29), although the number of different species is great. In temperate waters there is a sharp rise in the phytoplankton in the early spring as soon as there is sufficient warmth to stabilize the surface water. This stabilization prevents the plants from being carried by convection currents beyond the limit of light penetration so that the start of their growth will depend on a relationship between light penetration and turbulence. The

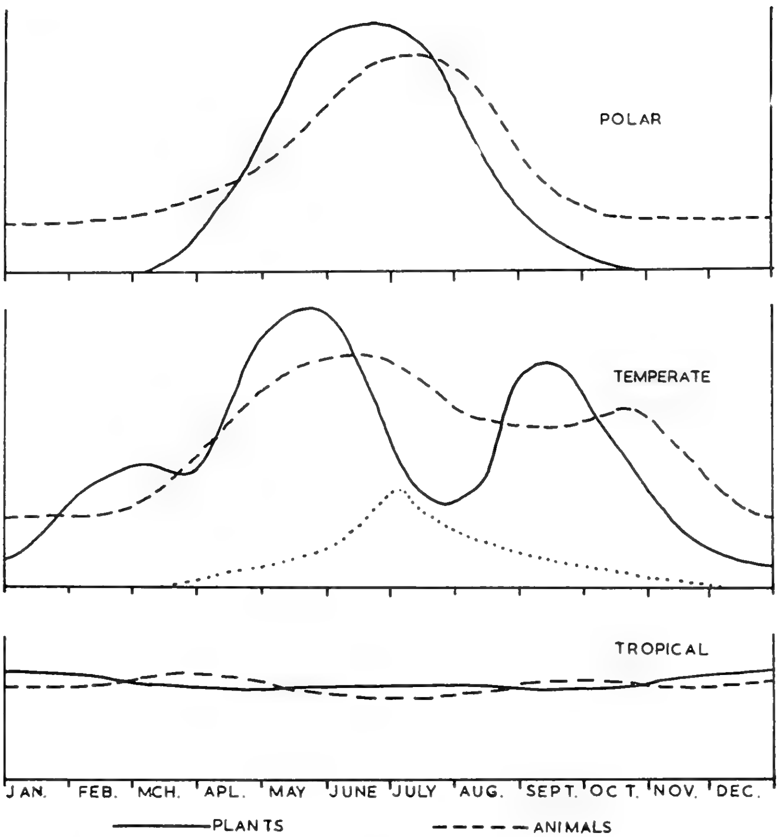


FIG. 29. The seasonal variations of plant and animal plankton in polar, temperate and tropical zones. Note that the increase in plants takes place first, when food is available the animals increase and graze down the plants. The dotted line in the temperate zone represents the abundance of dinoflagellates (see pp. 37–38).

shallower the water the earlier the growth will be because the light reaches all the way to the bottom and water movement cannot carry the plants away from it. We find the onset as early as February or March in coastal estuaries etc., March or April in the North Sea and as late as June in the open ocean.

The spring plant growth in shelf water continues until the winter accumulation of nutrients is diminished and the plant numbers are then much reduced because they are grazed by the herbivorous zooplankton. There is always some replacement of nutrients from the metabolic products of the animals feeding on the plants and from the disintegration of dead plants and animals, enough to maintain a reduced summer population. In the autumn while there is sufficient light left, and the thermocline is less intense because of surface cooling and wind turbulence, a secondary outburst will occur as the surface water is replenished with nutrient rich water from below. The amount will depend on the varying factors, for instance, a short turbulence at just the right time will enrich the surface waters without too much interference, but a continuous autumn turbulence will distribute too many of the plants into waters too deep and dark to make use of the nutrients. This of course happens in the winter when there is a complete mixing of the waters.

In polar seas the stabilizing effect of a thermocline does not exist to the same extent. There we have a six month period of light and growth and a six month period of darkness and no plant growth. In spite of this six months of darkness, plankton is richer in polar waters than in the tropics due partly to the continuous supply of nutrients for the plants in the continuous light of summer and partly because the organisms in the plankton tend to have a longer individual life span in the cold water. This is due to a slower metabolic rate, and they take longer to use the same amount of food. Under the ice of the poles, of course, plankton is reduced but is not absent any more than it is in deep water.

Why are the deeper waters rich in nutrients? Only in the light zone does the utilization of dissolved nutrients take place. Feeding on the plants in the light zone are the herbivorous animals; these migrate up and down in a night and day movement (p. 155) and they in turn form the food of the carnivores, fed on by other carnivores deeper and deeper in the water. During life all these animals release their waste products into the sea and on death these organisms, plant and animal, gradually sink so that regeneration of nutrients always tends to be in the deeper water. Any regeneration that occurs in the light zone is usually used up on the spot.

The major plankton distribution is thus largely based on temperature, but it is locally upset by other factors, especially those that cause upwelling of deep water into the productive light zone. For example, the almost constant trade winds off the coast of Peru are offshore winds which blow the surface waters away from the land with the result that the deep water must upwell to replace it. Here, then, we have light, warmth and nutrients and one of the richest areas of production of plankton in the world. Millions of small plants via the zooplankton feed small pelagic fish, millions of birds harvest some $2\frac{1}{2}$ million tons of these fish each year, reckoned to be about 10 per cent of the total catch of the world's fisheries, and their droppings on the land form the rich guano deposits. There is now a fishery for these small fish, mostly anchovies, which are used for fish meal, and this has rapidly increased in recent years. In 1956, 27,791 tons of meal were exported, but in 1959 this had risen to 200,000 tons, and to produce this figure a million tons of anchovies were landed by some 500 purse seine vessels manned by 5,000 men. And yet if a trick of fate changes the wind for a short time the cycle stops and there is catastrophe for all concerned, known as El Niño, until conditions return to normal again. A similar but perhaps less spectacular situation is found off the west coast of South Africa.

In our northern hemisphere an important cause of upwelling is the impact of currents against the continental shelves, and of course the breakdown of the thermocline in the colder regions. A chart of the distribution of plankton in the North Atlantic, taken from the book by Russell and Yonge, is given in Fig. 30.

The seasonal distribution of phytoplankton in temperate waters, following the stability of the water, has been mentioned (p. 110). One of the first diatoms to bloom in early spring in coastal waters is *Skeletonema* followed by *Thalassiosira* (Frontispiece; 7 and 4) which blooms further offshore. These two species alone usually form about 90 per cent of the spring plankton in the shelf waters of the north temperate Atlantic. Later a more mixed flora is found, depending a good deal on the amount of admixture of oceanic water. The autumn dominants are usually species of the needle-shaped *Rhizosolenia*, and when these are very abundant they cause a distinctive smell which the fisherman call 'baccy juice', and water so affected has an adverse effect on herring fishing (p. 133).

This richer plant growth in the shelf water compared with the open ocean results in a marked difference in colour easily distinguishable from a ship. Shelf water, particularly in spring, has a distinctly green appearance, but oceanic water with its paucity of surface phytoplankton is blue, and crystal clear. The blue Mediterranean is famous, its blue being derived from the extreme clarity of the water and the lack of plankton due to the warmth of the surface waters, and the consequent lack of nutrients there.

The spring outburst of plant growth is the new season's food supply and leads to a corresponding but slightly delayed increase in the zooplankton as it starts its multiplication. At this season many of the truly planktonic species reproduce, and there is a spate of spring and summer planktonic larvae, from the bottom-living and attached species as well as from the plankton itself. Most of the species that reproduce once a year do so in spring; less do so in summer although there is a group that utilize the more chancy autumn outburst. Others will reproduce at any time or fairly continuously throughout the summer six months. Survival depends on food; very few young animals appear in the plankton during the winter, and those are either carnivorous from the start or detritus feeders—but more of the food cycle in the next chapter.

The distribution of the planktonic stages of bottom-living and attached species is thus closely related to the current systems, and—need so obvious a factor be stated?—on where the adults are living. The spring plankton in water bathing a rocky coast will thus be different from that in a sandy area,

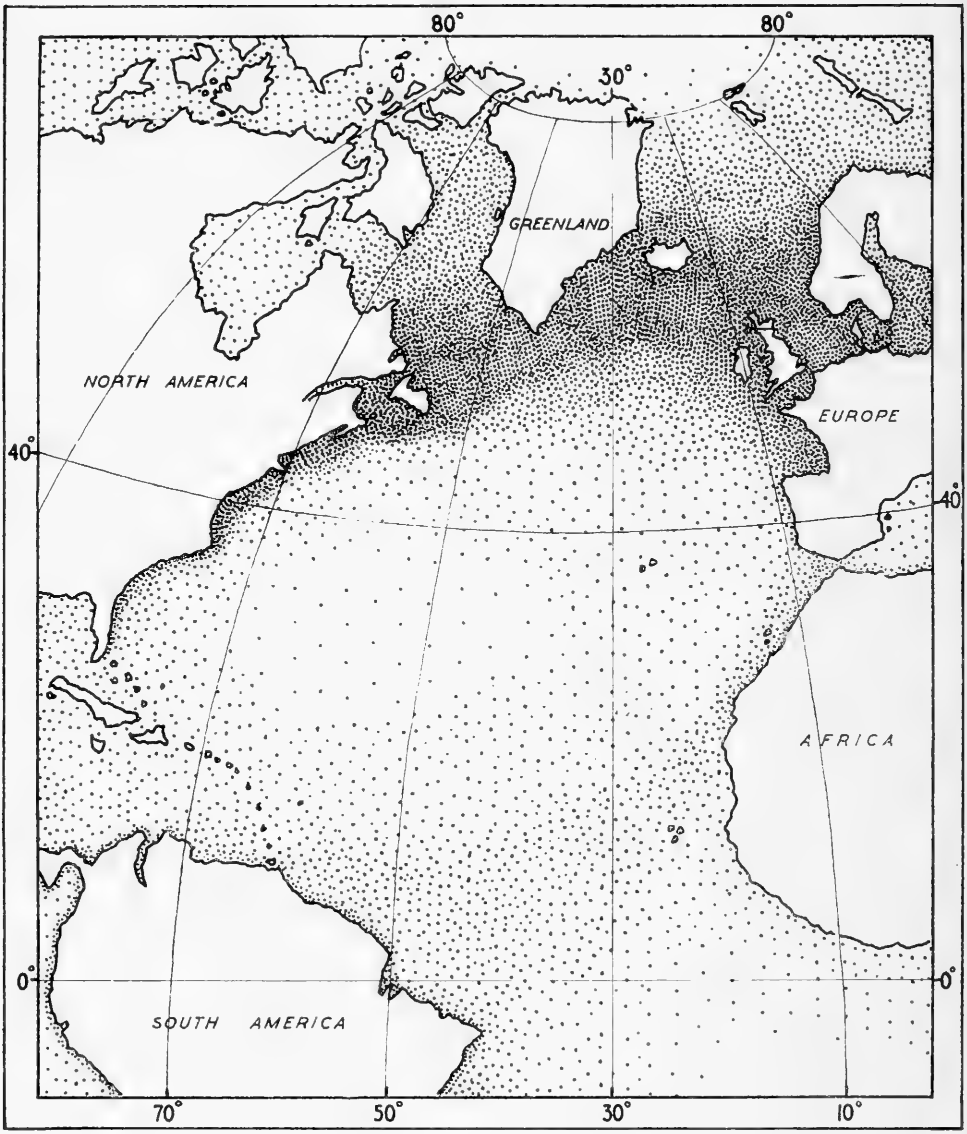


Fig. 30. The general abundance of plankton in the North Atlantic. After Russell and Yonge.

and shallow water plankton different from that over deep water. A buoy marking a channel, if placed in the spring of the year, will provide a settlement area for the spring larvae of mussels, and have a luxuriant crop of small mussels a year later, and quite big ones in two years' time. If it is not placed until the end of June it will be too late and get no mussels until the following spring and after two years will only have the equivalent mussel crop of the earlier buoy after one year.

It is, too, this dispersal of free living planktonic larvae in the sea that is responsible for ships' fouling, an expensive nuisance in time and money (Plate XXXIII). Increased drag means slower speeds and increased fuel costs, and delays are necessary for dry docking and scraping. Special anti-fouling paints have to be used—a double expense as these paints tend to cause corrosion if applied directly to the hull of a ship and a coat of normal paint has to be applied first. Anti-fouling paints usually contain copper, as red cuprous oxide, and this is why most ships' hulls are painted red below the water line. But whatever treatment is used, new methods of cathodic protection, paint or scraping, it is expensive and the cause of the expense lies in the plankton.

The severity of fouling depends on a number of factors including the ships' routine movements. Sudden changes of salinity on passing between fresh water and the sea kill off some species; others are strongly resistant to a quick change but cannot feed in fresh water and so die if the ship stays in river water for considerable periods. Scouring action in rivers where there is a strong tide carrying sand has a sandblasting effect if sufficiently prolonged. Ships normally travelling at a good speed at sea between river berths are less severely affected than those which have periods of immobility in salt water harbours. Ships' routine movements make a distinct difference to the type of fouling as well as its severity. For example, ships that spend months in warm waters get a different fauna from those that stay in the higher latitudes. It depends on where the ship happens to be when the larvae of the fouling organisms are in the planktonic stage and whether her movements take her to places where the conditions are suitable for their growth and survival.

To illustrate this point the hulls of two ships being scraped in a dry dock at Liverpool can be compared. Both ships spent their whole time in the Liverpool area; one was a tug which spent much of its time in and out of the docks and in the Mersey estuary, the other was a hopper that spent most of its time within the extensive Liverpool dock area, rarely being taken into the river. The hull of the hopper was luxuriantly coated with masses of large sea squirts, animals which feed by filtering small planktonic organisms from the water, but the tug had no sea squirts at all. In the quiet waters of the docks the worst of the mud and silt tends to settle, and the sea squirts lived on the rich micro-fauna associated with the dock water, which is essentially the same as that outside. In the Mersey estuary, however, the mud is constantly being churned up by strong tidal currents and chokes the filtering mechanism of any squirts that try to grow on the tug.

Fouling not only occurs on ships' bottoms, piers and the like, but inside pipes. Here, indeed, some of the worst fouling occurs as conditions are usually ideal. The pipes, particularly the stationary pipes to shore installations, are usually handling the same kind of water, and the water in which the larvae lived is also right for the adults. The constant stream of water into the pipe brings a continued supply of oxygen and food. Mussels and other fouling organisms grow bigger and so reduce the effective diameter of the pipe until it is eventually blocked (Plate XXXIII). At times a mass of mussels may break away and be carried along the pipe to jam valves or choke the smaller subsidiary pipes. This is especially liable if the current is suddenly increased, e.g. during a fire, and the blockage then occurs when the water is most wanted. If the mussels are killed by poisoning, the dead shells remain and the trouble is not relieved, and the only solution is the expensive dismantling of the pipes. The settlement cannot be prevented by filtering off the planktonic larvae as these are too small to be retained by any filter that will allow a reasonable water-flow to pass. The only preventative is the constant addition of a poison such as chlorine to the pipe for the whole period of the planktonic stage, and as different species breed at different seasons this is, in effect, the whole year.

To return to the main subject of this chapter—we find that temperature is not only an important factor in seasonal distribution but it is also responsible for determining the limits of the geographical distribution of many species. Just as on the land there are some cold-living species, but many more that need warmth, there are planktonic species confined to tropical and subtropical seas. They include many exotic species that are a real joy to the naturalist, but to the fish or other animals looking for food on the whole less of a joy than are the less bizarre species of the temperate and colder waters. If the cold-water lovers can withstand life in the cold, dark waters of the deep oceans they are found there also, and are then usually found in the upper layers of water in both the Arctic and the Antarctic. If they cannot, then they are usually confined to either one pole or the other, though no doubt they could live at either given the chance to get there in sufficient numbers to start a successful reproduction.

Then there are other species whose habitat is confined to the depths, and here it is not a temperature-controlled factor as these species are not found in the surface polar regions. They form an important part of the world's total plankton as 84 per cent of the sea area is deeper than 2,000 metres—indeed

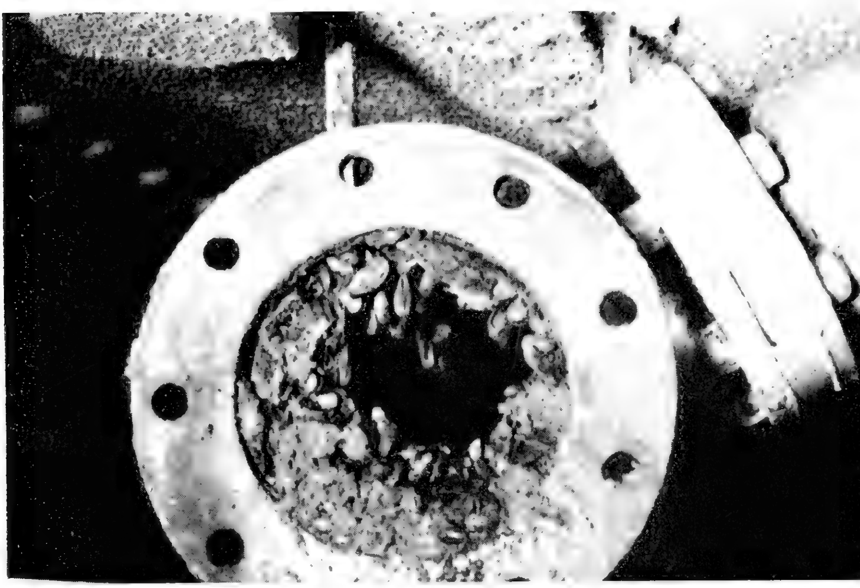


Plate XXXIII.

(*Top*) Fouling, chiefly sea squirts, *Ciona intestinalis,* on H.M.S. *Leviathan.*
(*Bottom*) A ship's fire main choked with mussels and entrapped mud.

Photographs Crown Copyright—reproduced by permission from the *Journal of the R.N. Scientific Service* about 75 per cent is between 2,000 and 6,000 metres. Pressures in deep water are extremely high, increasing by about one atmosphere in every 10 metres, so that the pressure at 1,000 metres is 1,470 lb per square inch, or 100 atmospheres. Yet depth itself is only partially a controlling factor as organisms living under these pressures have the same internal pressure as outside, so that there is no sensation of pressure there any more than we feel the air pressure of 15 lb per square inch. It is sudden changes of pressure that are troublesome and only severely so if there is an air bladder as there is in some fish (and of course in divers!). Water is so little compressible that delicate animals can be brought up from the bottom quite quickly with little or no apparent damage, and will swim about merrily in a tank. Gases are very compressible. This means that a small swim bladder of air, say 100 cubic millimetres, at 500 metres depth, will try to expand to 850 cubic millimetres at only 50 metres depth, and 5,100 cubic millimetres at the surface. A fish with a swim bladder wishing to change its depth must do so slowly allowing time for the expanded gas to be absorbed, or additional gas produced for a downward journey. If it climbs too quickly, or is forced to do so when caught in a net, the bladder expands and as it is a very tough elastic structure it forces the stomach and other internal organs out through the mouth causing the death of the fish even if the swim bladder does not reach bursting point.

The most important factor, associated with depth, that controls distribution is light. Marine animals in the plankton are usually extremely sensitive to light and vary their depth to give them the most suitable amount of light. This results in an up and down movement by night and day that is more fully discussed in Chapter 12 on behaviour. Plankton adapted to everlasting twilight or eternal dark in the depths can be killed on capture merely by the unaccustomed brightness at the surface. Watching the stars at night one can readily see how the fainter stars become visible only as the last remnants of twilight fade and the night gets really dark. Stars of the first magnitude can be seen soon after dusk, those of the third magnitude when it seems quite dark, yet only when it is really dark does one see the fourth magnitude stars. Experiments have shown that some planktonic worms, for example, are sufficiently sensitive to small light intensities that their reactions change very markedly in intensities that correspond to the difference that makes fourth magnitude stars visible to us instead of only the third.

The depth that light will penetrate into the sea depends on the angle of the sun and the clarity of the water. An overhead sun will penetrate deeper than when it is lower in the sky, and the clarity of the water is associated with the amount of mud in inshore waters and the amount of plankton. Light therefore penetrates much deeper in the blue ocean water than in the green shelf water. Even in the clear tropical waters of the Mariana Trench the divers in the bathyscaphe found it to be a dark twilight at 500 feet and quite dark at 1,000 feet.

The distribution of plankton according to depth can be investigated by means of closing nets (p. 18) that sample the plankton only within certain limits, and such samples can be examined in detail in the laboratory. Another and recent method which has given valuable results is by viewing the plankton from the window of a bathyscaphe. This method as yet can give no samples for analysis so that the value of the observations will depend on the experience of the observer. To get the best out of such an expensive dive it should be manned by the scientist available with the most experience in the field to be explored. Diving off Toulon to a depth of 2,100 metres, Professor Bernard of Algiers noted the sequence of the abundance of plankton. The average number of organisms he could see per second of descent is given in the table.

0–200	metres	poor	4·7
200–650	metres	rich	47
650–900	metres	very rich	225
900–1900	metres	poor	4·7
1900–bottom		moderate	21·5

This was in the intensely blue water of the Mediterranean, and as explained on page 113 the surface plankton here is very sparse indeed compared with the shelf water surrounding the British Isles and similar places. The increase of life in the intermediate layers is here in part associated with the distribution of coccolithophores, small plants that thrive in reduced light intensities (p. 41). Note, too the increase close to the bottom which will be explained on page 125.

Some planktonic animals are confined within certain salinity tolerances, irrespective of temperature or depth. Much more subtle are those distributions which are dependent upon some vitamin, hormone or other microchemical constituent. Although often subtle, and as yet even quite inexplicable, these delicate niceties of distribution can be extremely important; so often the plankton animals concerned are the food of fish etc. Some of these subtle factors are associated with the different water masses and are widespread in their effect; others are extremely local and result in patchiness in the plankton.

We are used to patchiness in the plant and animal distribution on the land, vaguely associating it with man's interference. Indeed often it is so caused, but not all clumps of trees have been deliberately planted nor are all nettle patches associated with man's habitation. Midges gather in clusters under a tree and are absent a yard away. Plankton is patchy in just the same way, and sometimes this may be due to a congregation of species, a kind of shoal as in the example of the midges. Often we can find no satisfactory explanation; it may be caused by patchy distribution of micro-chemicals, it may be just a random chance. Whatever the cause, the patchiness is very real and makes it difficult to assess plankton with any quantitative accuracy. Two nets towed side by side may easily differ in their catch by as much as three times; samples taken one after the other, in as near as possible the same water, are just as different. To smooth out these differences a long tow helps, or one can take an average of several replicate samples. One can get fairly detailed pictures of the plankton content of a small body of water, the smaller the more detailed, but only rough estimations of a large area. It is impracticable to sample in detail the plankton of the North Atlantic Ocean, or even of the North Sea, but as long as the investigator is aware of the probable limits of error in his samples he can make reasonable assumptions.

This chapter has tried to show how distributions vary and some of the causes of these variations. Some are physical, chemical or other external factors which affect the well-being of the organisms themselves, or perhaps their predators or their food. Food is *the* basic necessity, for without it the populations cannot exist, no matter how favourable their physical environment. We thus have to be careful to distinguish distribution due to the organisms' own constitution, and those due to the limited tolerances of their favourite food supply. This difference is important in the plankton itself, but it is much more obvious in fish and swimming creatures that can deliberately change their location in the search for food.

CHAPTER 9

The food chain in the sea

FOOD IS indeed so important that it must have a chapter to itself although it has so often necessarily been mentioned in the preceding chapters. The distribution of plankton is dependent on its food supply, and the structure of the various species is closely related to the type of food they eat, the method of feeding and the way they find their food. The reader will already have grasped the main principles of the food chain in the sea, but these need to be reiterated and elaborated: they are shown in Fig. 31, where the complicated story is reduced to very simple terms.

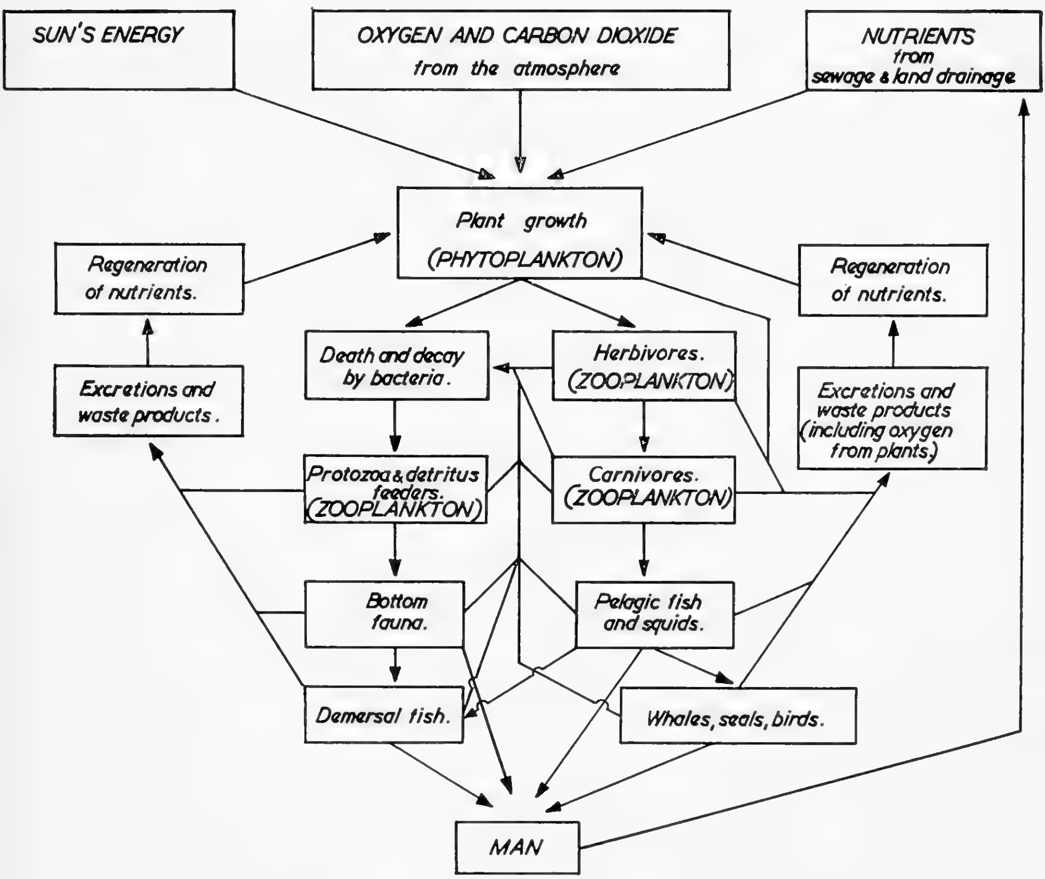


FIG. 31. Diagram of the most important elements in the food cycle in the sea.

The basic sources in the sea, just as on the land, are the green plants. They alone can combine the inorganic nutrients—the nitrates, phosphates etc.—with the dissolved carbon dioxide to form organic compounds that can be used as animal food—the carbohydrates, proteins, oils and fats. To do this they use the sun's energy and they need the green pigment chlorophyll to act as a catalyst—a chemical the very nature of which enables the combination to occur and to go on occurring without itself changing. The food of the green plant is therefore the dissolved salts and carbon dioxide, and plants can thrive only in the light and as long as these nutrients last or are replenished. This replenishment will depend on the regeneration of nutrients from the waste products of animals, and from the decay of plant and animal tissue by the help of bacteria. The distribution of the nutrients into the light zone is a feature of the current systems, both in horizontal transport and in the vertical turbulence of convection currents and upwelling.

In addition to these main nutrients the plants require minute amounts of metabolites—growth-promoting substances, vitamins and the like—some of which are manufactured only by bacteria, others by the plants themselves. Free bacteria in the sea are not very abundant but they do live in close association with any solid surfaces including, of course, the plants and animals. It is this necessity for metabolites that makes it difficult to grow things in artificial sea water, no matter how carefully prepared, unless some 'soil extract' or other complex witch's brew is added. The bacteria are thus a very important link in the food chain. It should be emphasized, of course, that these bacteria are not connected with any disease and that the number of beneficial bacteria in the world in general, and the sea in particular, far exceeds the harmful ones.

To remain in the light zone the plants must be attached at the coast in extremely shallow water, or else float; and as the coastal area is so limited compared with the total surface of the sea, it is the floating plants that really matter in the marine food chain. Some types of these plants have been described in Chapter 3, the most important being the very minute nanoplankton, the diatoms and the dinoflagellates. With the onset of stable conditions in the spring (p. 110) the nanoplankton and the diatoms start to multiply rapidly by simple division, and as a generation is measured in minutes and hours it does not take long to establish a population. The wag who said that political troubles are the only things that can be multiplied by division was not a biologist!

The dinoflagellates follow later. The process of rapid reproduction, reaching a peak and then dying down, is called 'blooming' or 'flowering'. There is a succession, not only of these types but of the different species of diatoms. This is only in part due to seasonal variation in the current systems and the environmental condition associated with them. It is also due to the individual metabolic requirements of the species themselves. As yet we know very little about their intimate chemistry, we partly know, and partly suspect that, as each individual species grows, absorbing nutrients, it secretes minute amounts of organic compounds into the water around it, to be acted on by the bacteria. As these differ slightly the resultant bacterial effect is also slightly different and the chemistry of the sea is then more suited to another species. The first dies down having reached some limiting factor in its requirements to be replaced by a second, and so on. This starts a biological history of the water, to add complexity to its physical history, and here the disintegration of the nanoplankton may be as important as its growth and survival. The spring and early summer diatoms are, in general, followed by the dinoflagellates as these can exist in a lower nutrient concentration, in part due to an ability to use dissolved or particulate organic matter as well as inorganic nutrients and sunlight (pp. 38, 39 and Fig. 29). Again the species of dinoflagellate to thrive will be dependent on the biological history of the water. Sometimes there are mixtures but very often one species outnumbers all the others put together and is dominant over perhaps a hundred square miles or more, whilst an adjoining water mass will be dominated by a different species.

On these plants feed the herbivorous animals which form a large proportion of the general plankton and an even greater proportion of the planktonic larvae of the bottom-living species. But not all are capable of feeding on any species of plant, so that the biological history of the water which has helped to determine the plant species is responsible in turn for the type of animals that thrive. Generally speaking only the very smallest of the animals, especially the small invertebrate larvae, feed entirely on the nanoplankton, the others are unable to filter off such minute organisms in sufficient quantity, an exception being *Oikopleura* (Plate XIX). Others might take some nanoplankton but it would be so rapidly digested that it would be difficult to recognize in the stomach contents; the actual structure of the filtering mechanisms suggests that many do not do so to any extent. Animals feeding on diatoms and dinoflagellates are limited in their choice by the size and shape of the food and whether they ingest the food whole, or break it up first. Copepod nauplii, for example (p. 68), and even the dinoflagellate *Noctiluca* (Plate IX), ingest their food whole, and complete diatoms such as *Skeletonema* and *Thalassiosira*, and dinoflagellates such as *Peridinium* and *Dinophysis* can be seen inside them; but the spiny species of *Chaetoceros*, the long *Rhizosolenia* and the horny *Ceratium* are not often taken. This applies also to the very smallest stages of the young fish larvae.

On the other hand the adult herbivorous copepods can usually break up the larger diatoms, as well as swallow the more convenient ones whole. Copepods are the most important of the herbivorous zooplankton, although some copepods are carnivores and others are detritus feeders. Other notable herbivores are the salps and doliolids (pp. 78, 80 and Fig. 23), which pump water through a perforated gill for breathing and at the same time filter off the phytoplankton as food.

The next link in the food chain is the feeding of carnivorous species on the herbivores or on other carnivores. When thinking of land animals the name carnivore conjures up the fierce lions, tigers, jaguars and the other big cats. In the plankton so often it is the apparently harmless creatures that are the most voracious carnivores, the worst offenders being the small jellyfish and sea gooseberries. These have no powerful claws or teeth; the jellies and the siphonophores (Figs. 13–17) quietly paralyse their prey with stinging cells and the gooseberries catch theirs by entanglement in sticky tentacles (p 57). However there are also the carnivores that actively chase their prey and are well equipped with powerful seizing jaws—e.g. the arrow-worms, p. 59. Others grab their food in their mouths, e.g. young fish and adult pelagic fish such as herring, or they catch their food with modified legs or other appendages—e.g. copepods and other carnivorous crustacea, and indeed these legs may be provided with pincers as in the larval lobsters, crabs, some shrimps and amphipods.

Not all the plants are eaten by herbivores, and not all the animals by carnivores, many simply die a natural death due to lack of food or intolerable conditions of temperature, salinity, depth or other factors. These are disintegrated by bacteria, and the products of disintegration including the bacteria themselves, then form the food of innumerable filter and detritus feeders in the plankton. Many invertebrate larvae in the plankton feed this way and also copepods, some euphausids and amphipods, feeding more or less indiscriminately on whatever particles they filter, digesting what they can and ejecting the remainder. Even the faecal pellets contain something of value to some other creatures and are included in the detritus they feed on. When the plant food is particularly abundant the herbivores feed to excess and this has the two-fold effect of grazing down the plants, thus slowing down their use of nutrients and extending the growing season; also, as the animals cannot digest all they feed on, there is a great increase of food value in the faecal pellets. These, being heavier than the water, sink and help to provide food more quickly and abundantly in the sub-surface and deeper layers.

There are hosts of bottom-dwellers and attached animals that feed on detritus, including most of the bivalve molluscs—the cockles and mussels and their kin—the barnacles, and the worms. These, too, take their place in this food chain as the main food of the demersal fish and so in the economy of the sea. There are even heterotrophic diatoms, flagellates, bacteria and protozoa on the sea floor which use what is left by the coarser filter feeders.

Food originally produced at the surface is used over and over again as one animal feeds on another, or on its waste products. Creatures living below the surface are thus not starved, though they tend to get scarcer in deeper water until quite near the bottom. Here, there is a further supply of food available as the bottom acts as a physical barrier to further sinking, and so concentrates what is left to be used by detritus feeders and those that prey on them.

All the organisms in the sea, alive, dead or disintegrated, form the food of something else, and any organic material not re-absorbed by animals is regenerated by bacteria into the basic inorganic nutrients which will eventually nourish new plants. Nothing is useless in this great cycle of continuously interdependent events. The only losses from the sea are those deliberately removed as fish etc by man or by birds. These losses in actual protein add up each year to an enormous figure (Chapter 10), but are compensated by the return to the sea of sewage, detritus and nutrients, and the drainage of fertilizers from of the land. Most the droppings of the sea birds, and their bodies after death, fall back into the sea. The sea is, in fact, probably becoming rather richer than poorer every year in its total productive capacity, helped also by the increase in atmospheric carbon dioxide due to man's use of fuel in industry.

CHAPTER 10

Plankton and its relationship with the fisheries

It will have been realized, from the preceding chapter in particular, that the food supply of the fish themselves is fundamentally the phytoplankton, so that the importance of plankton to the fisheries is indeed basic. This is true whether the fish are plankton feeders like the herring, bottom feeders like plaice, or really deep-sea fish like halibut. The relationship has been nicely depicted by Professor Hardy, and his figure is reproduced here as Fig. 32.

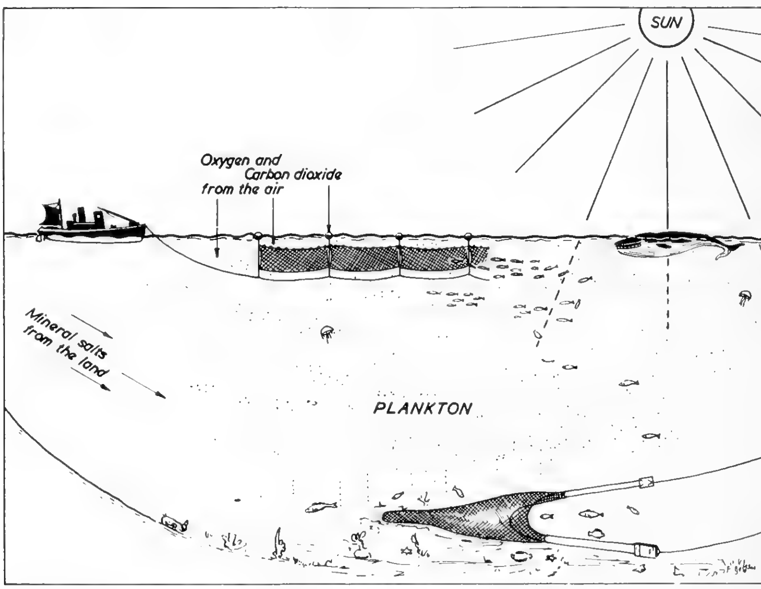


Fig. 32. A diagrammatic sketch illustrating the general economy of the sea. From Hardy.

It has, too, already been explained that the richness of plankton production depends on the mixing of the waters so that nutrient-rich water from the deeper layers is brought to the surface layers where the plants can use it. The intimate chemical and biological factors in the history of the water have their importance in the succession of the various plankton species with their different food values or availability as food. In the higher latitudes plankton is richer in food value than in the tropics (Fig. 30). It is thus no accident that the richest fisheries of the world are related to the areas of richest plankton production and are on the continental shelves, where there is good feeding and depths which can be economically fished.

There are a number of aspects of this relationship that are worth further

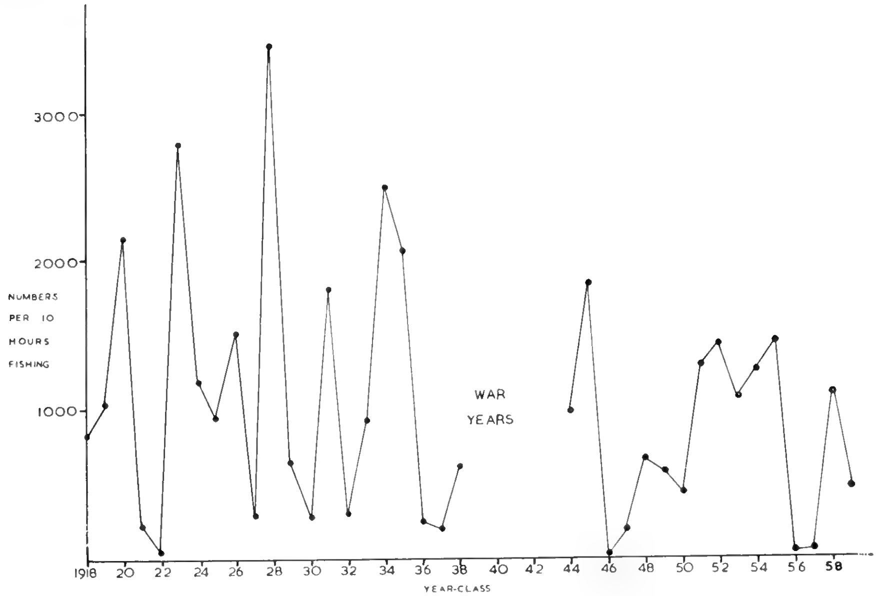


FIG. 33. Fluctuations in year class strength of haddock in the northern North Sea. Haddock spawn in February–March each year, and by the autumn of the following year the new recruits to the stocks are large enough to be retained in the commercial fishing nets.

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consideration and it is convenient to divide this chapter into three major sections; one dealing with the larval fish which are themselves planktonic, and the others with the fish as adults, the plankton feeders and those which live on or near the sea floor.

Starting with the egg stage, we have already seen (p. 97) that the eggs of almost all the commercial fish, except herring, float in the plankton, and that the female fish produce vast numbers of eggs. It was mentioned that a haddock, for example, spawns over $\frac{1}{2}$ million eggs, and she may spawn for several successive years before being caught. Supposing she lays 4 million eggs, only two of these, a male and a female, need reach maturity to maintain the population at the present level. The rest, one way or another, form the food of other creatures, including man. This is a mortality of 99·99995 per cent! Should the mortality, for some reason or other, be changed to 99·9995 per cent the difference would seem so slight as to be almost ineffectual, but in fact the survival rate is ten times as great. If this were kept up for several years haddock would be tremendously abundant. Natural fluctuations greater than this do occur, as is shown in Fig. 33, but big increases can never be maintained because there would be insufficient food for all the extra haddock, and in turn there would be an increase in the number of predators to feed on them, which could result in very poor broods indeed.

The numbers of young recruited each year to the fisheries is thus not so much dependent on the number of eggs laid as on what happens to them afterwards. It is most unlikely that egg production could ever be too severely curtailed by overfishing: if fish were as scarce as that it would not be economical to catch them. No marine fish are therefore likely to become extinct through exploitation as actually occurred with the dodo and nearly with the bison.

How is the survival rate of the young fish affected by the plankton conditions? There are three main ways. First: the young fish after hatching feed in the plankton and there must be enough food of the right type available for them. Second: the eggs and the young fish are ideal food for a host of carnivores in the plankton, including other fish. Third: being part of the plankton they are drifted by the currents, perhaps to unsuitable areas for their later development. The chances of surviving all these hazards is indeed small.

Taking each of these in turn we can look at them more closely.

When the larvae hatch and first start to feed they are very small, only a few millimetres long and they cannot be expected to hunt far and wide for their food. Food must be available in plenty in the plankton and it must be of the right type. Small fish select their food but only within certain limits, some being less particular than others, and they feed largely on what is available. However, some organisms are too spiny or awkwardly shaped, some too big or too active to be caught, or of inadequate food value if not actually unpalatable, so that mere availability is not everything. Whilst some plant material may be taken in the very earliest stages, animal material is also necessary. The most favoured food is undoubtedly the early nauplius stages of copepods, which are feeding on the spring outburst of the plant growth and are most abundant then. It is therefore not surprising that cod roe is at its best in the fishmongers in late winter, for this is just before the eggs are spawned to develop and hatch when the wealth of spring food is available.

The larvae are planktonic for three months or so and during all this time they need planktonic food. Is it any wonder that *all* the millions of larvae cannot find food *all* the time and so there are large losses? In an ordinary year these losses amount to about 10 per cent per day, but they can be less or a lot greater. Conditions that are not conducive to the production of good food supplies are therefore partly responsible for poor brood survivals. These conditions have already been referred to in the preceding chapters but can be repeated very briefly. Insufficient mixing of the water-masses is one of the most important causes of failure as this means inadequate nutrients for the plant growth and so paucity of the right kind of animal plankton as food for the young fish.

Two arrow-worms are of special interest here as one, *Sagitta elegans*, is associated with mixed waters and the other, *Sagitta setosa* (Plate XXXVI), with unmixed water in the North Sea and English Channel. These associations will be more fully dealt with in the next chapter but here it is sufficient to note the relationship with the survival of fish larvae. Sometimes there is an incursion of western water, a mixed water, into the English Channel which pushes the local water farther east, and we can distinguish the two masses by the arrow-worms present. When *S. elegans* is present, i.e. with a greater inflow and mixture of western water, young fish are fairly abundant in the Plymouth area: when *S. setosa* is present and Channel water is unmixed the young fish are scarce. The same feature is also found in the northern North Sea where, again, *S. elegans* indicates the presence of the North Sea water mixed with (not replaced by) oceanic water entering from the north. Over a period of years the number of larvae of bottom-living fish found in the plankton associated with *S. elegans* always averaged more than if *S. elegans* were absent. These differences are, of course, nothing to do with the presence of the arrow-worms, but with the mixed conditions that *S. elegans* also needs. Just as too little inflow of new water to mix with the local water leads to poorer food supply so does too great an inflow which actually displaces the local water, at least until it has had time to mix.

The previous biological history of the water is in part responsible for the types of planktonic organisms that thrive and these may or may not be suitable as food. This is particularly important for those young fish which are very selective in their food, e.g. plaice and lemon sole which feed so much on *Oikopleura* (Plate XIX).

Another condition that reduces the available food supply is an abundant population of salps (Fig. 23) which filter off the plants extremely effectively. An incursion of *Salpa fusiformis*, such as that which came into the northern North Sea in 1958 and also flooded the area south-west and west of Iceland, can virtually deprive hundreds and hundreds of square miles of water of its phytoplankton, thus leaving too little food for the animals which in turn would have been eaten by the young fish.

The second major hazard for the young fish larvae is being eaten by predators. The jellyfish, sea gooseberries and arrow-worms are the worst offenders in the plankton. The method of feeding of the jellies and sea gooseberries has already been described (pp. 48, 57). When they swarm they can have a very serious predatory effect and this is increased by the severe depletion of other animals that could be used by fish larvae as food. Swarms of *Pleurobrachia* in particular can be so dense that after a short time there is almost nothing else to be found. Other important predators of young fish are adult pelagic fish such as herring and mackerel. A point to remember here is that adult fish (as any trout fisherman will know) have a tendency to continue feeding on the same acceptable food while the supply lasts, ignoring other foods for the time being. This means that if larval fish are plentiful and adult fish are taking them they will tend to continue doing so, therefore the greater the numbers of young fish the greater the hazard.

The third major factor is the actual transport of the larvae by water movements. Some fish like a sandy bottom, others a stony or a rocky bottom, either because of their own likes and dislikes or because their favourite foods are associated with such a bottom. Some fish, e.g. plaice, need to be in very shallow sandy bays during their first year, and so their nursery grounds are very close inshore. Who has not paddled in a sandy pool left by the tide and not seen the tiny plaice, the size of a big-toe nail, scudding along on being disturbed? Even haddock, that as babies do not mind fairly deep water, cannot stand it too deep. It follows, then, that if currents carry the young fish to places where, when they go to the bottom, they cannot find a suitable habitat they will be doomed. Again, taking plaice as an example, the main spawning grounds of the southern North Sea are so sited that the normal currents there carry the young to the very suitable sandy shallows of the Dutch, German and Danish coasts. How many other species are usually so consistently lucky, especially in areas where currents are far from constant?

Taking all three major hazards, is it any wonder that survival rates are so low, so variable and so dependent on plankton? Recruits to the cod stocks in the area of the Bear Island fishery have been shown to vary with the abundance of *Calanus* there, in turn depending on the planktonic conditions and the amount of the north-flowing warm water. This is, of course, also correlated with the weather conditions—a point nicely illustrated recently in Norway, where it has been found that the cod stocks at the Lofoten fishery vary from year to year with an extraordinary similarity to the growth of the nearby pine trees, judged by the distance between the growth rings seen when the wood is cut. Recent Russian work has shown that when the northern sea gooseberry is abundant the rest of the plankton is poor and cod stocks are affected, but when *Beroë* (p. 58) is numerous this eats the sea gooseberries, plankton thrives and so do the young cod.

Turning now to the relationship between plankton and adult fish we can first consider the adult pelagic fish such as herring, mackerel, pilchard, sprat etc, which are plankton feeders. Here it is obvious again that the main relationship is a direct one of food supply, and it must be emphasized yet again that in their own turn these food organisms are dependent on others in the plankton right down to basic plant production.

The copepods, chiefly *Calanus* (Plate XVII), are responsible on the average for about 21 per cent of herring food but with a much higher percentage in summer. Although herring will take other foods when necessary they prefer *Calanus* if available in sufficient quantity. In the colder waters such as the Barents Sea, *Calanus* forms about 80 per cent of the total weight of all zooplankton species together. When *Calanus* feeds on the living diatoms etc. in the phytoplankton near the surface they are rather pale in colour, but if they feed largely on distintegrating material, as they must do in deeper water, they are red and very oily. The herring feeding on *Calanus* are correspondingly oily and if there is too much oil the herring can be too rich for proper curing. Hence *too* rich a food supply is not necessarily a good thing for the market. Herring when full of *Calanus* have what is called 'red gut' and as a rule are in excellent condition. If they feed on the small mollusc *Spiratella* with its black shell and strong smell they have 'black gut' and do not keep so well nor fetch so good a price on the market.

If *Calanus* is such an important part of herring food could one assume that herring would be more abundant where this kind of food is? If so would it then be possible to increase the catch by fishing only in areas where a plankton sample showed that *Calanus* was common? In 1932 this experiment was tried on the North Sea herring grounds. Fishermen co-operating in the experiments towed a 'Hardy' Plankton Indicator (Fig. 5) for a mile before shooting their nets and the plankton was analysed and associated with the resultant catch. By and large the experiment worked, not always but on the average, as shown in the table and in Fig. 34. For example, when *Calanus*

	In poorer *Calanus* water		In richer *Calanus* water	
	Calanus numbers	Herring (in crans)	*Calanus* numbers	Herring (in crans)
	1	0	120	36
	1	24	125	47
	20	20	165	2
	25	4¾	180	9½
	40	0	204	61
	42	4½	245	37½
	68	¾	280	63
	88	72	330	59½
	96	30	332	10¾
	101	1	480	19
	105	0	1,420	0
Totals	587	157	3,881	345¼
Averages	53	14¼	353	31½

was below the average of the sample the average catch was fourteen and a quarter crans; against thirty one and a half crans if *Calanus* was above average.

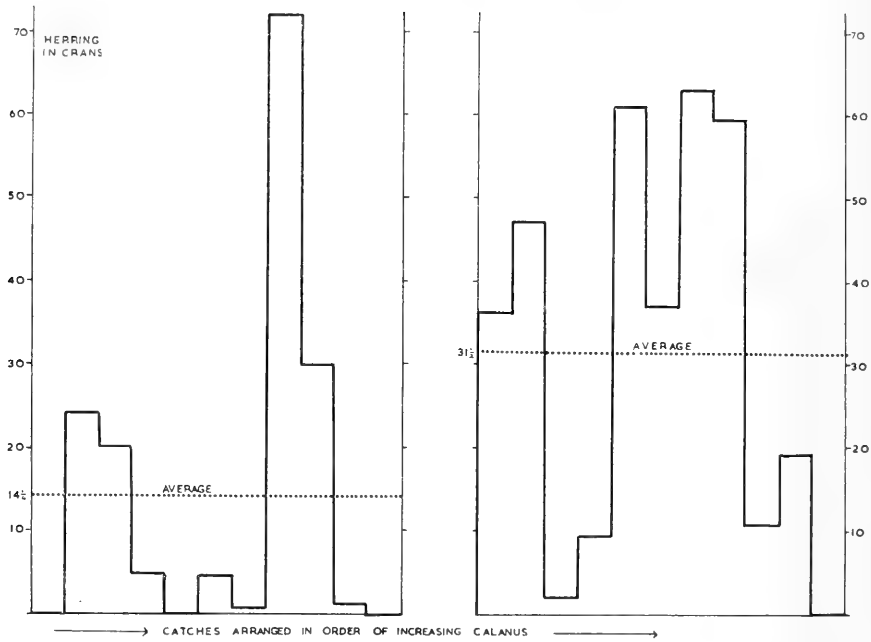


FIG. 34. Catches of herring compared with the number of *Calanus* taken at the same time and place by the 'Hardy' Plankton Indicator. The samples are arranged in order of increasing numbers of *Calanus*, and divided into two blocks of eleven samples each, to show the greater average catch of herring in the richer water. Adapted from Hardy.

It does not always work out that way, indeed the highest catch of the sample was in the lower *Calanus* group and no herring at all were caught with the sample of maximum *Calanus*. Why is this? There are several reasons.

A big shoal of herring will graze down the *Calanus* so that the shoal may be found where *Calanus* have been abundant, but before the herring have moved on to new feeding grounds. If food is abundant there may be plenty on the edge of the *Calanus* patch so that the richest areas are not reached. When herring are about to spawn they are then most concentrated and most easily caught, but they are then just not interested in food. The herring/*Calanus* relationship has yielded even better results in the Icelandic area. The method has fallen out of favour as a commercial venture since the introduction of the echo-sounder which can locate the actual shoals very accurately and independently of biological theories and practice.

Calanus is not, of course, the only food of herring and most other species of zooplankton are taken and young sandeels are particularly important as they average about 40 per cent of the total herring food. Incidentally, about 70 per cent of sandeel food is *Calanus*.

Herring are migratory fish, moving in shoals in complicated and not too well understood paths between feeding and spawning areas. These paths therefore vary according to the distribution of suitable hydrographic conditions and the abundance of food, so that in turn this has its effect on the disposition of the fishing. This effect is not only that herring search for food but also that they will avoid distasteful water. On page 113 reference was made to 'baccy juice' when the diatom *Rhizosolenia* is abundant and that herring avoid such patches. Avoidance of dense phytoplankton seems fairly characteristic even if we have no evidence of a distasteful effect. A rich patch of diatoms may occur just because there are too few herbivores to graze on them and there may be few herring there due simply to the lack of copepods etc. 'White water' due to the presence of coccolithophores (p. 42) is an indicator of the mixed conditions that are good for plankton production, so that 'white water' is considered a good omen for herring fishing. But not all 'white water' is due to coccolithophores, some is due to minute globules of herring oil making the water milky or even to the presence of brushed off scales. These would obviously indicate the presence of fish and perhaps the more direct relationships have helped to give rise to the suggestions about the other!

Plankton conditions can thus affect not only the food supply but the movement of herring, and so affect their availability to the fishermen independently of their actual numbers. Pilchard feed more directly on the phytoplankton than the other fish of the herring family and so have an even more direct dependence.

One of the biggest fish in the seas around the British coasts is the basking shark which reaches about 30 feet in length. Although it is a true shark it is not a ferocious fish and it feeds almost entirely on plankton. This it gets by cruising slowly along with the wide gape of its mouth open, rather like a plankton net, and the plankton is filtered off by a series of special combs of 'gill-rakers' attached to the gills. The food is mostly the rich oily *Calanus* and euphausids. Basking sharks may be seen cruising at the very surface on a calm warm sunny day with the dorsal fin out of the water (Plate XXXIV). They are not at all aggressive and only cause damage to fishing nets when they accidentally get entangled—can you blame them! A sudden swish of the huge tail can easily upset a rowing boat but this would only happen if the shark had been suddenly disturbed. Strangely enough they lose their gill rakers in the autumn and 'hibernate' on the sea bed until the new ones have grown in February.

Whales are not fish, of course, but they deserve a paragraph here. Whales are of two main types, the toothed whales like the sperm whale, and the whalebone or baleen whales which feed on plankton. The blue whale, the largest mammal that has ever existed and which may reach nearly 100 feet and weigh 120 tons, is a plankton feeder. Like the other baleen whales it

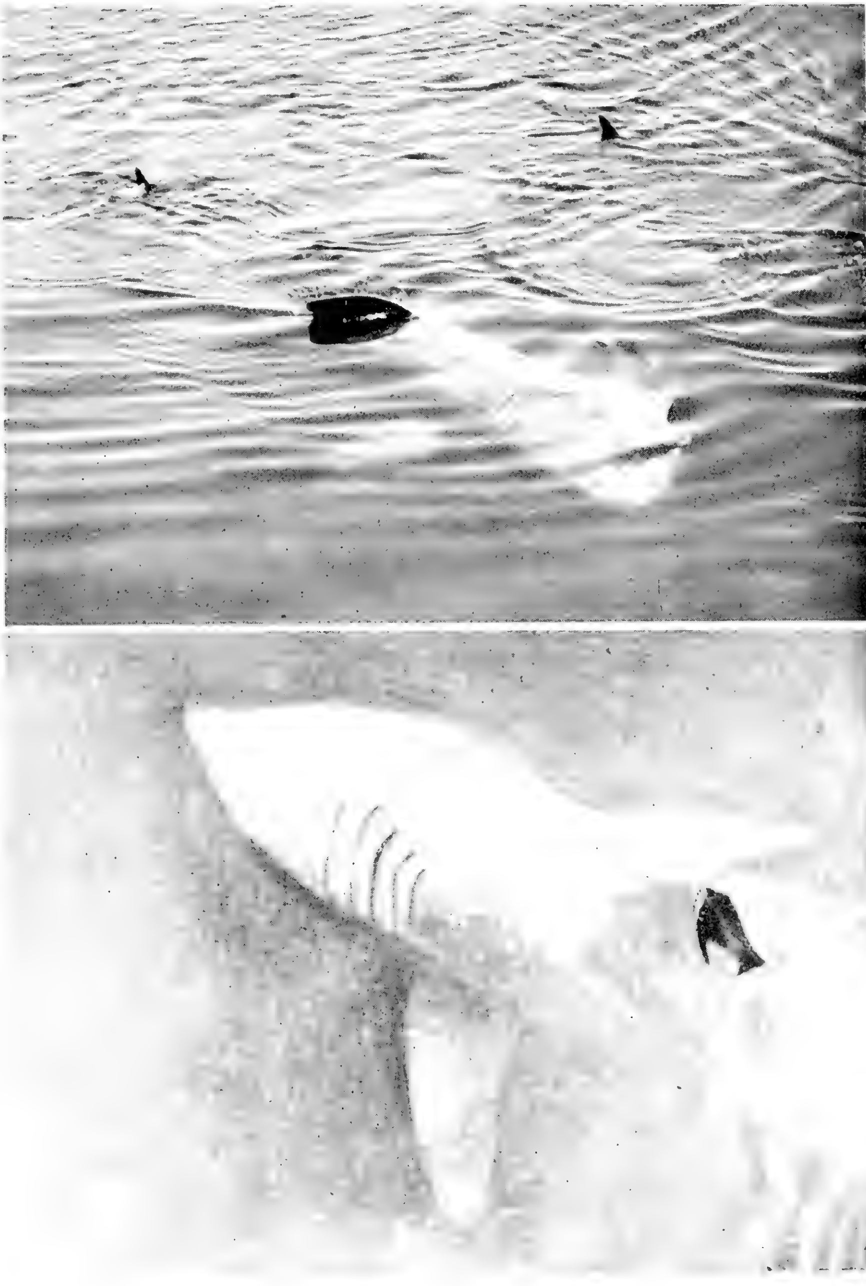


PLATE XXXIV. Basking sharks, taken from the bow of the research ship *Scotia* in the Firth of Clyde.

(*Top*) Approaching the shark. Its mouth is wide open filtering off the plankton—note the gill rakers in the mouth, the gill slits and the widespread pectoral fins. The tip of the snout is just touching the surface, and the dorsal fin and the upper part of the tail are above the surface. The tail of a second shark, swimming slowly parallel to the first is also seen.

(*Bottom*) Looking down from almost directly above the shark.

Photographs by James Fraser

filters the plankton with a sieve made of a series of brushes, which are the hairy fringes of the baleen plates (Plate XXXV). Its main area of feeding is in the Antarctic during the southern spring and summer where the planktonic krill (*Euphausia superba*) is abundant. A blue whale stomach may contain tons of euphausids. An idea of the richness of this food is obtained from its rate of growth. The calf is about 26 feet long and weighs 12 tons at birth after one year's gestation, and during six or seven months lactation its weight increases at about half a ton a week until it starts to feed for itself. After two years it may weigh 60 or 70 tons.

Although most of the larger whales are more or less universally distributed in the oceans, one of the more abundant in the northern areas and in part responsible for the whaling of these areas, is the sei whale. Here in the northern waters the main food is another euphausid, the 'northern krill' (*Meganyctiphanes norvegica*, Fig. 22; 5). The smaller toothed whales in this area are mostly fish feeders and not therefore the concern of this book. The harp seal and some sea birds too are keen on euphausids, notably the fulmar in the north and the short-tailed shearwater in Australia.

Adult fish living on the bottom are also dependent on the plankton, not so directly as the larvae and the pelagic fish, but nevertheless just as truly. We have already seen that the young stages of very many bottom-living animals—the food of the bottom-living fish—are planktonic. It is thus clear that their abundance and their distribution are directly linked to the plankton. Because the food supply of these bottom-living animals is in turn largely derived from the plankton, their survival and growth is also dependent on it. The richness of the food affects the growth rate of the fish; for example a five-year-old haddock living on the moderately good food supply of the central North Sea grows to a length of 31·6 centimetres (just over 12 inches), but a five-year-old haddock from the rich feeding Icelandic waters grows to about 55 centimetres (nearly 22 inches) which is about five times the weight (see the final paragraph in Chapter 2).

Recent changes in climate are affecting the temperature of the northern seas and ice has gradually been receding. This has meant a northerly extension of areas in which fish—especially cod—can live. When such changes take place, a re-colonization of the sea floor by animals suited to the new conditions occurs and these, of course, are the food for the fish in these new grounds. Although it is a gradual change, it is not so gradual that small bottom-living animals could crawl fast enough to keep pace, and re-colonization depends on the transport of planktonic larvae by the currents actively associated with the climatic change.

Plankton is thus of fundamental importance to the fisheries through a shorter or longer food chain according to the type of food the fish eat, but beginning always with the green plants of the phytoplankton. It has been estimated that the annual production of green plants in the seas of the world amounts to something like 150,000 million tons. This is, of course, only a very rough estimate based on a few calculations in isolated parts of the ocean and it is only possible to guess what is happening elsewhere. This figure is not too different from production on the land. At each stage of the food chain about 90 per cent is lost so that 100,000 lb of green plant yield 10,000 lb of herbivorous zooplankton, 1,000 lb of carnivore and 100 lb of fish if it feeds at this stage, 10 lb or 1 lb of fish if it feeds at one or two stages further removed. The 150,000 million tons of green plants in fact yield some 30 million tons on the world's fish markets, a yield of 0·02 per cent or 1 in 5,000, but this covers a large area of ocean where little commercial fishing is possible. In areas such as the North Sea, or the Icelandic shelf about 0·2 to 0·3 per cent of the yield is taken out as fish. This high figure is partly due to the large proportion of herring which are mostly feeding on herbivores or at one stage further removed from the primary production. It is also probably in part due to the current systems which bring into these areas the middle stages of the food chain which have had their primary plant stage outside.

The word fisheries used in the title of this chapter includes the catching of fish as well as their abundance in the sea. Plankton in the form of jellyfish can be a serious hindrance to successful fishing, and in Faroese waters, in particular, they can be sufficiently numerous to spoil the fishery. After living near the surface in the summer, the jellies, when they are quite big, go to the bottom in August or September, or even as late as October. Here they congregate in such numbers that they become a serious menace to trawling, and catches are so poor that the trawlers have to go elsewhere. We are not quite sure how the jellies affect the fish; they may cause the fish to rise above the bottom where the trawl is, they may possibly be driving the fish off the grounds, but most likely they are just so numerous that the nets become choked and heavy and cannot catch the fish with their usual efficiency. Some skippers report that the nets become full of jellies almost as soon as they get to the bottom and on hauling their sheer weight bursts the net. Later in the year, about November, the grounds clear and fishing then becomes more profitable.

Stake nets around the shores for catching salmon also choke with jellies and spoil the fishing. In the Baltic, fish traps can become so heavy with *Aurelia* that they break when lifted and the fishery for herring and sprat is spoiled. The jellies penetrate so far into the fresher waters of the Gulf of Finland that they affect the pike fishery there. They seem to be most prolific in warm summers.

This chapter and the preceding two chapters have tried to show how a

PLATE XXXV.

(*Top*) Dr. S. G. Gibbons holding the baleen plate of a plankton-feeding whale. Note the fringes which filter the plankton from the water.

Photograph by James Fraser

(*Bottom*) A view of the upper jaw of a fin whale showing the baleen plates in position. This particular whale had a large tumour—marine creatures are not immune from such afflictions!

Photograph by D. F. S. Raitt

good fertility of the water, through the plankton, can yield a good fishery. It does not always work out quite that way, especially if the change is too sudden. An example is the 'red tide' mentioned at the end of Chapter 3; this name is given to a sudden bloom of a toxic dinoflagellate associated with an exceptionally rich nutrient supply. One occurred off the west Florida beaches in 1959, the fourth in ten years. Red tides can have a serious adverse effect on the local fisheries and amenities. The nutrients are so rich in the area affected that the dinoflagellates can multiply extremely rapidly and reach such enormous numbers that the toxin given off can poison many of the fish. Other fish die through lack of oxygen in the water because it has been absorbed by the bacteria during the process of decay of the fish and other creatures.

The spray blown ashore by the wind may contain enough poison to cause an irritation to those ashore and this can be serious to those with chest or heart troubles. This, and the smell of decaying fish, makes these otherwise popular seaside resorts thoroughly unpleasant, with the resulting loss of tourist trade. As the dinoflagellates multiply they use more and more of the nutrient until it is exhausted and there follows the sudden death of multi-millions of them through sheer starvation.

Red tides occur in places other than Florida; in India, Japan, Australia and Chile, for example. They are also known from fresh or brackish waters in the Mediterranean area and as near home as Belgium and Denmark, but not to anything like such a severe degree as at Florida. What can sometimes happen is a case of indirect poisoning. Shellfish such as mussels feed on bacteria and other small organisms including dinoflagellates—mostly of course the non-poisonous ones. If they happen to include too many poisonous ones in their diet, and are then eaten, they can cause poisoning even after cooking. The chance of this is rare, and in Britain it is particularly remote as the Shellfish Purification Schemes, designed to get rid of pathogenic bacteria, would naturally free them from poisonous dinoflagellates too.

CHAPTER 11

'Indicator' species and water movements

Living things are all adapted to certain conditions of life, but some are much more tolerant than others. For example, polar bears live in the cold climate of the Arctic and penguins in the Antarctic; a giraffe prefers it warm; a hippopotamus likes it wet; a parrot prefers a forest but a bison the open plain. All of them will survive in the very similar conditions in a temperate zoo when protected and given the right food, because they are fairly tolerant. Many tropical species just will not live in zoos except in specially heated animal-houses because they are less tolerant of the colder temperate climate. Some will happily take a variety of foods and are not difficult to rear, but a panda is most particular about his bamboo shoots.

So it is, too, amongst the plants and animals of the plankton, and we find those that are associated only with a high salinity, others with a lower salinity, and yet others where salinity does not seem to matter. Other limiting factors are temperature, depth, food, and also those more delicate chemical factors such as vitamin and hormone content. Thus the different species in the plankton are distributed according to environmental conditions, the tolerant ones rather loosely, and the less tolerant ones between quite closely defined limits. This was mentioned in Chapter 8 (p. 110) as it affects the geographic or seasonal distribution of the plankton.

We can, however, take it a step farther than this. By choosing suitable species and studying their distribution we can follow their movements and so learn more about the currents that carry them. The principle is quite simple. As water moves from one place to another it gradually mixes with the surrounding water, and it will become cooler, or warmer as the case may be. Its physical and chemical characteristics also mix until its identity is lost and the differences can no longer be measured. But although the plankton also becomes mixed the actual individuals carried by the currents cannot be changed and they remain recognizable until they die and disintegrate. If the chosen organisms are easily identified the water mass can be labelled at sight simply by towing a plankton net and looking at the catch. This has been realized for centuries, but only in a vague way until 1935 when Dr. F. S. Russell of the Plymouth Laboratory pointed out how useful such labels were and how easily they could be obtained. Since then most of the water masses in the north-east Atlantic, and in several other places in the world, have been labelled. Because certain species in the plankton could be used to indicate the

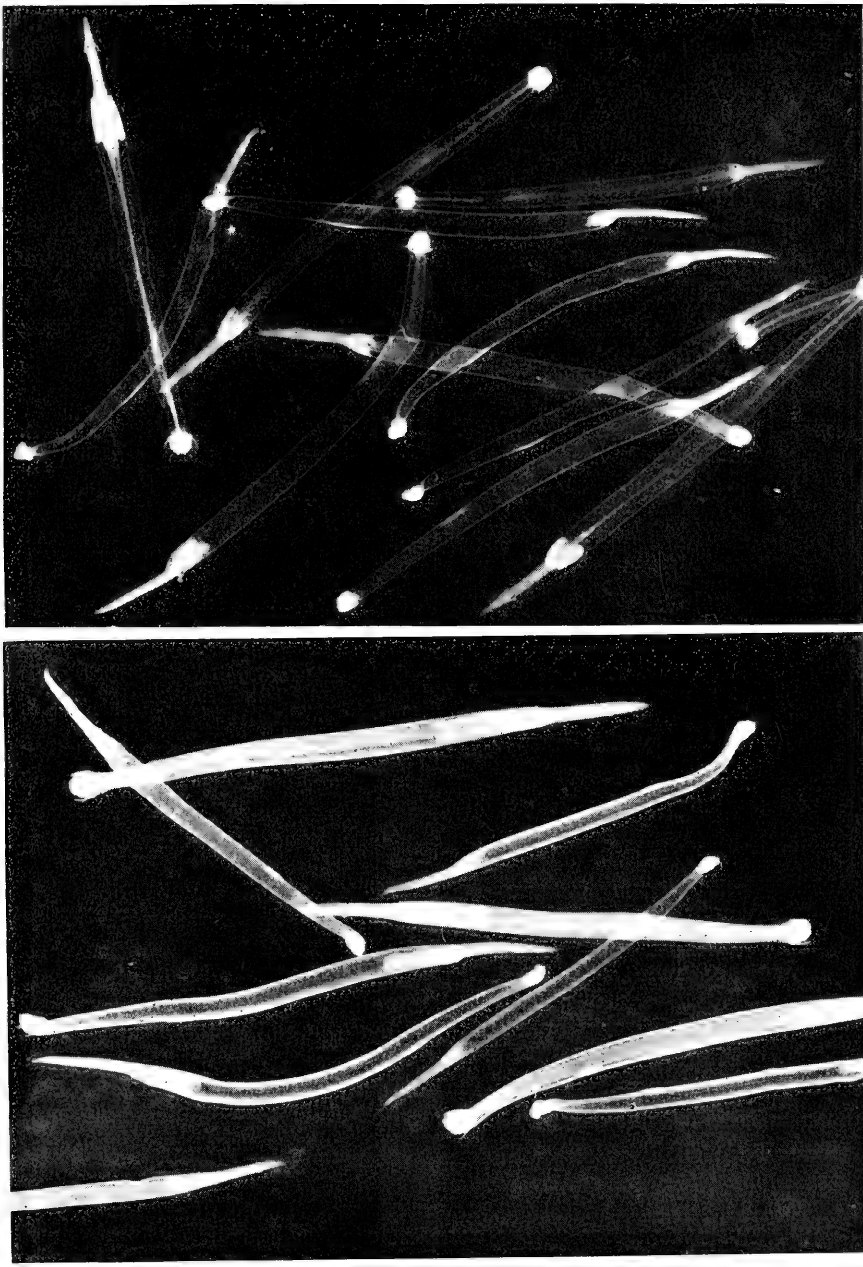


PLATE XXXVI. The two types of *Sagitta* used as indicators in the English Channel, North Sea and Irish Sea.

(*Top*) *Sagitta setosa* from the local water.

(*Bottom*) *Sagitta elegans* from mixed local and oceanic water.

Photographs by James Fraser

origin of the water mass containing them Russell coined the term 'plankton indicator species'.

Most species, including the plankton indicators, are much more tolerant as individuals than as a race because, although they can live—according to their degree of tolerance—in a somewhat changed habitat they can only breed within much closer limits. This means that the dispersal of water over a fairly wide area, accompanied by physical changes, can still be linked with one or more closely defined origins.

By using a sequence of species with a range of tolerance to change, followed by those suited to the new conditions, an even wider dispersal can be traced. As an example we can later try to trace the sources of origin and the mixing of the different water masses comprising the North Sea, but before doing so we must first obtain some information about the species themselves.

The arrow-worms, the Chaetognatha (p. 59), are one of the most useful groups. There are several species found in the area in the neighbourhood of the British Isles, each readily distinguished with a little practice. *Sagitta setosa* (Plate XXXVI *top*) likes a moderately low salinity, not high enough to let it live in the open ocean, and not low enough to let it live in the Baltic. It is found in North Sea water, in the Irish Sea, in estuaries like the Gironde, in parts of the Mediterranean, the Black Sea and near Labrador. *Sagitta elegans* (Plate XXXVI *bottom*) likes a rather higher salinity but this must be linked with a mixture of oceanic and coastal water so that it is rare where oceanic water does not reach, and it is not often found in the open ocean. It is thus found in the mixed waters of the North Sea, off the west coast of the British Isles, Norway, Faroe, Iceland and the American and Canadian coasts. *Sagitta serratodentata* likes a high salinity but it will not thrive in very deep water. *Sagitta lyra* prefers it warm and moderately deep. *Sagitta maxima* likes it cold, and it does not matter whether it is the cold near the surface in the Arctic or the cold in the deep underlying water much farther south. *Sagitta macrocephala* and *S. zetesios* are only found in deep water.

The copepods (p. 65) can be similarly used, and there are vast numbers of species compared with the arrow-worms. To name a mere selection, we have *Labidocera wollastoni* in the North Sea uninfluenced by oceanic inflow, *Metridia lucens* in the mixed water, *Calanus hyperboreus* in the cold water, *Pareuchaeta barbata* in the cold and deep, and *Pleuromamma abdominalis* in the warmer but fairly deep water. There are many other groups also, so that when thinking along these lines the plankton must be considered as a community of many species of similar tastes living together. They say that one swallow does not make a summer: neither does one *Sagitta* indicate a water mass, but if accompanied by the others of the same community the inference is proportionately stronger.

Sheer numbers of indicator species, although labelling the water mass the more certainly, do not necessarily mean a proportionate increase in the volume of water being transported. They may do so, because the greater the volume of water the more slowly it will be affected by outside influences and the favourable conditions will last all the longer. They may, however, be due simply to an unusual abundance of the species at the source, or conditions may be favourable enough for the organism to reproduce whilst in transit. It is sometimes possible to distinguish between the few older individuals that have themselves been carried all the way, and the more numerous young ones born *en route*.

Some species are useful indicators in spite of a wide tolerance because their origin is controlled by some other factor. A good example is the medusa of *Obelia* (Plate XII). This is a very tolerant form, but is always associated with a coastal origin because the hydroid stage in its life history (p. 85) is coastal, whether an open Atlantic seaboard such as the west of Ireland or the Hebrides, or perhaps in a very different type of water, such as the coast of Kent. Similarly the larval stages of shore crabs and acorn barnacles, and the empty cast skins of the barnacles, indicate coastal associations of the water in which they have been.

A small cladoceran (Fig. 19) *Podon polyphemoides* can be used as an indicator of Nile flood water as far as the coast of Israel. Turtles from Mexico, *Colopochelys kempi*, were drifted to the west of Ireland in 1928 and 1934, and it is probable that other turtles, *Caretta caretta*, found occasionally are also of Mexican origin, as they are not known to breed in south European seas. Leathery turtles, *Dermochelys coriacea*, reached the northern North Sea and close to western Norway in 1956.

Deep-living species can be used to indicate places of upwelling. Hosts of examples from all over the world could be given.

There are five main water masses in the neighbourhood of the British Isles and each can be distinguished by its plankton content. So as not to make this section too cumbersome only a few indicators are mentioned here as examples, some of them are depicted in the figures associated with Chapters 4 and 5.

1. The local water of the North Sea, Irish Sea and similar local areas, (Plate XXXVII) with:

Sagitta setosa	arrow-worm
Labidocera wollastoni	copepods
Isias claviceps	
Tima bairdii	medusae
Eutonia indicans	

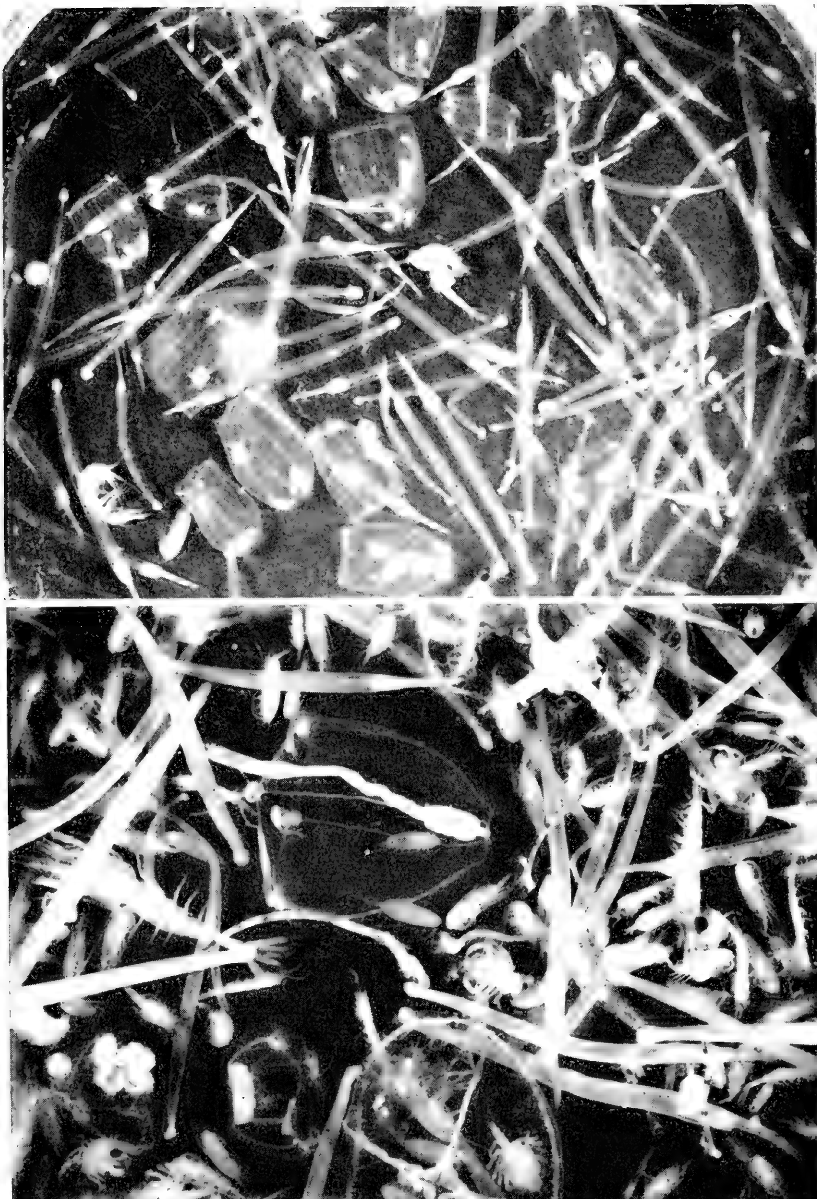


PLATE XXXVII. The plankton communities with the two species of *Sagitta* shown in Plate XXXVI.

(*Top*) *Sagitta setosa* with plankton of poor feeding value; also seen are the medusa *Aglantha*, a larval hermit crab, an amphipod and one fish egg (*left*).

(*Bottom*) *Sagitta elegans* with plankton of rich feeding value. There are many copepods—chiefly *Calanus*—euphausids, a shrimp, crab larvae, medusae, *Oikopleura* and young fish—chiefly lemon sole and witch.

Photographs by James Fraser

2. The mixed Atlantic and Shelf water, found in the northern North Sea (Plates XXXVII and XXXVIII), parts of the Irish Sea, the continental shelf of Britain, Norway, Faroe, Iceland etc with:

Sagitta elegans	arrow-worm
Metridia lucens *Candacia armata*	copepods
Thysanoessa inermis	euphausid
Clione limacina *Spiratella retroversa*	molluscs

3. The North Atlantic Drift with:

Sagitta serratodentata	arrow-worm
Rhincalanus nasutus *Euchaeta hebes*	copepods
Laodicea undulata *Cosmetira pilosella*	medusae
Lensia conoidea *Physophora hydrostatica* *Agalma elegans* *Dimophyes arctica*	siphonophores
Lepas species	stalked barnacles
Salpa fusiformis *Doliolетta gegenbauri*	Thaliacea

4. The Lusitanian Stream (from the area near Gibraltar and the Bay of Biscay) with:

Sagitta lyra	arrow-worm
Siphonophores (except those in 3)	
Phyllosoma larvae of spiny lobster	
Phronima	amphipod
Thalia democratica *Doliolina mulleri*	Thaliacea

5. Water of arctic or boreal origin, with:

Sagitta maxima *Eukrohnia hamata*	arrow-worms
Calanus hyperboreus *Metridia longa* *Pareuchaeta barbata*	copepods
Spiratella helicina	mollusc

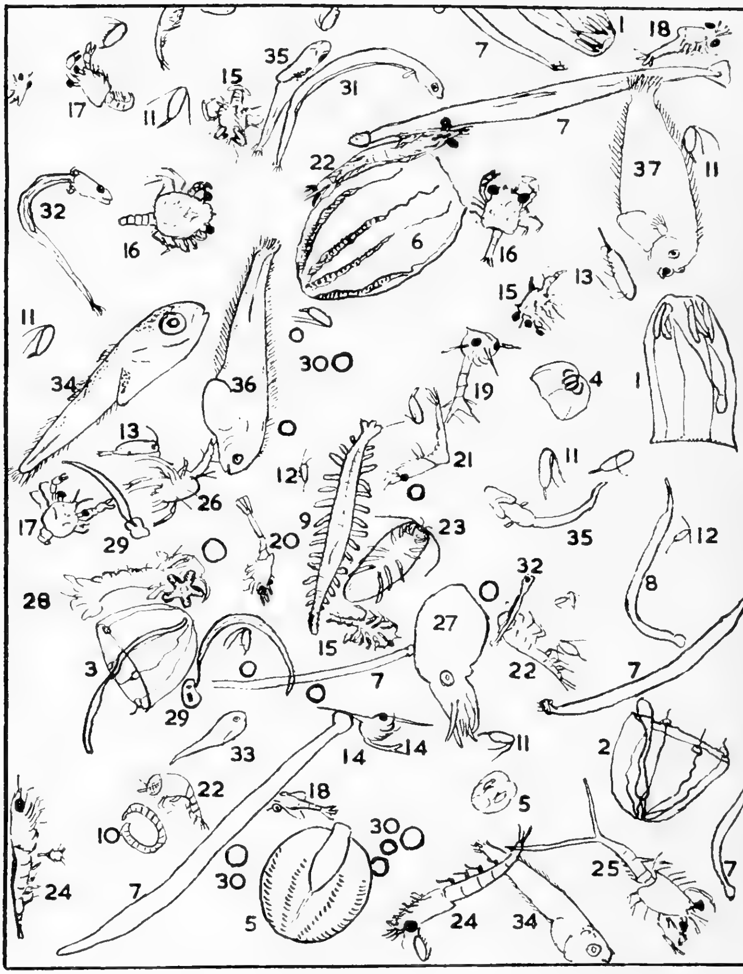
This gradually merges into the cold deep water below the North Atlantic Drift and there occur also:

Sagitta macrocephala	arrow-worms
Sagitta zetesios	
Gaetanus pileatus	copepod
Amalopenaeus elegans	decapod
Spiratella helicoides	mollusc

With information of this type we can, as an example, trace the inflow and mixture of Atlantic water into the North Sea from the north. The currents and their immense significance in the biology of the seas have already been briefly dealt with in Chapter 8: west of the British Isles we find the main mass of Atlantic water with the cosmopolitan oceanic plankton including the indicator species mentioned under 3 above. Just beyond the edge of the shelf there is the Lusitanian Stream; some years it is hardly present at all but in other years quite marked. Where it is present we find the indicator species under 4 above mixed with the others, not replacing them. In an ordinary year these can be clearly traced west of Ireland and Scotland and continuing close to the edge of the shelf and so into the Faroe-Shetland Channel. The plankton selected for the photographs produced as Plate XXXIX were taken from this mixed oceanic water mass. The indicator species gradually die out *en route* according to their tolerance and usually only the hardiest members will reach near Orkney or Shetland. In years when the water movement is unusually strong, e.g. in 1953 and 1954, they can be found in the North Sea itself. As the stream flows so close to the edge of the shelf it gradually upwells into the shallower water to mix along the north coastal area of Scotland towards Orkney. It is important to realize that the total volume of water in this Lusitanian stream is very small indeed compared with the main water mass, even west of Ireland, but it can be traced because of its plankton long after its physical characteristics have disappeared.

The main Atlantic inflow passes through the Faroe-Shetland Channel, taking with it the more cosmopolitan oceanic species, but again mixing on the way so that the less tolerant species die out and are replaced by those species which need the mixed conditions. A mixed water species, such as *Sagitta elegans* or *Metridia lucens*, found off the west Atlantic coasts thus indicates a mixture of coastal water with the Atlantic, but the same species in the North Sea, Irish Sea or other shelf waters indicates the mixing of oceanic water.

Because the origin of the plankton species is linked with their breeding, the indicators tend to come in groups at the same time each year, giving a



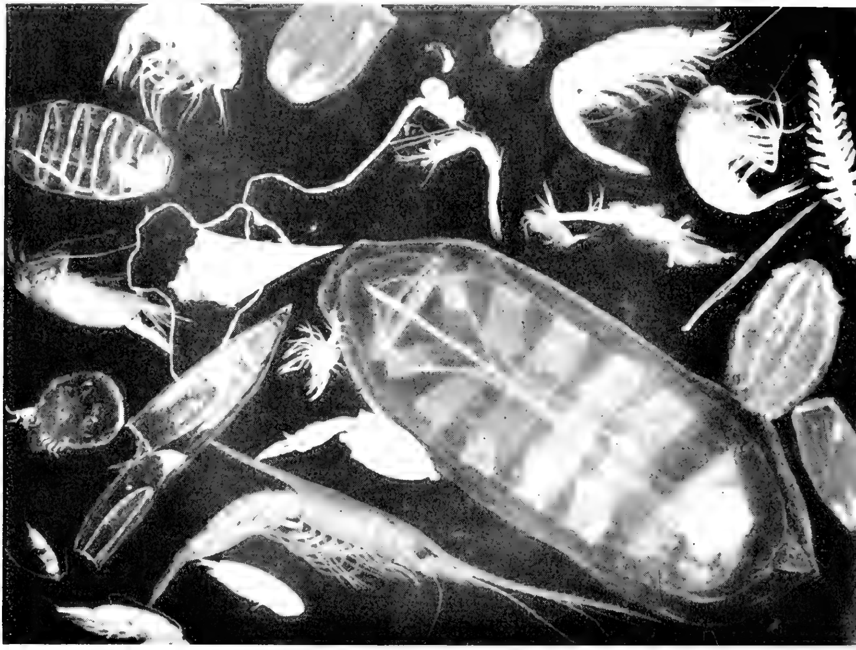
Key to organisms photographed in Plate XXXVIII.

1. *Aglantha digitale* (medusa)
3. *Dipurena ophiogaster* (medusa)
5. *Pleurobrachia pileus* (ctenophore)
7. *Sagitta elegans* (chaetognath)
9. *Tomopteris septentrionalis* (polychaete)
11. *Calanus finmarchicus* (copepod)
13. *Anomalocera patersoni* (copepod)
15. Megalopa of *Hyas* (crab)
17. Larva of *Eupagurus* (hermit crab)
19. Larva of *Munida* (squat lobster)
21. Larva of *Nematocarcinus* (shrimp)
23. *Eurydice spinigera* (isopod)
25. Larva of *Nephrops* (Norway lobster)
27. Larva of *Eledone* (octopus)
29. *Oikopleura* (tunicate)
31. Young herring
33. Young shore sucker (*Liparis*)
35. Young cod
37. Young plaice

2. *Sarsia tubulosa* (medusa)
4. *Bougainvillia* (medusa)
6. *Beroe cucumis* (ctenophore)
8. *Sagitta setosa* (chaetognath)
10. *Peocilochaetus serpens* (polychaete)
12. *Metridia lucens* (copepod)
14. Zoea of *Corystes* (crab)
16. Megalopa of *Portunus* (crab)
18. Larva of *Galathea* (squat lobster)
20. Larva of *Pandalus* (prawn)
22. *Themisto gracilipes* (amphipod)
24. *Thysanoessa inermis* (euphausid)
26. Larva of *Sergestes* (oceanic prawn)
28. Metamorphosing *Asterias* (starfish)
30. Fish eggs (various)
32. Young sandeel
34. Young haddock
36. Young lemon sole

PLATE XXXVIII. Some animals from the zooplankton. A key to help in identifying them is given opposite.

Photograph by James Fraser



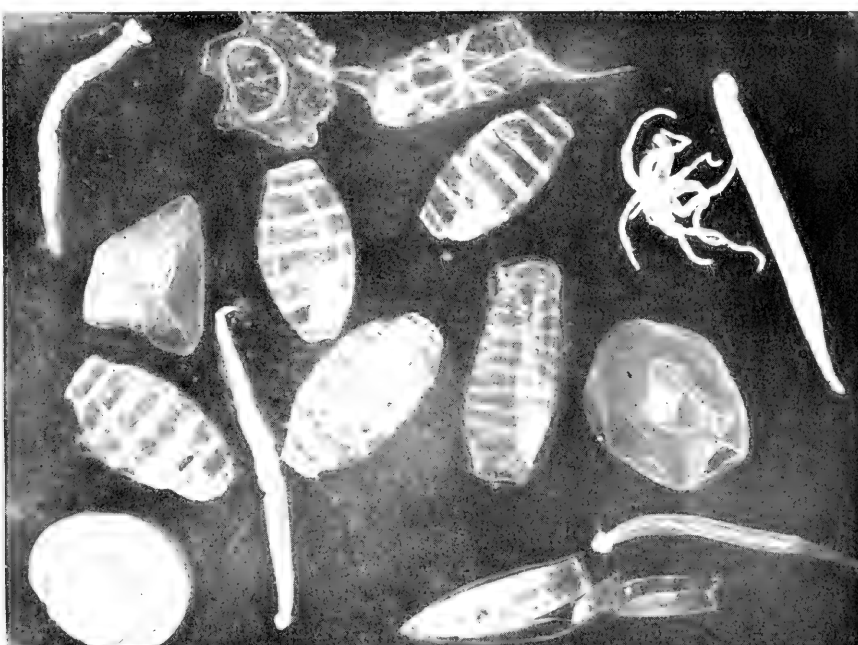
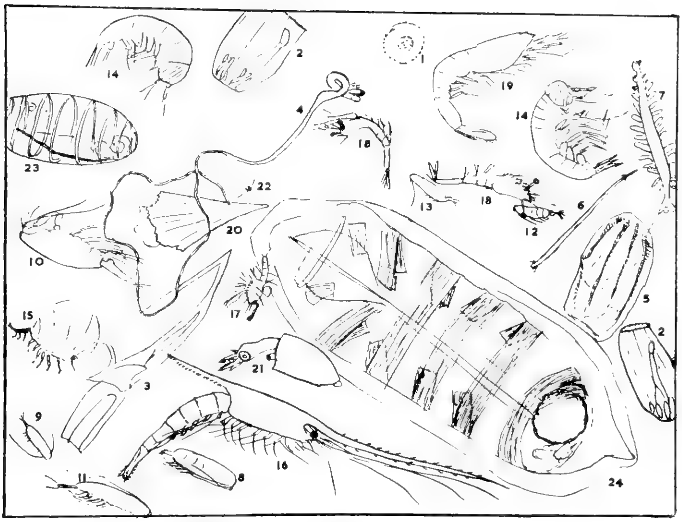
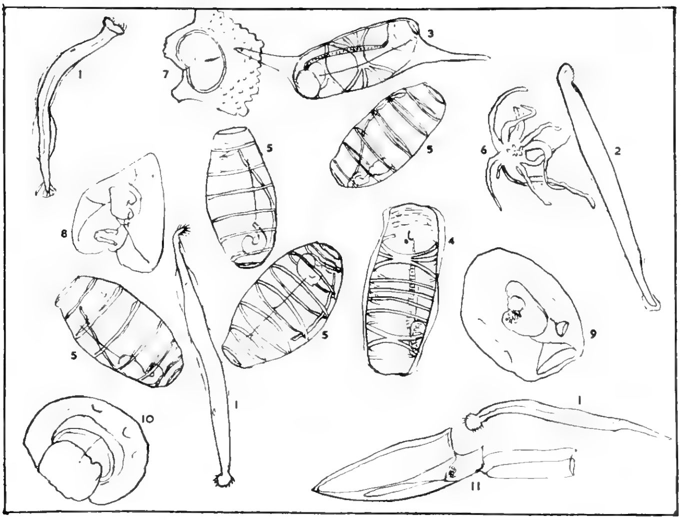


PLATE XXXIX. Some oceanic plankton animals. The lower photograph contains a greater proportion of 'Lusitanian' species. Keys are given opposite.

Photographs by James Fraser





Key to organisms photographed in Plate XXXIX.

Upper

1. *Thalassicolla nucleata,* radiolarian
2. *Aglantha digitale,* medusa
3. *Chelophyes appendiculata,* siphonophore
4. *Agalma elegans,* siphonophore
5. *Beroe cucumis,* ctenophore
6. *Sagitta serratodentata,* chaetognath
7. *Tomopteris septentrionalis,* polychaete worm
8. *Calanus hyperboreus,* copepod
9. *Eucalanus elongatus,* copepod
10. *Pareuchaeta barbata,* copepod
11. *Pareuchata norvegica,* copepod
12. *Scottocalanus securifrons,* copepod
13. *Undeuchaeta major* (stage V), copepod
14. *Themisto gracilipes,* amphipod
15. *Mimonectes loveni,* amphipod
16. *Gnathophausia zoea,* mysid
17. *Sergestes* (larva), decapod
18. *Sergestes* (young), decapod
19. *Amalopenaeus elegans,* decapod
20. *Clio pyramidata,* pteropod
21. *Brachioteuthis riseii* (young), cephalopod
22. Ophiopluteus larva, brittle starfish
23. *Dolioletta gegenbauri,* doliolid
24. *Iasis zonaria,* salp

Lower

1. *Sagitta lyra,* chaetognath
2. *Sagitta zetesios,* chaetognath
3. *Salpa fusiformis* (aggregate stage), salp
4. *Salpa fusiformis* (solitary stage), salp
5. *Dolioletta gegenbauri* variety *tritonis,* doliolid
6. Arachnactis larva of sea anemone (*Cerianthus*)
7. *Vogtia spinosa,* siphonophore
8. *Nectopyramis thetis,* siphonophore
9. *Rosacea plicata,* siphonophore
10. *Hippopodius hippopus,* siphonophore
11. *Chelophyes appendiculata,* siphonophore

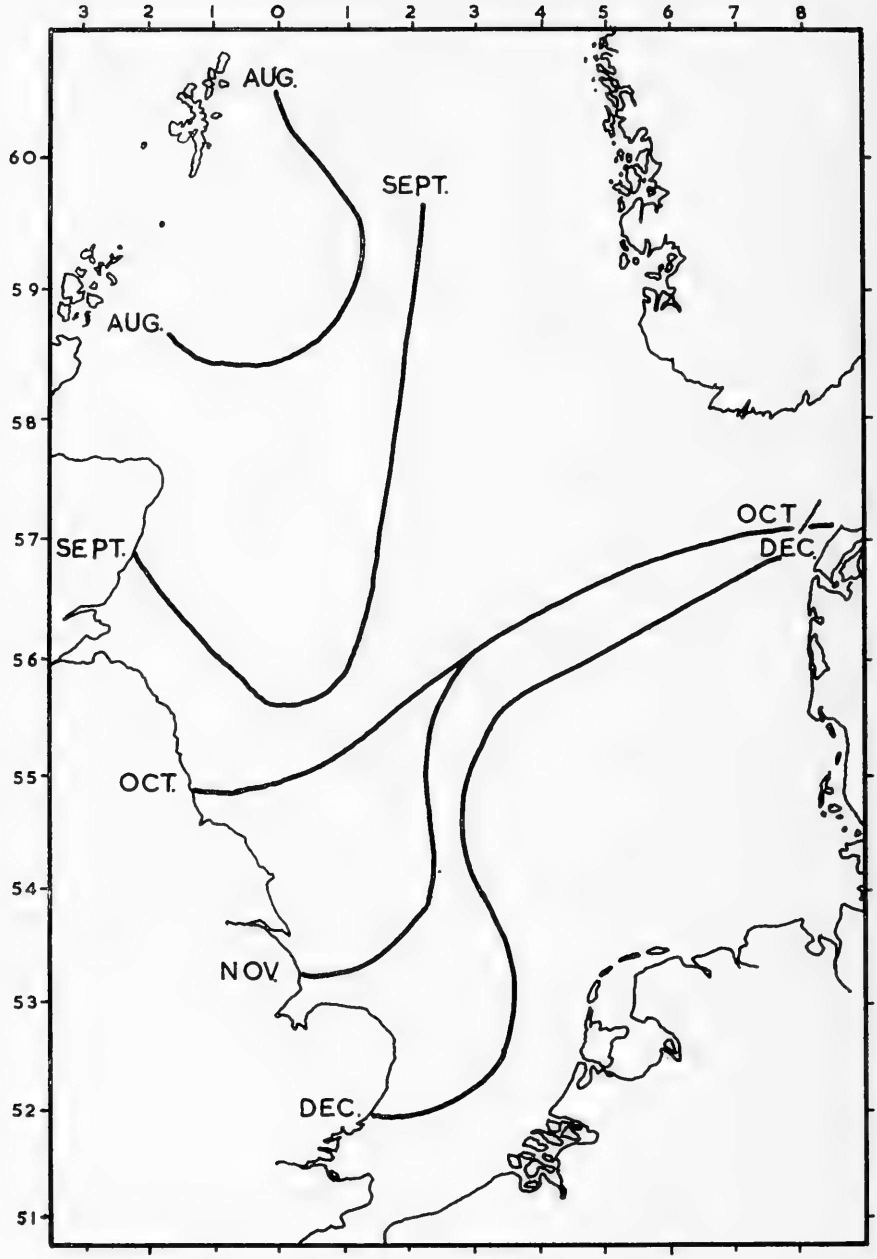


FIG. 35. Chart of the North Sea showing, month by month, the southern limit of distribution of plankton indicative of the flow of mixed water from the north. After Glover.

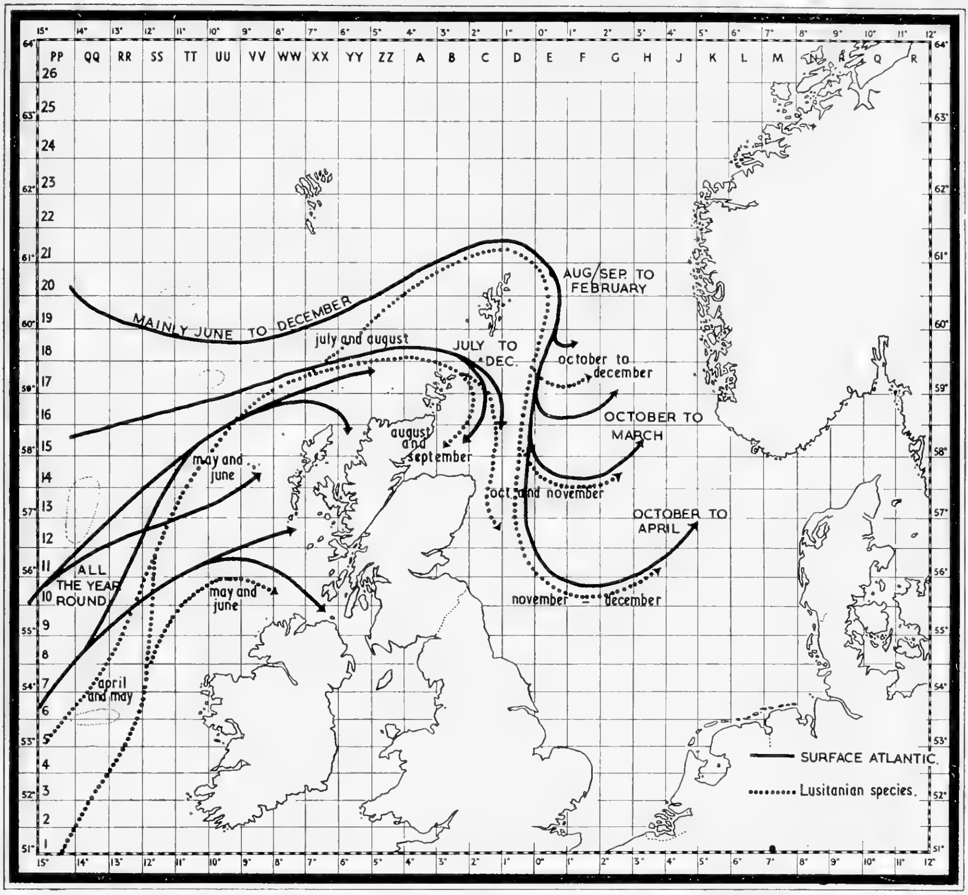


FIG. 36. Chart showing the route and times of approach to the British Isles of Atlantic and 'Lusitanian' plankton indicator species.

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sense of annual pulsation of the current which is not necessarily a true one. The currents have periods of maximum and minimum inflow of their own which are not always connected with the abundance of indicators.

To follow the further penetration of the mixed water into the North Sea the true oceanic species are no longer so useful as indicators as they have mostly died out, but the mixed water indicators take their place and a picture such as that given by Glover (Fig. 35) is seen. Taking a general view of the whole example, one can produce a chart (Fig. 36) which gives an idea of the average route taken and the times of arrival of the indicator species.

This principle applies elsewhere of course, and passing mention can be made of the inflow of salps into Norwegian waters in September 1955 and the inflow of salps west of Iceland in September 1958 which even continued round the North Cape.

Salps, too, can be used in this way off the east coast of Australia, arrow-worms can be used off Peru and in the North Pacific, and off the Atlantic coasts of America and Africa. Oceanic fish are used to determine the penetration of water into the Strait of Georgia between Vancouver Island and the coast of Canada.

Some of the sea shore-animals like barnacles and limpets, and bottom-living animals too, can be used in a similar way. As their distributions are usually less transient than in the plankton they can be used in determining the long-term trends associated with climatic changes rather than the more immediate changes. A warning, however, needs to be given, as some bottom-living animals have been transported by man to new surroundings and have managed to survive there. The Chinese mitten crab is an example; it became established, as an adult, in the German rivers like the Elbe from which it has gradually dispersed, causing worry because of the damage it does by burrowing into the soft banks of river estuaries. This artificial introduction rarely happens to plankton organisms but it has occurred, for example with the diatom *Biddulphia sinensis* (p. 36).

Although only a few species have been named in this chapter the list could be very greatly extended, and indeed many of the microscopic forms found in the phytoplankton could also be included. Ease of identification on the spot has, however, such an advantage that those species that require specialist techniques are not so readily accepted as practical indicators.

Indicators are used not only for labelling water masses to trace the movement of the currents but, as shown in the previous chapter, these labels also indicate the boundaries of the various water masses and the mixtures of these that have different fertilities. Even more importantly they indicate the biological changes occurring *en route*. It should be emphasized that those indicator organisms may play only an insignificant part in the whole plankton community; it is their value as labels that is important. We need the labels because the different water masses have different abilities to support production of plankton, of fish food and so of the fish themselves.

Some fish are also drifted out of their normal range and fishermen often come across such strangers. The fishery laboratories are glad to receive these unusual specimens as the records help them to understand the ever-changing conditions at sea. In return for the help given they will identify the fish, or whatever it is, and send the finder a short comment about it.

CHAPTER 12

Behaviour

THE PREVIOUS chapter, and indeed the very name plankton, emphasizes that these organisms drift where the currents take them, and suggest that their own swimming powers are negligible. This is true in the broad sense but, although they cannot swim to stem a current or to migrate in the way fish can, most zooplankton organisms are capable of quite definite movements which can be classed as behaviour, and these need a chapter to themselves.

First they swim to catch their food, vigorously if they are carnivorous predators actively searching out their prey, less actively perhaps if they are herbivores or detritus feeders swimming about to bring new pastures within their range. We are so accustomed to the almost universal use of sight by the familiar land animals in finding their food, especially the carnivores, that it is difficult to realize how little importance is attached to sight in aquatic invertebrates. Certainly the vertebrate fish have efficient sight and so have the cephalopods (the squids and octopuses, p. 62) whose eyes are very reminiscent of mammalian eyes. Some crustacea and their larvae have compound eyes not unlike those of insects. Though it is certain that many fish and the cephalopods use their eyes to see their food, many of the planktonic crustacea being filter feeders probably use theirs instead for seeing movement rather than detail and so escaping from their enemies. Most planktonic animals are quite blind or have eye-spots that are sensitive to light but not to details of shape.

Water, being almost incompressible compared with air, is a much better medium for transmitting small pressure differences and one of the most important senses of marine creatures is their highly developed sense of 'touch'. It seems as though this enables them to perceive the vibrations in the water made by the movements of other creatures, and perhaps also the echoes they receive back from stones and other objects whose presence they could then sense, and so take any necessary avoiding action. It is uncanny to watch an arrow-worm chasing a copepod and realize that both are sightless, and yet arrow-worms can successfully catch fast swimming young fish (Plate XXXII), and a medusa can stretch out its extensible stomach to grab a passing small fish. Blind fish can swim in aquarium tanks without bumping into the walls.

Smell, too, is a highly developed sense in marine animals, more efficient than we humans can appreciate—the story of the eels finding the fresh water rivers given on page 102 is one example. Many find their food or their mates by smell and it is worth commenting on these two different origins of the smell; the one an extraneous source from the food, alive or dead, and the other from its own species. The name 'pheromones' (from the Greek pherein, to transfer) has been given to those substances secreted to the outside by an individual which cause a reaction in another individual of the same species. The best known pheromones are probably those liberated into the air by female moths and which can attract the males from amazing distances. We know so little about their occurrence in the sea that there is a whole field of research waiting to be done, but it is very probable that the attraction between male and female plankton organisms is by pheromones.

Lantern fish may be an exception. They have luminous organs, photophores, arranged in specific patterns (Plate XXXI) which we find most useful for identification. It has been suggested, but without any evidence to prove it, that the lantern fishes also use them for the same purpose and so find the right mates. Light from the photophores may also serve to attract other curious animals and lure them close enough to be seen by the owners. The luminous lure of the angler fish, dangling immediately above a large gaping mouth, certainly serves such a purpose.

Deep-sea fish are not the only luminous creatures in the plankton. Many squids also have specific patterns of photophores (Plate XV). Look over the side of the ship on a really dark night, especially towards the summer in the higher latitudes. Every ripple in the water seems incandescent, and every wave breaking on the beach has its shimmer of light. A general greenish glow with no definable points of light is probably caused by millions of dinoflagellates, each too small to be seen by the naked eye. Minute pin-pricks of light are probably due to the larger dinoflagellate *Noctiluca* or to small copepods. Bigger and more bluish flashes are caused by larger copepods, euphausids, planktonic worms or small fish. A large disc of pale light is probably a single medusa. Comb jellies are luminous and the colonial *Pyrosoma* (p. 80) is a particularly brilliant form. One might add to this list almost to the extent of asking if there are any planktonic organisms which are *not* phosphorescent!

A last example of marine luminescence, not strictly planktonic but too familiar to be overlooked, is that caused by bacteria in rotting fish. When a fish is kept rather too long, it glows brilliantly in the dark. Such fish, the trails they leave behind when moved and on fishermen's working clothes have been the real origin of many a spooky story.

We have yet a lot to learn about 'bioluminescence' as it is called. It can usually be stimulated by disturbance in the water, but on some dark nights when plankton is there all right, and the disturbance is there, we hardly get any sparklers. Sometimes at sea the light will flash in rhythm with the ship's propeller—understandable as vibrations are carried so well in water, but more inexplicably it is reported to respond to the ship's radar, disappearing when the radar is switched off as if something in the transmission stimulates the organisms to light up. At other times a flash of light can be seen to move across the water at a speed of 100 knots, reminiscent of the streamers of the aurora, and possibly stimulated by electrical or magnetic disturbances in the earth.

What are photophores, and how does the light work? There are various differences in detail, but mostly each consists of a ball with a silvery reflector behind and a transparent lens in front so that the maximum efficiency is obtained—and it *is* efficient too, only about 10 per cent of the light energy is lost in heat. Some photophores work by a chemical reaction which results in the production of light and this seems to be at the control of the owner. Others are cells containing luminous bacteria and some of these can be controlled by a shutter like an eyelid. Some squids can change the colour of their lights by covering them with a red skin.

Most photophores point downwards (Plate XXXI) and the reason is not really understood. Photophores, as distinct from a general all-over phosphorescence, seem most common amongst those organisms that live in the middle depths and migrate towards the surface after dark (see below). One plausible reason is that one creature below another would see it as a black silhouette against the slightly illuminated blue background above. Bluish photophores under the body would tend to neutralize this effect, but if photophores were on the back, then the animal would show up against the black background of the depths. This is, in effect, the same type of adaptation that makes a fish silvery underneath but dark on top.

The second form of swimming behaviour to be mentioned in this chapter is that of 'diurnal migration' where so many species move towards the surface at night and go down again to deeper layers in the daytime. There seems to be no doubt at all that this is related to the light intensity, even though such a large proportion of the species that do so are sightless in the accepted sense. Nevertheless, they are very sensitive to light and cannot tolerate an excess. In order to keep at their own preferred light intensity, they remain submerged during the day, but as sunset approaches they start to climb upwards reaching the surface layers in the twilight. In total darkness there is no directional stimulus so they become scattered, only to reassemble near the surface as dawn approaches. As the light increases down they go again (Fig. 37). The copepod *Calanus* will daily climb and sink again through some 300 feet. Although only about $\frac{1}{8}$ inch long, it can climb

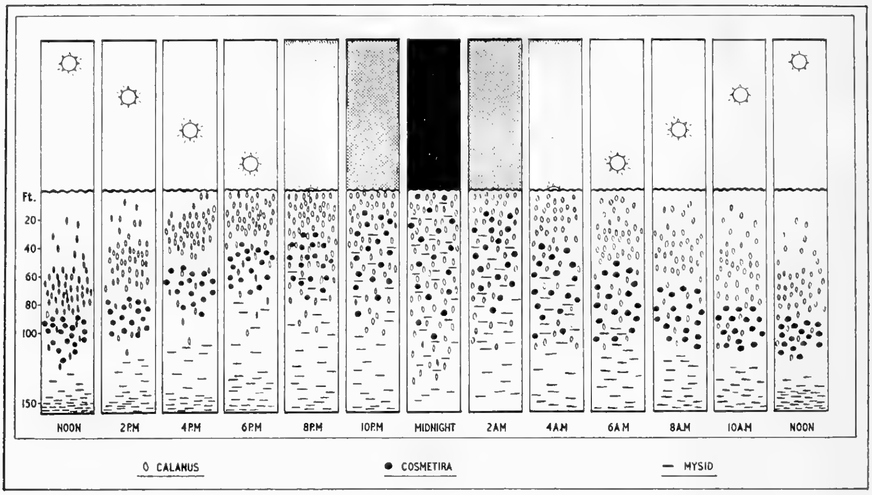

Fig. 37. Diagrammatic representation of the diurnal vertical migration of three common species in the plankton; a copepod, a jellyfish and a fairy shrimp. After Russell.

at 50 feet per hour and sink at three times that speed. The larger euphausid *Meganyctiphanes* can climb at 300 feet per hour, and sink at 420 feet per hour, though in short two-minute bursts it dives at speeds of 700 feet per hour.

Another reason for diurnal migration, to be considered with light intensity, is that of self defence. Animals migrate to the surface at night in order to feed, but as daylight approaches they sink into dark regions so as to avoid being seen by predators such as fish which are dependent on sight. Herring, for example, a plankton feeding fish, cannot see to feed at depths below about 100 metres. Associated with this, the zooplankton species which have daily migrations tend to have a longer life span, one to three years as against one to three months, and lay fewer eggs than those which do not migrate. To produce large numbers of eggs in a short time requires a corresponding increase of food intake and the non-migratory species get this by staying in the region of maximum food. The survival of the race is ensured on the one hand by evasion of capture, and on the other by excess egg production.

Migratory species which are drifted by the currents to shallow waters where they cannot sink into darkness during the day help to form the food of cod and haddock and other fish usually less dependent on plankton than are the pelagic fish such as herring.

Migrations of this sort mean that herbivores like *Calanus* are to be found during the night up near the surface amongst their food, the phytoplankton, and they sink during the day where they release the products of metabolism to enrich the deeper layers (p. 124). As the currents at the surface and below will not be identical, the animals will not be in quite the same place when they ascend the next night. Such movements are usually helpful in dispersion, but on the other hand in some places they seem to be essential in keeping the plankton in the same place. For example, during the colder weather the water surrounding an island will cool and so sink, taking the plankton with it, but at night the plankton will rise to the surface again and be returned to the waters converging on the island.

Light intensity is, however, not the whole story in diurnal migrations, for sometimes *Calanus* can be found at bright noon in calm weather dancing at the actual surface. Experiments have shown that at other times a few hours of bright sunshine is lethal; although sometimes *Calanus* recovered after four hours' exposure, they never did after eight!

What is an optimum light intensity for one organism is not necessarily the best for others, so that as the plankton in the upper layers moves towards the surface at night it is partly replaced by an upward movement of deeper and darker-loving species, while the faster swimmers from quite deep water—such as lantern fish, squids and euphausids—will swarm at the actual surface. The phenomenon of diurnal migration appears in very deep water also. These layers are not easy to sample in detail with closing nets but the behaviour pattern can be quite readily seen on the echo-sounder.

The echo-sounder (Plate XL) is an instrument originally designed for navigational purposes, its main function being to find and record the depth of water under the ship. It works by sending down a sound impulse which is then echoed back from the sea floor and the echo received is electrically amplified on board the ship. As the time taken for the sound impulse to go to the sea floor and back is in direct relationship to the depth a very accurate measurement of the depth is obtained. The electrical impulse can be made to mark a slowly moving paper band so that a continuous picture of the bottom is obtained. If the instrument is made sensitive enough, echoes will be received from any obstruction between the ship and the bottom, such as a shoal of fish. Whether or not an echo is received will depend on the sensitivity of the instrument, and on the size and texture of the obstruction. Fish with air bladders give very effective echoes, but jellyfish and many other plankton organisms have a composition so nearly the same as sea water that they are not nearly such good sound reflectors. Some of the larger plankton organisms like squids or the hard-shelled prawns can give a good echo and so can very small planktonic fish if they have small swim-bladders.

The echo-sounder, then, can be used to watch diurnal migration of those planktonic organisms capable of reflecting enough sound to record on the sensitive paper, and we can thus study their movements at sea under natural conditions, instead of in the laboratory, and follow differences such as on moonlight and dark nights. The echo-sounder revealed, too, that there is a 'deep scattering layer', a layer of 'something', not yet thoroughly investigated, which returns echoes of sound from the midwater layers of all the oceans of the world. It also showed that this deep scattering layer moves up and down every day, being as low as 400 fathoms or so in the day and coming up to 100 fathoms or less at night, sometimes reaching the surface. Because of its regular diurnal movement it is obviously a 'living layer' and not some physical difference of temperature or salinity. Because most planktonic organisms are not good sound reflectors, the actual sound scattering is thought to be mostly due to small fish with swim bladders, but euphausids and other larger creatures may also be partly responsible; these may of course be associated with large numbers of non-reflecting organisms. What is probably happening is that the associated plankton is regularly moving up and down according to the light conditions, and that the sound-scattering fish etc. are following the plankton to feed.

When the after effect of the atomic explosion at Bikini was being investigated, a curious problem arose. During the first day the radiation level of ships in the vicinity was not very great, but it gradually increased during the night. The key to the problem lies in this diurnal migration of the plankton. The micro-organisms in the lagoon were affected, but, being so small, each carried only a small dose. At night they followed their normal behaviour of climbing to the surface. Here they formed the food of the barnacles attached to the ships and, as each barnacle could capture a large number of the affected plankton animals, their radiation level increased sufficiently to affect the value given the ship as a whole.

Vertical movement of plankton in the sea raises the question of buoyancy. Protein, and skeletal parts, often the main body constituents of plankton, are heavier than water and dead plankton sinks fairly rapidly. How does

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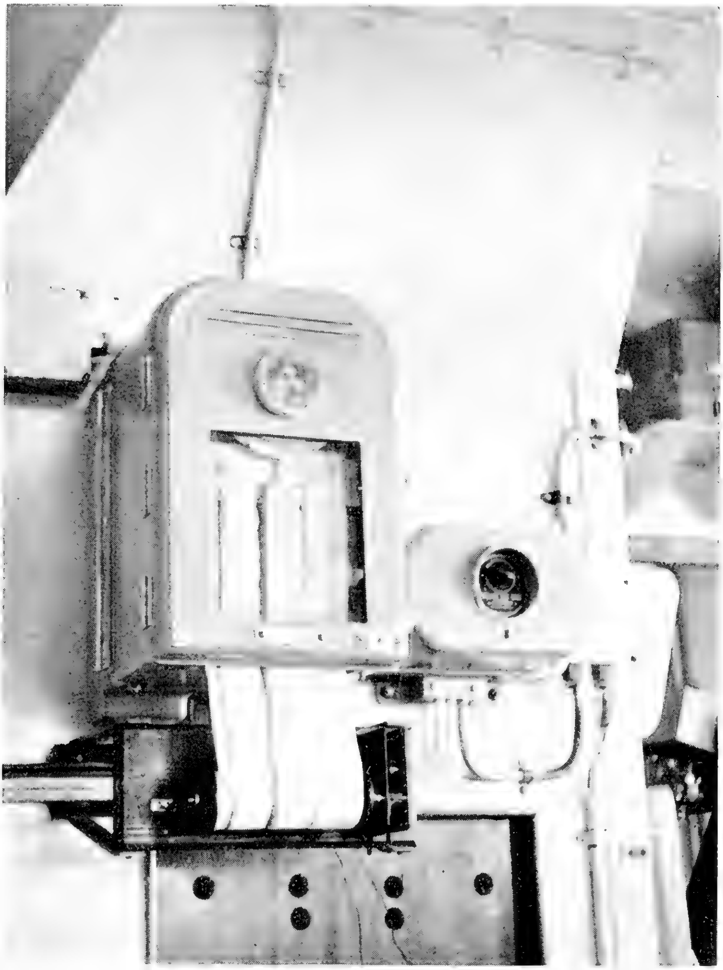
PLATE XL.

(*Top*) The echo-sounder (Kelvin Hughes MS24G) fitted in the laboratory of the research ship *Explorer* (see Plate I). The unit to the right contains the sensitivity control. A roll of special paper is being marked by the echo as it appears immediately below the transparent disc graduated in depths in fathoms, and the paper is being wound on to a storage spool below. The regular ticks to the left of the paper are at two-minute time intervals, and the dark line next to them represents the position of the surface of the sea. The dark marking near the centre depicts the sea bed and a 'double echo' is seen at twice the depth and is due to the sound impulse being reflected from the sea bottom to the ship's hull and back to the bottom again before being picked up on board. Echo traces from organisms (fish or plankton, see p. 157) near the surface of the sea can be seen on the paper close to the storage spool and also through the glass panel of the instrument.

(*Bottom*) Part of the echo-trace taken by *Scotia* at the edge of the continental shelf west of Scotland, 56° 46′ N 8° 52′ W on 14 July 1955. The depth of water on the shelf is about 60 fathoms, but the edge is very steep and the depth increases quickly to about 1,000 fathoms, and so beyond the limits of the scale shown here. The 'double echo' is seen in the shallow water and the two-minute time marks are also shown. There are two distinct traces, one near the surface to about 16 fathoms depth, and a deeper one which is seen upwelling at the edge of the shelf and then settles down at about 30 fathoms.

Photographs by James Fraser (Crown Copyright reserved on the echo-trace)




0
40
80
120

the living plankton maintain its level or change it to suit a changing environment?

The plants, as discussed in Chapter 3, are small, often with long spines, so that their ratio of surface area to weight is very high. Some contain oil globules which increase the buoyancy, whilst the very tiny nanoplankton organisms are often motile and can actively swim towards the light.

The animals are mostly much more able to swim and many do keep their level by swimming upwards, and gradually falling back in a resting phase before repeating the process, but many must be incessantly active. Fish with swim-bladders adjust the amount of gas in them and so are able to achieve a true balance; most fish without swim-bladders are deep-sea fish with reduced skeletal parts and they are often fatty which reduces their weight. Their body fluids are less salty than sea water and this, too, helps to give them a positive buoyancy. Their muscles (which are chiefly of the relatively heavy protein) are reduced and weak because the fish attract their prey by lures instead of chasing.

Cuttlefish possess a 'bone' (it is frequently given to canaries and other caged birds to exercise their beaks on) which is very light and contains gas spaces which make it buoyant thus reducing the weight of the cuttlefish in water to almost nothing. One deep-sea squid achieves this neutral buoyancy by having a very large cavity inside it equivalent to two or three times the rest of the animal (Plate XV) and this cavity is filled with a liquid lighter than the sea water. This is achieved by replacing the sodium part of the salt of sea water by the ammonium ion, which is naturally produced as a product of excretion.

Some siphonophores produce a gas-filled float (Fig. 17; 2, 3 and 4). Many copepods and other crustacea store oil or fat, particularly in the colder waters where the food is richer, but must rely on their own muscular powers when food is less abundant. It is significant that warm water is less dense than cold water and animals have therefore more work to do in warm water to keep from sinking. One way of easing the difficulty is to follow the lead of the diatoms and grow long feathery hairs which increase the surface area and hence very considerably the resistance to sinking. Copepods of the same species, for example, are often very much more feathery in the tropics than in cold water, the hairs becoming little plumes (Fig. 38).

By and large, however, the planktonic organisms keep to, or change, their level by their own unceasing efforts. These may be momentarily relaxed, but only to have the lapse made up by increased effort. There is no real rest for them, and for so very many of them the bottom is two miles or so below and in everlasting darkness, a most inhospitable environment for all except those specially adapted to live there.

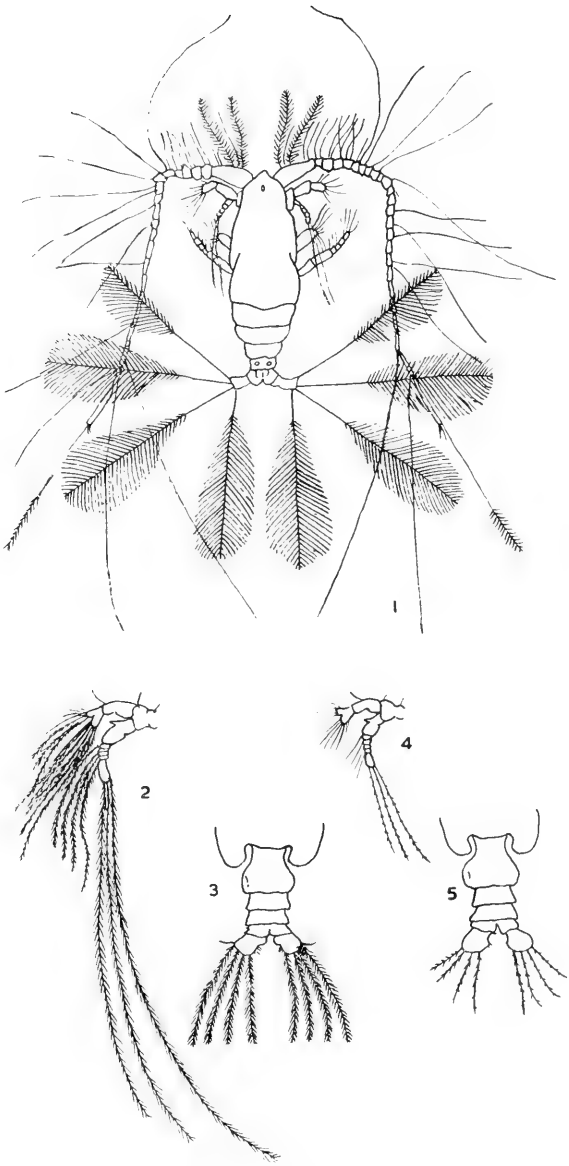


FIG. 38. 1, A warm-water plumose copepod *Calocalanus pavo*; 2 and 3, a 2nd antenna and tail fan of the copepod *Euchirella truncata*, plumose variety from the Lusitanian stream; 4 and 5, the same parts from the normal type of the same species.

CHAPTER 13

Plankton as food for man, and the possibilities of fertilizing the sea

If so much life in the sea depends on plankton, it is very natural to ask if plankton cannot be caught commercially, perhaps for human food, perhaps to supplement animal feeding stuffs, and so to lead to increased supplies of human food.

On page 136 it was stated that the total annual production of green plants in the sea amounted to 150,000 million tons, which yields only about 30 million tons, or 0·02 per cent, on the world's fish markets. Can we not use some of the 99·98 per cent of this lost production? Properly treated, the plants *could* form excellent silage. Or even if we reduce this surplus to one-tenth or even one-hundredth and concentrate on catching only the zooplankton, this should leave us some 1,500 million tons a year to tap. Certainly there is plenty of plankton in the sea to be had for the taking—but can we take it?

Collecting marine plankton for food can be considered under two quite separate topics: as an emergency food for shipwrecked mariners, and as an economic proposition aimed at feeding the world's ever-increasing populations.

The shipwrecked mariner in his lifeboat or on his raft needs to eke out his existence, to remain in sufficient health long enough to be rescued and enable him to recover completely. His main needs, apart from protection, are water, food and vitamins. Plankton can supply all these, not ideally, possibly somewhat dangerously—but the alternative is so much worse! Dr. Alain Bombard cast himself adrift in the Atlantic in 1952 to prove to others that man could survive under such conditions, living exclusively on what he could get from the sea, for much longer than the normally expected ten days. He advocated small doses of sea water during the first few days, and while the body still possessed its normal water content, but beyond this first period taking any sea water can only make things worse. Sea water contains about 3½ per cent salt, while the kidneys can only deal with a little over 1 per cent, and this figure is soon reached in the blood if natural water losses are not replaced. Taking more salt can then be fatal due to acute nephritis. Dr. Bombard's idea was that as the normal blood contains less than 1 per cent of salt it can accept sea water with its essential liquid until the limit of salt concentration is reached—but not beyond it—thereby delaying the first onset of dehydration.

The body fluids of fish and plankton mostly contain much less salt than sea water, and so can be taken to increase the water content of the body. Fish juices are probably fairly reliable but plankton juices less so because of the very varying nature of plankton. Plankton is good food, high in protein and fat content, perhaps not so good as fish either physically or psychologically, but limited amounts, if fish cannot be obtained, would help to eke out an existence and increase the chances of a successful rescue. 'Eke out' is probably a suitable phrase, as, even if abundant, plankton would not be safe to eat in quantity because of the possibility of excesses of nauseating or unpalatable flavours and over-rich fats and vitamins which in excess can be fatal. Some plankton, even if fish is plentiful, would be advisable in the diet of the shipwrecked mariner because it does contain some of the vitamins, especially 'C', which are lacking in fish, although fish livers in particular contain ample vitamin 'A'.

Unfortunately, the best catches would be made at night (p. 155) when it is too dark to see what is happening and to sort out the catch, but nevertheless plankton is there, and to have a small net for catching it might make all the difference between life and death. Dr. Bombard survived for sixty-five days, drifting from the Canaries to the West Indies. He had no rain for twenty-three days; he drank sea water for the first fourteen and fish juices for forty-three, and his plankton diet kept up his vitamin supply. It cannot be said that it was a pleasure trip and he suffered very greatly, but he did arrive alive, and he recovered at least sufficiently to write his book even though his later death would be in part due to his severe privations. Nevertheless, though far from ideal, in such circumstances plankton as food is most certainly worth while.

As a commercial concern, catching plankton for food, be it for human food direct or for animal feeding stuffs, is quite a different proposition. Before welcoming plankton as one possible answer to the world's food supply, it is first essential to look at some of the difficulties.

Let us admit that plankton in what seems like unlimited quantities is there for the taking, that its protein value is high and indeed that there is the basis of a rich supply of food available to anyone who troubles to collect it. The problems are in the collecting and are not so much biological as engineering, and they are concerned with separating it from the sea water and the salt. The often-used metaphor of a 'soup' of plankton rarely exists in nature and the total volume of plankton compared with the water in which it lives is extremely small.

The first choice would be to use a plankton net or a similar filtering device. This at once leads us into difficulties about mesh size. The finer the mesh the more slowly it will filter the water and the more easily the meshes will become choked. The larger the mesh the greater the loss of the smaller organisms through the net. Because plankton has such a range of sizes there is no ideal size of mesh; either we use a fine mesh in an attempt to capture a large proportion of the plankton present in a small volume of water, or we use a coarser mesh and catch only the larger animals from a larger volume of water.

If we use a centrifuge instead of a net the same principle applies, we can either extract only the larger organisms from a relatively short or slow spin or we can extract also the smaller ones using a longer or a faster spin.

The next problem is that of dealing with the immense quantities of water, and this is a double problem, one of handling the water and one of supplying the necessary power, using either nets or a centrifuge. The cost of the power must be deducted from the returns and unless free power is available this is a very serious item. Free power could be available in tidal estuaries—where there is usually more silt than plankton—or in certain places round the coast where there is a strong tidal run. These places do not, as a rule, have a reliable plankton content; sometimes it will be moderately rich, at others very poor, or made up of comb-jellies and other unwanted species. The richest and most reliable sources are those of the cold waters of the Arctic and Antarctic, miles from the places where plankton is most wanted, and miles away from laid-on power supplies.

This leads us to the next difficulty, one of preservation. Once it is caught plankton will not keep long, and the time will depend on temperature. In the tropics it would be rancid or putrid within a hour or so, and it cannot be stored in quantity in ice in a fish hold to keep during transit from the Arctic as can individually handled fish. Plankton would need to be deep frozen, or much more preferably, dried on the spot using the same type of machinery that is used to produce dried milk. The apparatus, the power to work it, the personnel to use and maintain it, must all be on the spot, again adding to the production costs.

Towing a plankton net for a biological sample is all right, but it is not feasible merely to increase the size of the net to give a larger sample. Fine-meshed netting offers a big resistance to the water, it is delicate and easily torn by sudden surges due to waves or the ship's motion, so that a very large net is not a practicability and it would be impossible to handle large fine nets from a ship, or in a tideway, especially in bad weather—and it will often be bad weather where the plankton is richest!

Perhaps the most efficient method would be to build an artificial whale or basking shark in the form of a ship with an 'open mouth' below the surface—so as to avoid all floating debris such as timber, straw, seaweeds, bottles, feathers etc. This open mouth would lead to revolving fine-meshed drums of monel metal netting, revolving to reduce choking, and constantly passing the plankton to the ends from which it could be continuously extracted in a concentrated form by pumps. Then it would need to be reconcentrated to remove all the surplus sea water before being passed to the drier otherwise the deliquescent sea salts would attract the moisture again. All the salt could not be removed, however, and the dried plankton would still have to be packed in airtight containers. To increase the filtering efficiency the ship's propellers could be inside the stern of this plankton tunnel. Such a ship could surely catch plankton in quantity, but could it do so economically? Because of its design and the special apparatus it contains it might well cost twice the price of a conventional trawler to build. Because of its shape and the resistance of the filters it would cost more in fuel to run than a trawler. The fact that the delicate parts could only be serviced or repaired in dry dock would reduce the available time at sea and add heavily to maintenance costs.

Assuming such a ship to be the same size as a trawler, the gape of the 'mouth' could scarcely exceed an oval 15 feet × 6 feet or about 50 square feet. This is seven times the area of a 1-metre plankton net but it could fish twenty-four hours a day at perhaps 6 knots and so catch 2,000 times as much in a day as the plankton net catches in a quarter hour at 2 knots. In an average area the 1-metre net might be expected to catch $\frac{1}{4}$ lb though it would often be less; in a rich area the catch might reach 5 lb but would average about 2 lb. In other words our ship could catch 500 lb a day steaming to and from rich grounds where it might catch 4,000 lb a day. For a twenty-one-day trip this could be 2,500 + 44,000 + 2,500 lb or about 22 tons wet weight yielding about $2\frac{3}{4}$ tons of dry weight plankton. A trawler on a similar trip will catch 500-2,000 kit or 30-120 tons of white fish (wet weight) at less than half the cost and worth a great deal more per ton in the market. This in home waters does not look like being a commercial proposition. It does not mean that it never will be, and indeed the prospects in the rich plankton area off Peru (p. 112) offer much brighter hopes—but the fish are easier to catch there too!

If a conventional type trawler towed several large plankton nets, say six nets of 2 metres in diameter, the total cost of the dried plankton caught would be about £2,000 per ton and on only the basis of the amount of protein present would be about 20 times the price of fish. This ignores any psychological factors and the serious possibilities of unknown toxins and excess vitamins that might reduce its value or even make it dangerous.

Out of the many millions of tons of plankton in all the oceans of the world what proportion could we hope to filter out? We should lose such a large proportion of the minute organisms through our filters that we would be doing well to retain a third of the plankton out of the water we actually filter, but this is a minor point compared with the proportion of water we could handle. The sea is so vast that even a tremendous human effort would seem quite negligible. The whole Gulf Stream, for example, is only a small part of the world's ocean mass, yet as said on page 108 more water flows in the Gulf Stream in a day than in Niagara in three years. There is an anonymous verse which runs:

> If all the sea
> were one sea
> That would be
> 1,370,232,000,000,000,000,000,000 cc.

One cubic centimetre is not very much but this figure is equal to 301,471,060,000,000,000,000 gallons. If we had 10,000 extremely efficient filtering stations, each dealing with 100 million gallons a day it would take about a million years to deal with the equivalent of all the sea water once. As things are at present it pays us far better to let nature takes its own course and let the fish feed on the plankton, even at several stages removed, feeding sometimes twenty-four hours a day and certainly seven days a week, no overhead costs, no labour difficulties, and then catch the fish even if our present catch is only 0·02 per cent of the ocean's productivity, though we certainly could catch more than we now do by exploiting the world's fisheries more rationally.

Changes in costs, a product of pharmaceutical value from plankton out of all proportion to its mere food value, or a radically new engineering design are of course all possibilities, and might easily change the arguments used here against the commercial catching of plankton in any indiscriminate way.

There are, however, several successful commercial ventures for catching plankton which should really be classed as 'fisheries' as are the shrimp 'fisheries'. Three examples can be given here: the mysid fishery in India, the krill fishery for *Meganyctiphanes* (Fig. 22; 5) in the Mediterranean, and the fisheries for larger planktonic prawns (Peneidae) in several places in the tropics. Each of these is based on the catching of fairly large crustacea, sometimes attracted by lights, and they are not indiscriminate plankton fisheries.

It has been said that, as the world's population increases, the need for food will outweigh the pure economics and that plankton will then need to be caught at whatever cost. With the coming of the atomic age there may be possibilities, but with conventional power supplies the shortage of fuel would be every bit as important as a shortage of food.

As an alternative to catching plankton as food, can we artificially enrich the sea to increase the growth of plankton and so increase the fish supply?

This method of fish farming is very effective indeed in fresh-water ponds in the middle and far east, and yields very striking economic returns in ponds specially built for the purpose and as an 'extra' in places like the rice paddy fields. Can the same principle be used in the sea? Before attempting to answer this, it is first necessary to consider the factors that contribute to making fish farming a success and then weigh the difficulties in applying the same ideas in the sea. The greatest successes have so far been in warm countries, and in ponds or lakes where the water is either retained in the pond or changed very slowly. The fertilizers are thus retained and are under proper control, the process can be watched and the effects can be properly assessed. The fish grown in these ponds are largely herbivores, feeding directly on the increased plant growth supplemented to some extent on herbivorous copepods etc., at only one stage removed. In the colder climates it has been shown that the addition of fertilizers and lime can increase the amount of insect life etc. in trout lochs and give a substantial increase in yield, but these fish are caught primarily for sport and the economics of the cost of the treatment compared with the actual food value of the increased yield are of only secondary significance.

Most marine fish are carnivores, feeding at least at two or three stages removed from the original plant production, and part of the food of the bottom-living fish may be four, five or even more stages removed. As was seen in Chapter 10, only 10 per cent of food eaten becomes established in the next stage so that a much greater total increase of plant growth is needed to produce the same increase of yield of carnivorous fish as of herbivores. These extra stages in the food chain also increase the chances of some link in the chain getting out of hand so that the final result is not according to plan.

Because of the size of the sea, it is advisable to consider the problem at three distinct levels: the small almost enclosed body of sea water with a restricted exchange of water with the outside, such as a shallow fjord or the Scottish west coast lochs in which preliminary experiments have been done; a relatively small but unrestricted area such as an open bay; and the sea itself.

The first factor to be considered is what happens to the added fertilizer, will it be absorbed or will it be washed away? Experiments have shown that the extraction of the fertilizer from the water is remarkably fast, taking less than seven days, partly due to the immediate utilization of it by the plants and partly because it is adsorbed by the mud particles (i.e. it adheres firmly to the outside of the grains of mud) from which it is only slowly liberated. This means that the fertilizer is largely retained *in situ* and not washed away as quickly as one might expect.

In our almost enclosed body of sea water the losses are thus negligible, but the fertilizers are nevertheless not used to our complete satisfaction.

These places usually contain a wealth of seaweeds and other attached algae and it is rather these than the plankton which seem to get the most benefit. The absorbed fertilizer is so slowly liberated from the muds that it is temporarily lost; although it would eventually be liberated it would take a long time. It is thus difficult to assess the actual amount used by the plankton, but it is a relatively small proportion and it is this that will benefit the fish most.

Further, such confined places rarely form a suitable habitat for the type of fish we would want to grow for economic purposes even though there are plenty of gobies and other shore fishes that can live there. We would thus have to 'weed' the area of unwanted fish and replace them by transplanted fish or fish bred in hatcheries. All of this is expensive, and only of doubtful value because the confined conditions would not be ideal and the fish would do their best to migrate out of the area. This is an important factor in marine fish which did not need to be taken into account in the fresh-water fish farms. Economically, it does not look too hopeful, as with the cost of fertilizer, labour, hatching or transplantation it would probably cost more to rear each fish than its market value.

If, instead, we consider an open bay some of these disadvantages disappear; the seaweeds are not a major item, the bay is an acceptable natural environment and would be naturally re-stocked. If we choose one where the tides do not replace the water each time we stand a good chance of a large proportion of the fertilizer being retained, and a consequent increased growth of plankton. The plankton, however, would tend to be washed out to sea gradually and lost, but some increase may be left to encourage the growth of the bottom fauna and so of the fish. But how much is 'some'? We do not know, and it would be very difficult to assess the real result in terms of fish. Shallow bays are often excellent nursery grounds for flat-fish, but before the fish reach marketable size they migrate to deeper water, and in a bay of this sort there is no barrier to prevent them. Trying to assess the benefit of such a fertilization would be very like assessing the value of fertilizing a farmer's field by estimating the increased growth of local foxes which had been eating the increased number of rabbits. It *might* be a good thing to do, but considering the small proportion of the fertilizer which would actually become fish flesh it seems rather unlikely!

Turning then to the third possibility, that of the open sea, we lose all the disadvantages mentioned for the other two, and we can make some calculations of costs and probable returns. The most important new factor that impresses us in these calculations is the enormous amount of water in the sea even in local areas. Farmers measure their holdings in acres, there are 640 acres in a square mile, and a square mile of sea is a very small unit indeed. However, we can use this small unit as a basis for our calculations. Thinking first in the terms of phosphate content we learn from the marine chemist that the summer level in the sea is about 0·2 microgram atoms of phosphate/phosphorus per litre. Translated into terms of sodium phosphate, and considering only the top 50 metres of water (the photic depth, at which there is enough light for the plants to grow) this works out at 1·64 grams per square metre of surface, or 1,406 lb per acre, or about 4 tons per square mile. The summer level of phosphate in the sea is the depleted figure after the plants have had their spring growth, and we should want to double this figure to give any real increase in phosphate content. After the summer growing season, and after many of the plants and animals have died off there is a regeneration of nutrients from their decay and with the winter mixing (p. 111). This results in a winter level of about four times the summer level so that doubling the summer level would not be at all excessive. Not only do we want to double the summer level of phosphate, but we want to maintain it at the higher level so that a single fertilization is grossly inadequate. To maintain the level we should need to add our fertilizer about every two weeks during the spring increase of plant growth and monthly thereafter for about four months only, a total of about ten applications per year.

Using superphosphate, which has only about one-quarter of the phosphate content of sodium phosphate, but which is the usual form of fertilizer, we would need sixteen tons per square mile at each application. We would also need to add other fertilizers in proportion, especially nitrate, and the total tonnage needed would be about four times the superphosphate. It would be pointless to apply one without the others as the plankton growth would be limited by whichever substance was in shortest supply. Basing our calculations on superphosphate at £15 per ton, and sodium nitrate at £25 per ton, this works out at £1,440 per square mile for each application, or £14,400 per year without any allowances for transport and labour in distributing it. The North Sea has an area of about 125,000 square miles! The annual yield of fish from the North Sea is in the order of £50 million or an average of £400 per square mile, though certain parts will yield much less than the average and other parts considerably more, as much as £1,000 per square mile. But is it worth spending £14,000 to double the plant production even in the best areas, when double the yield would only give an extra £1,000?

More than that, doubling the plant production would be no guarantee at all of doubling the yield of fish; there are so many stages in the food chain, as well as losses at each stage, and things can go wrong at any of them. One example of this was given on page 138 in reference to 'red tides'. Here an abnormal increase of fertilizer brings about the sudden increase of a toxic dinoflagellate instead of the normal plankton, and this results in wholesale destruction of fish and the ruination of tourist trade to popular seaside resorts.

When the extra fertilizer is used up, the organisms of the red-tide die off in their millions and millions and things gradually return to normal. If there is fertilizer to spare, how much better to put it on the land and increase our crops under proper control with a reasonable hope of a fair economic return and extra food for the world! Indeed, there is so much rich fertilizer unused in the deep oceans that if we could do so it would be better to extract it from the sea instead of putting it back.

A more hopeful way of fertilizing the sea would be to increase the turnover between the nutrient rich deep layers and the depleted surface layers, especially in the warmer oceans. This is not a biological problem, but an engineering one, and not within the scope of this book which is, however, sufficiently ecological to remind the reader that transference by the bucketful, or even by the million gallons, is neither here nor there.

This rather discouraging chapter does not mean that all efforts to improve marine fisheries by artificial means are doomed to failure. In Chapter 10 it was emphasized that the greatest loss of fish occurred in the planktonic stages. If we can rear fish beyond that stage, simply by giving them enough food and protecting them from their natural enemies, we could increase the potential fish stocks—provided there is sufficient natural food for them where they are to be liberated. Another way of doing much the same thing is by catching large numbers of young fish in their natural nurseries and transplanting them to places where the food is more plentiful than it would be where the fish would normally migrate to. This has been done for a number of years in the North Sea, taking young plaice to the Dogger Bank which provides a better natural food supply than the shallow sandy shores of the continent. It would help, too, if we can increase the available food by reducing the numbers of other less valuable species eating the same foods. This could be a way of getting more human food out of the sea, but the economics depend on the ratio between the increased value of the fish caught and the cost of rearing and transplanting the fish, or the cost of the 'weeding' operations.

The world's population is increasing at a frightening rate, and increased populations mean increased need for food. The sea is an important source of this food and will give better and better yields as we learn more and more about it, and learn to exploit it in a controlled and rational way. This means the international co-operation of biologists, chemists, physicists, engineers, statisticians, politicians, fishermen and all the various ancillary vocations and trades. It can be done and, gradually, it is being done.

This book is about plankton, and the part plankton plays in this problem, it is not a book on the economics of world population. Nevertheless, plankton forms a natural community of living things and its study is bound to show many parallels with the populations of men as living things. In the previous chapters of this book, time and time again, the interdependence of one living thing with another is emphasized. Nothing is free from the complexity of its surroundings. If conditions are right, and there is adequate food, there will be something to eat it, and the more food the greater the numbers, but in turn there will be something else to eat those. As food becomes short the numbers dwindle but the result is a regeneration of the prime nutrients and so the cycle is constantly maintained. With humans, conditions are different as we have learned in part to control our environment, we warm our houses in cold weather, we store our food at harvest to spread it out over the whole year and we have organized transport to distribute it. How absolutely natural that our numbers have increased! On top of this we have reduced our worst natural enemy—disease—and are doing our utmost to prevent warfare. This inevitably means continued increase of population and continual demands for more and more food and more and more organization in distributing it. As Lord Adrian said in his Fawley lecture in November 1959—'Much remains to be done before the under-developed territories of the world can be freed from poverty and hard labour, but the objective cannot be attained if the timing is not adequately supervised, if the population of the world is allowed to increase more rapidly than we can increase our means for feeding it.' Sir James Gray in his presidential address to the British Association for the Advancement of Science at York in 1959 said 'the writing on the wall is tolerably clear; if Man behaves like an animal and allows his population to increase whilst each nation steadily increases the complexity and range of its environment, Nature must take her course and the Law of the Jungle prevail'.

Man is a live animal, and his populations are living communities, but he does have the potential ability to exercise control. Without it, the continued supply of increased food will mean more and more people to feed and greater demands for more food. Always, pending the ideal, there will be those near the sources of food and amply fed, always there will be those on the outskirts who cannot get enough—and always there will be more. With control of numbers—and the method we hope will have no parallel with plankton!—there could be ample food for all. Without it, more effort to find more food merely means that instead of starving millions eventually, like the dinoflagellates of the 'red tides', there will be starving multimillions. Until we learn that control we shall continue to look to the sea for more and more food, and always our sea-food will be linked with plankton.

INDEX