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INTRODUCTION

This book is a first attempt to present a unified account of algal ecology without the artificial division into freshwater and marine communities. The variation in salinity is continuous from rainwater, through freshwaters, the ocean and to hypersaline land-locked waters and similar basic principles apply to the study of all waters.

Ecology is the study of organisms in their natural environment and therefore the 'organisms' and 'environments' are of equal concern to the ecologist. However, both 'organisms' and 'environments' have intrinsic properties and these, though not directly the concern of the ecologists, nevertheless require understanding. For example, environmental factors include the anomalous properties of water, the solubility of gases and solids in water, the penetration of light, and temperature–density relationships, while organic factors include intrinsic growth rates, life cycles, dispersal mechanisms of species, etc. Some of these facets are to a varying degree independent of one another (e.g. the input of solar radiation, current effects, time of nuclear division, selection of certain metabolic pathways) and can be discussed in relative isolation, though it is well to realise that there is some inter-reaction between most, if not all, properties of the environment and of the organism. Other aspects are so interlocked that discussion of one in isolation is virtually meaningless, for example the availability of nutrients such as nitrogen, phosphorus and silicon is intricately bound up with the rate of cycling by organisms, and the rates of change of populations are inextricably bound up with the fluctuations of the physico-chemical factors. In the aquatic environment, much more so than on the land, the growth of the organisms themselves has a rapid and dramatic effect on the environment and whilst seasonal climatic changes mould the environment and are often intensively studied the effects of the organisms are less studied but often more dramatic. Inevitably some habitats have been given greater consideration – some deserve it – but equally the treatment is a reflection of the unequal effort in the field and I hope that I shall succeed in bringing neglected aspects to the consideration of the reader. On the land the angiosperms of the grasslands, forests, etc. provide the fixed carbon for utilisation by all other organisms but in the aquatic environment the algae almost alone, provide the complex organic molecules for the vast range of animals in the water. It is perhaps worth emphasising that the ocean waters form, by far, the world's largest habitat. As work on this book progressed I began to realise what a daunting task I had undertaken since the range of algal ecology is comparable to that of land ecology.

Clearly the literature is too vast to cover in detail but one of my aims is to lead the reader into the relevant literature by illustrating points with *quoted* examples rather than generalised statements. Most examples have been taken from recent accounts and to keep the literature list within reasonable limits I have not referred to much of the earlier work. This does not imply any criticism of the early workers, and students should certainly consult the historical data for there is much of value to be discovered and much modern work is merely repetitive; however, to have included the references would have doubled the number. No doubt I have failed to refer to some important papers and to many which readers regard as important, but a choice simply had to be made. Works which merely list species are often valuable for phytogeographical studies but I have quoted them only if they have some special value. Individual lakes, sites, etc. are quoted whenever possible. Although I realise they may have little relevance to many readers, they are nevertheless essential to ecologists since they enable future workers to return to sites to check earlier data, continuity, pollution effects, etc. It is as important to an ecologist to be able to return to a site as it is to a taxonomist or experimentalist to be able to obtain a type species or authenticated culture. A further aim is to pin-point the diverse aspects of algal ecology, references to many of which are buried in obscure journals, or journals outside the normal range consulted by botanists. This necessitates referring to topics which have been investigated only in a cursory manner and the numerous mentions in the text to the paucity of data are added purposely to highlight the need for intensive studies. No apologies are given, for many fields are utterly neglected and desperately require attention.

Throughout the reading of the literature, an obvious split between the floristic and experimental approaches is revealed: *both* are absolutely essential parts of ecology, but rare are the publications which attempt to combine them. Those workers who disapprove of lists of species are denying the reality of the complexity of algal communities which *must* be described somewhere. Poore (1962) summed this up neatly: 'the exact description and characterisation of the community thus becomes essential to all who work in the science of vegetation; for it is important that the ecological findings should be related to communities which are well described. Not to do so is tantamount to carrying out a physical experiment without stating the conditions'. Equally, those who do not welcome data based on chlorophyll estimations, ^{14}C uptake studies etc., are rejecting valuable even if simplified approaches to complex situations.

Both approaches are *essential* elements of ecology and neither takes precedence but data from the former have simply been accumulating over a longer period of time. There are unfortunate comments in the literature that the organismal–community approach is difficult and to be side-stepped wherever possible. It is not possible to do this and I can best quote Margalef & Estrada (1971): 'Identification of species is tedious and time consuming, but it brings high quality information – provided the identifications are reliable. *No short cuts exist* for this and of course nothing, no information – is given freely' and Nicholls & Dillon (1978) 'direct microscopic determination of biomass appears to provide the best estimate of phytoplankton biomass'. Nevertheless I have in the succeeding chapters cut down to a minimum the listing of species, though I realise this will be criticised by those who would like to have complete accounts of communities. The full data can however often be found in the quoted papers and one must remember that the large number of species in most associations is such that to quote them would make a most unwieldy account. I have therefore attempted to strike a balance and point out other facets of the biology of the species, associations, etc.

Ecologists are concerned with many levels of organisation although many workers confine themselves to one level and few publications attempt an overall view. This is not surprising since the levels of organisation involve single species, communities of many species, interacting communities and the ecosystem itself. At the first level there has been only slight study of genetic variability but this has been sufficient to show that such variability is considerable and important.

Some of the work in ecology is moving towards biochemical functioning within natural ecosystems rather than in the unnatural conditions in laboratories and indeed little ecological significance can be attached to many laboratory-based experiments until similar effects have been demonstrated in nature. The biochemical aspect is also compounded by interactions between algae and other organisms. Another approach, which is in its infancy and too often has to rely on extremely crude data, is that of mathematical modelling of the ecosystems. This relies on the skill with which the data are obtained from the traditional approaches and is only as good as the initial observations.

I have attempted to indicate areas where studies are needed but I am all too conscious that someone, somewhere, may have completed studies and it is I who have regrettably missed the appropriate publications; in all such instances I apologise and I shall be delighted to hear of the results.

The aquatic environment is not uniform but contains within it numerous spatial niches and these are each colonised by very well-defined communities of algae – the open water by the phytoplankton, the sediments by the epipelon, plant surfaces by the epiphyton, rock surfaces by the epilithon, etc. There is slight interplay between these communities but they have a high degree of independence and need to be discussed separately. The interactions with other communities and between species within the community are as yet largely undocumented.

Though the subject of this book is algal ecology this, like higher plant ecology, cannot be isolated from interaction with the animal world. The algae live in a solution of animal waste products of varying concentration, are grazed directly, or indirectly following bacterial decay, and in many habitats are increasingly influenced by the single most active animal – man. Algal ecology has, however, one fortunate feature which is absent from higher plant–animal ecology and that is the almost cosmopolitan distribution of most freshwater species, of oceanic phytoplankton and even of some seaweeds (though here the greatest degree of geographical isolation occurs). The genera therefore tend to be familiar to workers in different continents even if some of the species are different. Equally, however, algae are not ubiquitous throughout each habitat-type and each water body has its own peculiar selection of species.

As mentioned above there are two equally important sides to ecology and it is not always easy or desirable to separate them. One aspect is the detailed analysis of communities, the kinds and numbers of organisms and seasonal changes within each discrete community, and the second is the functional aspect of the individual species and of the communities as a whole. For the study of both aspects it is necessary to define quite clearly the individual, often restricted, habitats in which algae live and then to analyse the physico-chemical background of these habitats. The approach to community structure involves the use of precise sampling techniques and is dependent upon the continuing development of basic and all-important taxonomic revisions of groups of algae.* Here much remains to be achieved in spite of 150 or more years of study. Wherever the problems of identification are too great, effort can always be diverted from a synecological to an autecological approach in which a single, more readily identified, species is selected for study. The functional aspect is dependent upon developments in physiology and biochemistry. It requires the same attention to habitats but also to sophisticated techniques for detecting the operation of processes and for measuring the rate of such processes under natural conditions, for it is here in nature that the rates of carbon fixation, nitrogen fixation, carbohydrate secretion etc., are of prime significance.

Ideally it is possible to describe the conditions under which every alga lives, how its functioning is affected by and how it interacts with the habitat. Equally, the precise habitat of each alga is theoretically definable and this is easier since a relatively small number of habitats are occupied by a large number of species. However I find it difficult to define *some* of the rather diffuse habitats which algae occupy; it is essential for comparative purposes to be able to identify habitats precisely at numerous sites and many more detailed studies of microhabitats need to be undertaken. Few autecological studies of individual algae have been attempted (examples are *Ascophyllum nodosum* (Baardseth, 1970), *Laminaria hyperborea* (Kain, 1971)) and many more need tackling along the lines of the excellent Biological Flora accounts of the angiosperms published by the British Ecological Society; but even here only a fraction of the species has been tackled. The problems with algae are more acute than with angiosperms but they are not insurmountable and present a challenge to phycologists. A similar series of accounts of algae is slowly being published by the British Phycological Society, but there is a massive amount of work to complete throughout the world.

There is a direct interaction resulting from man's waste products but even more important are the indirect and often unconscious effects of his economic activities; these threaten to be even more disastrous than his natural activity. The study of ecology is thus in the broadest sense the study of interaction – give and take, stimulus and response, stimulation and feed-back. Since quantitative field and laboratory observations can be made, a mathematical base is being gradually defined and from the generalities of this base a new systems ecology is evolving.

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* As far as has been possible, names of European marine algae have been brought into line with the 3rd edition of Parke & Dixon (1976) *Checklist of British Marine Algae.* A few lists compiled by European workers have not been altered since there is some slight doubt about the application of the British names to the more distant material. The Cyanophyta have been quoted as in authors' papers and not altered since I believe that there are important ecological variants which should not be submerged in a few taxa. This does not imply that revisions are unnecessary, they are necessary, but must be based more on ecological–cultural studies.

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Algal ecology thus involves a continuum of web-like interactions between the environment, the algae themselves, the animals and man's industrial disturbance, but readers and publishers expect chapters and not a continuum of discussion. As previously suggested some sections of the subject can be isolated, e.g. the intrinsic physico-chemical environment (Chapter 1), the littoral benthos (Chapter 3), etc., but compartmentalisation into chapters inevitably tends to isolate the various aspects. One must always stress that nothing is operating in isolation in ecology and even where the data are sparse, e.g. in the all-important aspect of algal–animal relationships, their importance is immense and bears no relationship to the number of papers published. A further important aspect of algal ecology is the breakdown of algae by fungi and bacteria and the re-cycling of their components, but regrettably little can be written on this aspect because the literature is almost devoid of studies. Algae are the primary carbon fixing organisms in the aquatic environment and are thus an indispensable link between solar radiation, the complex solution of chemicals in the waters, *all* aquatic animals and eventually man, whose existence is dependent on oxygen evolved in plant photosynthesis; some 50–90% of this oxygen is estimated to come from algal growth. The original oxygen of the earth's atmosphere is presumed all to have been derived from algal photosynthesis (Cloud, 1968) and it plays a vital role in geochemical evolution of the lithosphere, hydrosphere and atmosphere (Cloud *et al.*, 1965).

Two branches of science, limnology and oceanography, have developed and have, unfortunately, to some extent grown apart. Limnology is concerned with the freshwaters on the land surface, and oceanography with saline water, though the most saline water occurs in inland lakes and the salinity of the seas varies from 'freshwater' (e.g. the melting ice of the polar regions and the upper regions of enclosed seas such as the northern part of the Baltic) to the somewhat more saline tropical evaporation basins (e.g. the Red Sea, Gulf of California, etc.). The distinctions within these compartments of science are thus merely of degree. Few if any organisms are present in both fresh and saline waters but the same *kinds* of organisms with *similar* life forms are present, as is obvious if one compares the forms of epiphytic or epipelic algae in marine and freshwater habitats (Fig. 2.1*a*). Many factors operate in a similar manner in the sea and in lakes, e.g. light penetration and temperature stratification, and can be discussed together. Techniques of sampling and of measurement are essentially similar and the distinction between the two is grossly distorted by the fact that sampling in the Atlantic Ocean or in the Pacific Ocean requires a large expensive ship whilst a rowing boat is adequate on the much studied Linsley Pond in Connecticut.

Another important habitat in which algae grow is the so-called sub-aerial habitat: they occur on the surfaces of plants, especially in the tropics but commonly on tree bark throughout the world and on soils of all types. Algal floras exist in such unlikely habitats as moist rock surfaces, even within rocks in arid zones, and on the surfaces of permanent snow fields. These floras tend to be confined to a relatively small number of highly characteristic species often with an almost world-wide distribution.

I see no virtue whatsoever in separating off a section of so-called applied algal ecology but considerable studies have been undertaken on man-made systems utilising water, e.g. sewage disposal and water supply installations, where the algae are beneficial or detrimental to the system. Thus algae in reasonable amounts provide oxygen, take up nutrients and *clean* the water but in too large amounts produce filtration problems (e.g. in waterworks) or decay and utilise excessive amounts of oxygen (e.g. in the deep waters of lakes such as Lake Erie and in relatively enclosed oceanic basins) with subsequent detrimental effects. Other systems have been evolved to utilise algal growth for food (especially in the Pacific region), for extraction of organic compounds, and for production of Crustacea and fish and all of these benefit from and contribute to the study of ecology. Their problems are intricately bound up with basic limnological and oceanographic studies and cannot be studied in isolation or without consideration of the natural systems.

The sequence of topics is deliberately chosen to deal first with a brief survey of the physico-chemical background (Chapter 1), followed by a general discussion of the habitats and communities (Chapter 2). Then habitats exposed first to rainwater as it falls, through increasing salinity and complexity due to percolation, flow and interaction of the water with sediments, etc. are discussed in more detail. Thus, Chapter 3 deals with the flora of bare rock surfaces on mountains subjected almost entirely to rainwater, then with that of the rock surfaces of streams, rivers and lakes and finally with the flora of the rocky sea shore. A similar but geographically restricted habitat involves the free-living species of the algal community of coral reefs and this is dealt with in Chapter 4. The breakdown of the rock and its intermixture with organic matter to give soil, and underwater sediments provides the next habitat group on the land surface, in rivers, lakes and shallow seas, all richly colonised by algae (Chapter 5). At some point a discussion of snow and ice algae had to be incorporated and since these both grow on 'sediments' they are described at the end of Chapter 5. Into this chapter I also fit the algae of hot springs since these algae are growing on and forming a thick mat over the sediments of the outflow streams. In the sediments (and on the rocks) macroscopic algae, other plants and animals grow and these are colonised by attached algae (Chapter 5). The water which has percolated, seeped and drifted past all these communities then collects in rivers, lakes and the open ocean and here the surface layers are colonised by the phytoplankton (Chapter 7). In the chapters devoted to habitats I have made no attempt to present a standardised account but have treated each in the way I felt to be most suitable. Algal floras are the appropriate place to find illustrations of all the algae mentioned. I have, however, included sufficient illustrations to show the diversity of form within each habitat. On these, no attempt has been made to draw the genera to scale but I have indicated the range in the captions.

The remaining chapters deal with certain general and inter-linked aspects – dispersal and phytogeography (Chapter 8), symbiosis–parasitism–grazing (Chapter 9), seasonal succession (Chapter 10), energy flow and cycling of nutrients (Chapter 11), sedimentation of algal remains (Chapter 12), palaeoecology (Chapter 13), and finally eutrophication and pollution (Chapter 14). I have not eliminated all mention of the latter aspects from the earlier chapters, especially when dealing with the less well-studied communities, where it seemed more appropriate to treat all aspects together.

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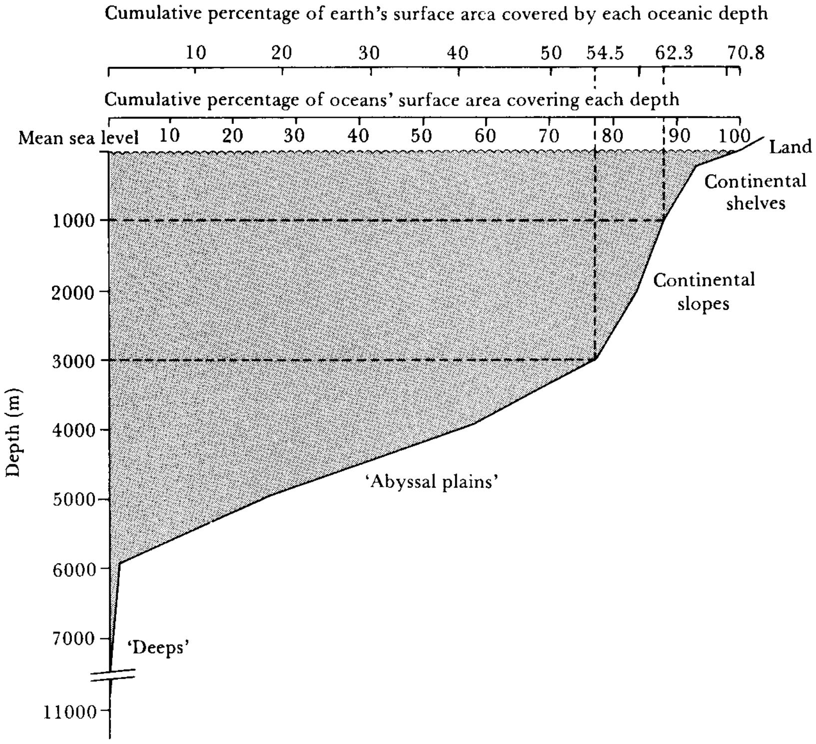
1 The physical and chemical characteristics of the environment

Slightly over 70% of the surface of this planet is submerged under water and much lies at great depths beneath the water. In fact 84% of the ocean has a depth of more than 2000 m (Fig. 1.1). It has been calculated that if the earth were smoothed out it would be covered by water to a depth of about 2440 m. There are two theories to explain the origin of the water on the earth's surface. The first assumes that heating of the material which accumulated to form the earth produced a metallic iron core accompanied by release of vapour and salts. This so-called 'degassing' process is presumed to have occurred primarily during the first 500000000 years of the earth's existence. The second theory only differs in that this 'degassing' process is presumed to continue throughout geological time so that the gaseous material released by volcanoes and hot springs has steadily accumulated. Whatever the process or processes giving rise to the aqueous media there can be no doubt that suitable, but changing,

Fig. 1.1. The fractions of the earth's and of the oceans' surface areas covered by each depth of water. From Russell-Hunter, 1970.



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conditions for algal growth have existed for a considerable part of geological time. Algal ecology is mainly concerned with the present-day situation, but some aspects require an appreciation of past climates, movement of land masses, etc. On the other side of the coin the residues from algal growth are contained in sediments and rocks and are of considerable importance in geological and geochemical studies.

Whilst the oceans are ancient features, lakes and rivers are relatively recent and the majority of the world's lakes are situated in temperate to subarctic regions. They have only existed since the last retreat of the Pleistocene ice sheet from their sites. Most of these lakes, from the smallest to the sea-like Laurentian Lakes, are the result of water accumulation in hollows deepened by the movement of the ice sheet and of glaciers over the surface of the land. They therefore vary in age from recently formed lakes abutting the present ice sheet to those more temperate lakes formed between 12000 and 15000 years ago. Lakes in tropical regions have a different origin, for here the water accumulates in basins formed by tectonic activity, e.g. the rift valley lakes of East Africa and the crater lakes located in extinct volcanic cones. There are many more minor agencies involved in lake formation and for a full and fascinating account the student should consult Hutchinson (1957).

Freshwaters form only about 1% of the total global area of water, so the total contribution to organic production from this source is relatively small. There are however large areas of bog and swamp, flood plains, etc. which are waterlogged (often termed wet lands, e.g. the Sud along the River Nile) and these are good habitats for the growth of algae though, as yet, little investigated.

Only a relatively small number of angiosperms, pteridophytes and bryophytes, form associations within the aquatic environment and they are abundant only in shallower waters and along some temperate and tropical coasts. Algae of course are intimately mixed into these associations though they do not dominate the scene. In the remaining water masses the algae alone of photosynthetic plants colonise the medium and fix carbon. Algae are however dependent upon the influx of solar radiation into the water and hence only grow in the surface veneer which is penetrated by this radiation. The vast mass of water lies below this veneer, which in depth is less than that represented by the wavy line of Fig. 1.1; the mean depth of the ocean is 3800 m whilst the depth to which photosynthetically usable light penetrates is less than 200 m even in the clearest water.

It is impossible to consider algal ecology without an appreciation of the physico-chemical environment and the remainder of this chapter gives a brief outline, for the greater the understanding of these aspects the more perceptive will be the algal ecology.

Circulation of water

No water mass is stationary and therefore aquatic algae are subjected to a flow of water. This relative movement between algae and water results in exposure of the algae to fresh media and a continual removal of extra-cellular products and only in very special circumstances is it reduced to a minimum, e.g. in brine cells in ice, on the surface of soil, in cavities within rock or in epiphytic situations such as within moss clumps. Even the water of the smallest ponds is moved by wind stress on the surface and by convection currents caused by diurnal heating and cooling.

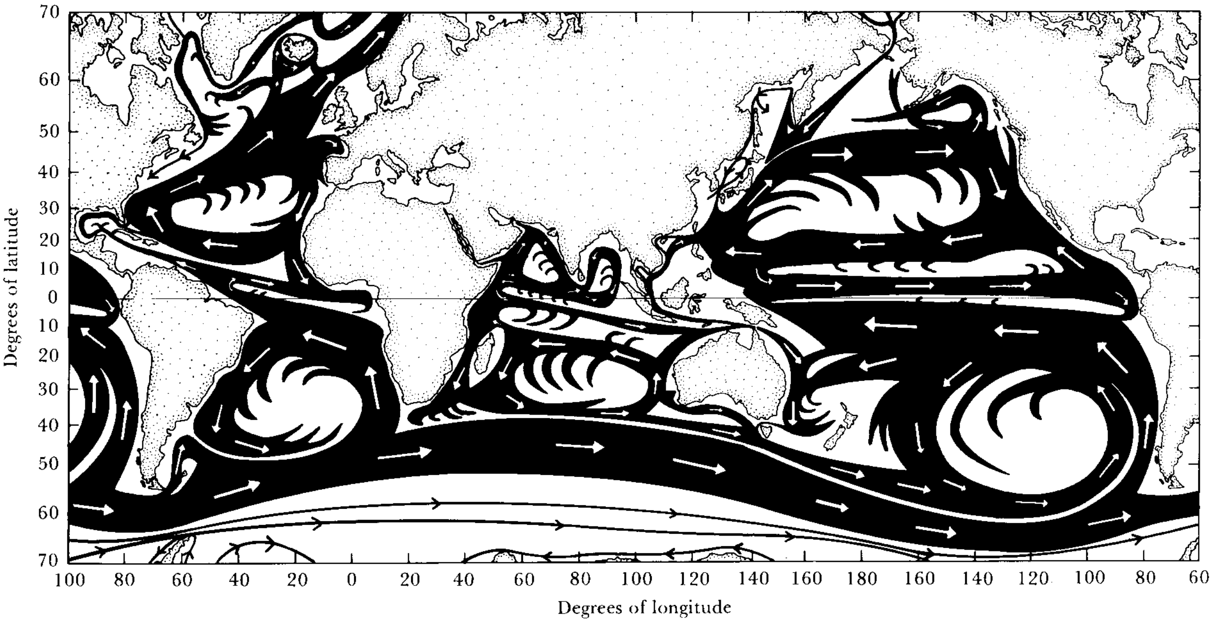
Inflow and outflow move water masses and their contained algae laterally through freshwaters, whilst turbulent mixing results in vertical movements. In large lakes, currents are generated by wind, by the earth's rotational forces (Coriolis Force) and by inflow–outflow movements. Oceanic circulation is even more complex for not only is there a system of surface currents but also a slower circulation of the deeper layers. The surface currents move algae from place to place and the circulation of the deep layers is in part responsible for the supply of nutrients for algal growth. The sun provides energy for algal growth, but is additionally linked to algal ecology, since solar energy generates the winds which couple with the surface layers of the ocean to produce the current systems. Basically these currents form large circular movements ('gyres') flowing clockwise in the northern hemisphere and anticlockwise in the southern (Fig. 1.2). The best known of these currents are the Gulf Stream in the North Atlantic Ocean and the Kuro Shio Current in the North Pacific Ocean. Where the wind blows off coasts, as it does along the western edges of the continents, the transport of surface water seaward results in upwelling of deep, and therefore nutrient-rich, waters and has a dramatic effect on plankton growth (*see* Chapter 7).

In recent years undercurrents have been found in the tropics flowing eastward along the equator; the Pacific undercurrent, also known as the Cromwell Current, is symmetrical about the equator, 300 km wide and has been followed some 3500 miles from 150° W to the Galapagos Islands. The upper boundary of this current is in places no deeper than 30 m and at its maximum velocity it moves at 150 cm s^{-1} or three times as fast as the South Equatorial Current flowing above it in the opposite direction (Knauss, 1965). Thus in this region phytoplankton assemblages can be mixing and moving in different directions within the upper 100 m, and this feature requires detailed study.

The deeper water can often be divided into four layers (upper, intermediate, deep, and bottom water) each characterised by different densities, dependent upon salinity and temperature. Owing to this relationship the deep circulation is often referred to as a thermohaline system. Water differing in salinity and/or temperature, and hence in density, arises in several ways, e.g. inflows of river water, evaporation in the tropics, formation of ice in polar regions. Two examples are often quoted; one is North Atlantic deep water, formed when highly saline Gulf Stream water flowing northward, meets cold, less saline Arctic water resulting in mixed dense water which sinks and drifts southward (Fig. 1.3), and the other example is Antarctic bottom water, which forms when sea ice accumulates as relatively salt-free ice crystals and leaves behind cold brine. This heavy brine sinks and forms the densest known bottom water which drifts northward and can be detected in the bottom of the North Atlantic Ocean (Figs. 1.3, 7.26). In general, most of the deep water is formed by sinking of surface water in the polar regions and to counteract this there is a general slow rise of deep water over the rest of the ocean. Such slow movement of bottom water may transport sedimented algae great distances from their original sites of initial sedimentation, e.g. diatoms from the Antarctic into South Atlantic sites.

At the surface, tongues of water of lower salinity outflowing from massive drainage basins, such as that of the Amazon, can be detected for hundreds of miles out to sea. This system alone is reckoned to discharge some 18% of the total river output of the world and the resulting dilution was thought to lead to a decrease in surface fertility over a million square miles (Ryther, Menzel & Corwin, 1967). More recent work (Cadée, 1975) has shown

Fig. 1.2. The major surface current systems in the oceans of the world.



that outflow of Amazon water does not decrease the nutrient content to the extent reported by Ryther *et al.* and productivity in the offshore waters is not particularly lower than the ocean average. Indeed from the numerous reports of optimal algal growth at salinities of 20–24‰ (e.g., Provasoli, 1965) one might expect greater production in the diluted water. In fact mixing of the Amazon water with water of the countercurrent system actually maintains the growth of the inshore species (Hulburt & Corwin, 1969). The immensity of some of these current systems can perhaps be illustrated by the statement of Pratt (1966*a*): 'The Gulf Stream carries a volume of water north through the Straits of Florida that is more than 70 times the combined flow of all the land rivers of the world'.

Some current systems alter their direction of flow at different times of the year and cause dramatic changes in phytoplankton production and migration of fish, e.g. along the Guinea Coast of Africa. If these currents change irregularly they can seriously alter fish production. The El Niño current which flows in a southerly direction along the west coast of South America brings warm water in contact with the cold Humboldt current flowing northward. The southerly current forms a wedge of nutrient-poor water in the coastal region and in turn depresses phytoplankton production: if this wedge becomes so wide that it spreads outward over the deep offshore water it drives the anchovy out to sea with disastrous effects on the coastal fisheries.

Water motion is a much neglected physical factor which operates on all algae. There are hardly any observations on the relationship between the form of the plankton and the degree of motion of the water. Schöne (1970) found that increasing sea force reduced the length of filamentous diatoms. He thought that the downward motion of air bubbles was responsible and in experiments using streams of air bubbles found that the chain length of *Skeletonema* could be reduced. In addition, the vigorous movement increased the number of cells in the culture, although the cell division of another alga (*Chaetoceros*) was reduced by excessive water movement. Turbulent seas also cause fragmentation of the colonies of the blue-green alga *Trichodesmium* (*Oscillatoria*) and this allows oxygen to enter the central colourless cells where nitrogen fixation normally occurs. The

Fig. 1.3. The surface water and deep-water circulation in the Atlantic Ocean. From Defant, 1961.

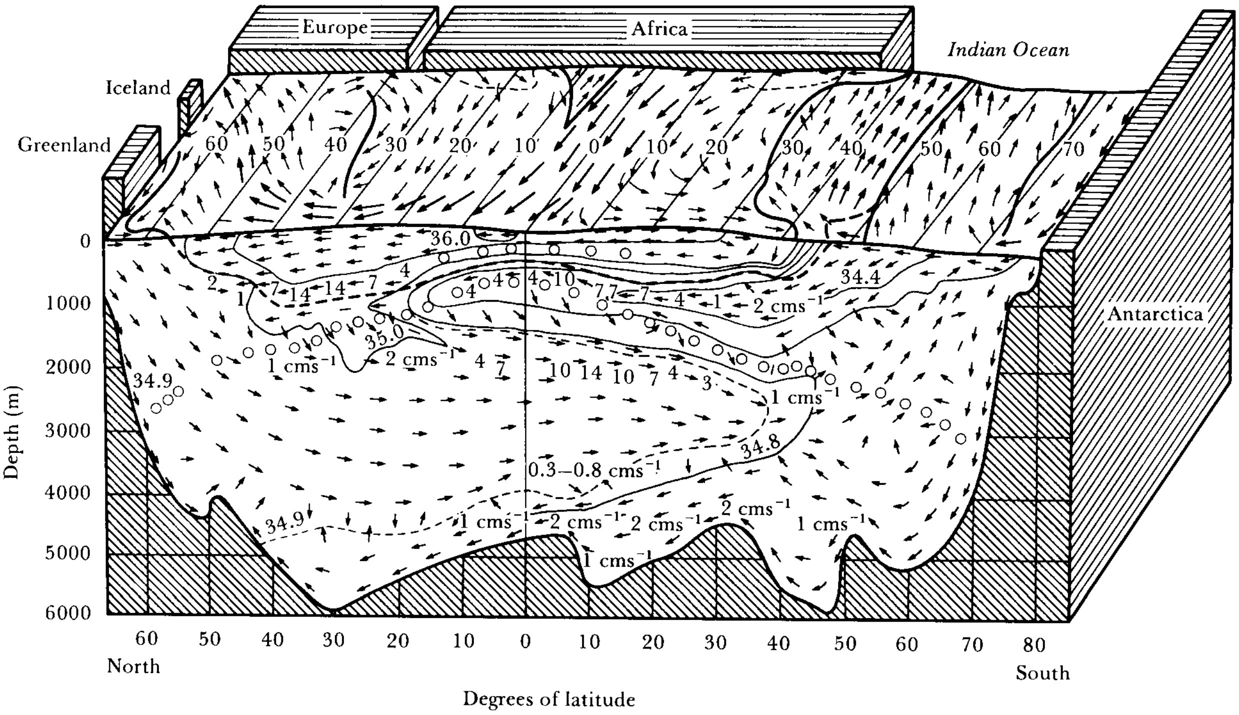


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Fig. 1.4. Some examples of different tidal patterns. *a*, *b*, *c*, predicted tides at three different localities, 18 June–18 July 1951; *d*, levels at San Francisco; *e*, predicted range of tides at Holyhead during 1959 showing the alternation of neap and spring tides, the annual variation in the range of neap and spring tides and the diurnal inequalities; *f*, data from *e* for 20–31 July 1959 enlarged on a day-to-day basis. MHWS, mean high water spring tide; MHWN, mean high water neap tide; MLWN, mean low water neap tide; MLWS, mean low water spring tide. *a*, *b*, *c*, *d* from Doty, 1957; *e*, *f* from Lewis, 1972.