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CHAPTER VI

PELAGIC PLANT LIFE

NOT many years have elapsed since the scientific world became aware that the sea contains plants in abundance floating on and beneath its surface, and that they build up the organic substances upon which marine animals depend. In the open sea the plants are too minute to be detected without the microscope ; so that, until this instrument came to be regularly employed by biologists, it was impossible to know anything about them. Historical introduction.

The first to use the microscope for studying unicellular organisms in the sea was the celebrated Danish zoologist, O. F. Müller, who, in 1777, described one of the most important plants of our northern waters, namely, *Ceratium tripos*. He was succeeded by the microscopist Ehrenberg, who laid the foundation of our knowledge regarding the multiplicity of forms, their wide distribution, and their significance in the economy of nature ; and also discovered the coverings of diatoms together with coccoliths and the skeletons of various unicellular animals (radiolaria, foraminifera) in deposits on the sea-bottom and in geological strata from previous ages. Ehrenberg aroused interest by pointing out the wonderful structure of these coverings, and improvements in the microscope have resulted in fresh wonders being disclosed, which have induced quite a number of capable amateurs to take up the study of diatoms. O. F. Müller.
Ehrenberg.

Classification of these algæ dates from about the middle of the nineteenth century. It is based on the shape and structure of the cell-wall, less attention having been given to the living contents and to the biology. The pelagic forms have as a rule thinner coverings, and a more indistinct structure, than the robust species nearer the coast, and have therefore been less studied. However, occasional samples have now and then been collected from the surface with nets, and researches have been carried out by J. W. Bailey in the waters off Kamchatka, by Brightwell along Bailey.
Brightwell.

Lauder. the shores of England, by Lauder at Hong-Kong, and by Cleve
 Cleve. in the North Polar Sea and at Java. A regular gold mine in the
 Wallich. way of rare pelagic forms was found by Wallich in the intestinal
 canals of *salpæ*, and this source has subsequently been utilised
 for procuring forms that our apparatus could not capture.

Pelagic algæ which have no skeletons of durable mineral
 constituents, such as silicic acid or lime, were in those days
 neglected. A few, no doubt, of the larger peridineæ were
 Nitsch. described by Nitsch, Ehrenberg, Bailey, Claparède, and
 Claparède. Lachmann; but there was very little progress made, and it
 Lachmann. was not till 1883 that T. R. von Stein published his first
 Stein. comprehensive monograph, a great deal of the material for
 Bergh. which had been taken from the stomachs of *salpæ*. R. S. Bergh
 had already issued, two years previously, a text-book on the
 organisation of these algæ.

Since 1870 important expeditions have been undertaken,
 one object of which was to study the pelagic organisms
 systematically. The "Challenger" Expedition, in particular,
 "Challenger"
 Expedition. collected quantities of material from all the seas of the world;
 though attention was still chiefly directed to those forms whose
 coverings are met with in deposits on the sea-bottom, that is to
 say, diatoms with their silicious coverings, and the remarkable
 little organisms forming the microscopic calcareous bodies which
 Ehrenberg had already designated coccoliths and rhabdoliths.
 John Murray. Murray pointed out that coccospheres and rhabdospheres, as
 they were termed, are really self-existent organisms in the
 surface-layers. He could obtain them by allowing a glass of
 sea-water to stand for a few hours, so that they sank to the
 bottom and attached themselves to threads placed there for
 purposes of experiment; and he also found numbers of them in
 the stomach-contents of *salpæ*, of which they often formed an
 essential part. It was possible, too, by noting the occurrence
 of their coverings in the bottom-samples, to obtain definite
 information regarding their geographical distribution. He
 observed that, while they are abundant in all tropical and sub-
 tropical waters in the open ocean, they are not found in arctic
 and antarctic waters having a temperature below 45° F., nor are
 they to be found in the deposits of the polar oceans. Murray
 further ascertained that diatoms are irregular in their occurrence,
 and that they are more numerous in coastal areas than out in
 the ocean. Unfortunately Castracane, when examining the
 diatoms collected by the expedition, was unable to find any
 conformity in the distribution of the different species.

The other expeditions that were sent out about the same time as the "Challenger" carried out their investigations on similar lines. G. O. Sars, who was a member of the Norwegian North Atlantic Expedition in 1876-1878, made a study on board ship of the luxuriant plant life near the ice-limit, and remarked, like CErsted before him, that plants are really the basis upon which the nutriment of animals is founded. It was not, however, till twenty years afterwards that an examination was made of the algæ in the comparatively small number of samples then collected.

G. O. Sars.

CErsted.

Soon after 1880 Hensen commenced a physiological study of the sea, and essayed principally to estimate its production of nutritive substances at different seasons. As a result the plants came more into notice than they had previously done; and it is significant that Hensen found it necessary to introduce the new name of "plankton" to designate generally all pelagic organisms, both plants and animals, regarded as one universal community. The term "plankton" is now used for all floating organisms which are passively carried along by currents, while "nekton"—a term introduced by Haeckel—is used to designate all pelagic animals which are able to swim against currents. During Hensen's Plankton Expedition in 1889 Schütt made the first investigations regarding the general biology of the plankton-algæ. His ingenious descriptions and admirable drawings explained the different ways in which the algæ adapt themselves to their floating existence.

Hensen.

"Plankton."

"Nekton."

Schütt.

An endeavour was made by Hensen to find a method of calculating the quantity of pelagic organisms occurring in different localities. He constructed nets to be drawn up for certain distances through the water, that were supposed to filter the whole column of liquid through which they passed, and to retain all the organisms existing therein. The total amount of these organisms was then measured by determining the volume, and a most careful enumeration was made of the number of individuals belonging to each species. The nets were drawn vertically through the whole zone where plant plankton is abundant, that is to say, from a depth of 200 metres to the surface; and Hensen attempted to utilise the results for measuring the production of life in a column of water whose superficial area is one square metre. He tried at the same time to solve important problems, such as the rate of augmentation of algæ, or what proportion of individuals disappears owing either to consumption by other organisms or unfavourable conditions of existence.

Quantitative estimations.

Hensen's work must not be disparaged because his aspirations have been more difficult to realise than he at first imagined. The difficulties are far from insurmountable, while Hensen himself will be always looked upon as one of the founders of the science of marine physiology.

In the biology of the sea we have also to consider the geographical distribution of the different species and their dependence upon ocean currents. The Swedish scientists, Cleve and Aurivillius, brought these two questions into special prominence, though no doubt they had been previously considered by others. But with the hydrographical investigations of Otto Pettersson and others the whole subject assumed a new aspect. Thanks to improved methods they succeeded in following the movements of the water-layers, by determining their salinity, temperature, and other hydrographical characteristics; and from this time forward the plankton was also enlisted as a supplemental means of characterising water-masses of different origin. Cleve with his marvellous power of distinguishing forms was able in a short space of time to determine numbers of species, animals as well as plants, and it is to him we owe the foundation of our knowledge regarding the distribution of plankton-algæ.

Since the international marine investigations were commenced about ten years ago, researches have been carried out in the Northern Atlantic, North Sea, and Baltic; and specialists from the different countries of North Europe have gradually extended our knowledge, as far as northern species are concerned.

Simultaneously great improvements have taken place in our methods of studying plankton. Lohmann has made it clear that the catches in the silk nets originally used incompletely represented the flora of the sea, owing to the fact that whole series of the most diminutive organisms slip through the meshes of even the finest straining-cloth. He devised methods for catching them by means of the filter and the centrifuge, and could thus estimate their numbers in a given quantity of sea-water. Coccolithophoridæ, which the "Challenger" Expedition claimed to have discovered, but which Hensen refused to recognise as self-existent plankton organisms, because he did not capture them himself, were now investigated, and Lohmann was able to declare confidently that they really are algæ, furnished with brown pigment granules, the physiological equivalent of chlorophyl, thus confirming the earlier discoveries of Sir John Murray, George Murray, Blackman, and Ostenfeld. Lohmann

Aurivillius.

Pettersson.

International investigations.

Lohmann.

G. Murray.
Blackman.
Ostenfeld.

has further, by his quantitative investigations of the variations in the plankton of Kiel Bay and off Syracuse, taught us the value of exact studies of this description.

Our future investigations will have to be conducted on three main lines:—

(1) In the first place, much study must be devoted to the biology, in the restricted sense of the word, of the algæ. We will have to learn how the forms adapt themselves to their conditions of life, and in particular to their floating existence. Here, however, a great advance should most certainly be made, now that W. Ostwald has shown us a new factor affecting their floating power, namely, the varying viscosity of sea-water, and since the instructive writings of Wesenberg-Lund have directed our attention to the seasonal modifications which the species adopt to suit variations in viscosity.

(2) In the second place, the distribution of the species throughout the seas of the world requires further investigation at different seasons, and this must be founded on a careful characterisation of the different species. In recent years the peridineæ, after a long period of neglect, have received due attention at the hands of Ostenfeld, Ove Paulsen, Pavillard, Jörgensen, Broch, and Kofoid. A great deal, however, still remains to be accomplished.

(3) In the third place, we will have to deal with the laws of production in the sea. This great physiological question calls for observations on a very comprehensive scale, if we are to be in a position to discuss the interesting theories put forward by Brandt, Nathansohn, and Pütter. A brief discussion of their theories will be found at the end of this chapter.

During the Atlantic Expedition of the "Michael Sars" we were able to make observations on all these three aspects of the subject; and in what follows I shall endeavour to summarise our results, and to consider, while doing so, the attitude at present taken up by the scientific world with regard to these three lines of investigation.

Most of the ocean plants exist in countless myriads of minute individuals, though they are invisible to the naked eye. Still, small as they are, they are in a way highly organised, and their organisation is in strict accordance with the particular conditions of life. On land a higher plant consists of a community of separate cells, each of which has a special function to perform in the service of the whole. It establishes an under-

Ostwald.

Wesenberg-Lund.

Paulsen.
Pavillard.
Jörgensen.
Broch.
Kofoid.Brandt.
Nathansohn
Pütter.General bio-
logy of the
pelagic algæ.

ground system of roots to collect moisture and nourishment from the soil, and its leaves are raised aloft on slender stems to derive benefit from the rays of light and build up organic substance out of carbonic acid and water. Ocean plants have no such *point d'appui*; they find their nourishment dissolved in sea-water and distributed uniformly all around them, and they get most benefit from the sunlight when they are regularly spread throughout the whole bulk of the water in the photic zone. Their diffusion is also their best defence against their enemies, for, while animals have no great difficulty in finding and consuming the larger plants, these creatures, scattered everywhere like dust amidst the immeasurable water-masses, are not so easily available. The majority of the floating plants pass their lives as single cells, though they are frequently far more highly organised than the single cells that go to form a higher plant.

As pelagic algæ have generally a greater density than the sea-water in which they live, they would sink out of range of the rays of light, and perish, if it were not for the fact that they are kept from descending either by their own exertions or by suspension organs which act as a parachute. The most noticeable features in their organisation are their different forms of structure, which are directly connected with the floating existence they lead. In what follows I shall describe the most important types, belonging to a limited number of classes, most of which have variously shaped pigment granules or chromatophores, consisting of brown colouring matter instead of green chlorophyl. Comprised in their number are diatoms, peridineæ, and brown flagellates, amongst which last we also include calcareous flagellates or coccolithophoridæ. In addition there are a few pelagic representatives of the green and blue-green algæ, which I will discuss separately.

A diatom can be distinguished from other algæ by its silicated cell-wall. This is composed of two quite similar halves, or valves as they are called, that are united to one another like the top and bottom of a pill-box (see Fig. 212). Inside the valves the protoplasm lines the wall like a thin sort of bladder, while the nucleus is frequently in the very centre surrounded by a denser mass of protoplasm connected to the bladder by bridges or strings. The rest of the cavity is full of a clear cell-fluid. The pigment granules, which are organs of nourishment, enable the diatom to collect rays of light and build

Suspension
organs.

Diatoms.

up organic substance out of carbonic acid. They usually lie in regular order along the cell-wall (Fig. 213, *a*); but if the light becomes too strong for them, they are able to huddle more closely together, either in the middle of the cell or

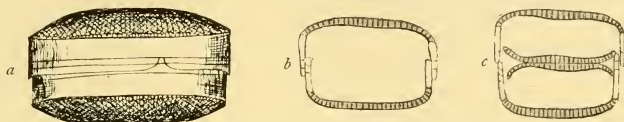


FIG. 212.—CELL-WALL OF A DIATOM (*COSCINODISCUS SUBBULLIENS*), $\frac{3}{10}$ °.
a, External view; *b*, vertical section; *c*, section in cell-division.

at some point where they can mutually protect each other from the harmful effects of the rays (Fig. 213, *b* and *c*). This has been demonstrated by Schimper. The assimilation of carbonic acid produces a fat oil, which may form into comparatively large drops.

Schimper.

Cells are produced by division. The nucleus and protoplasm divide into two parts, the valves are pushed a little apart, and two new valves develop within the old ones. Thus each of the daughter-cells gets one of the valves from the mother-cell and a new valve that joins on to it (see Fig. 212, *c*). When once the valves have acquired their shape they seem incapable of expanding, so that the cell generations will gradually become contracted in the plane in which division takes place.

Cell division.

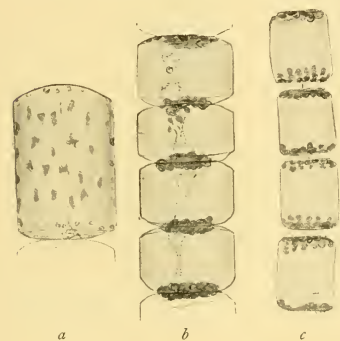


FIG. 213.

a, *b*, *Lauderia annulata*. *a*, Cell with the pigment granules (chromatophores) in normal position, collected early in the morning; *b*, chain from the surface of the sea, 3 P.M., chromatophores congregated at the ends of the cells; *c*, *Detonula schroederi* in the same condition. All $\frac{1}{10}$ °.

the perpendicular axis of the plane of division is frequently slightly prolonged. Algæ can, however, regenerate their original size, by throwing off their old valves, growing into a larger bladder with a thin expansible skin, and forming within it new valves that are two or three times as large as the old ones. This is the so-called auxospore development (see Fig. 214).

Auxospore development.

Diatoms occur in quantities over the whole world in both

Distribution
of diatoms.

fresh and salt water, and they are found not merely as floating forms, but also along the coasts, some of them attached to the bottom or to other algæ and animals; some are capable of motion, gliding over the mud in enclosed bays or among grains of sand near the seashore. The coast forms, however, are essentially different from the pelagic forms in their structure. Littoral diatoms are apt to have a comparatively thick and extremely silicated cell-wall with the characteristic patterns, ribs, and pores, that have made them such an attractive object of study to amateur scientists. Bilateral symmetry prevails, especially amongst forms that are capable of motion, which are as a rule pointed at the ends like the bows of a boat. Diatoms of

Littoral forms.

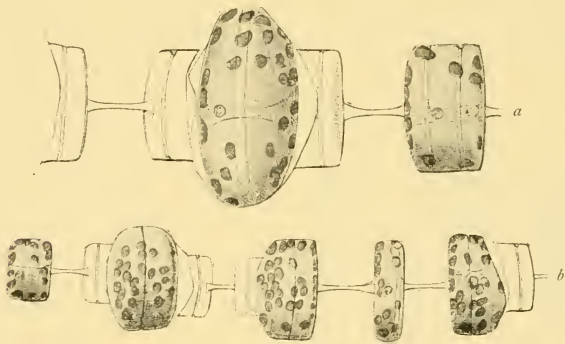


FIG. 214.—AUXOSPORE-FORMATION OF *THALASSIOSIRA GRAVIDA*.

a, Showing in the centre a newly-formed auxospore, the old cell-walls still lying outside ($\frac{200}{100}$); *b*, showing on the left a cell before auxospore-formation, succeeded by an auxospore during its first cell-division, the chain of five cells having originated from an auxospore ($\frac{200}{100}$).

this kind have a highly organised locomotion apparatus, which is differently constructed in the different genera, such as *Navicula* and *Nitzschia*. Attached forms show more variation. Symmetry with them depends upon the mode of attachment. *Licmophora* and *Gomphonema* are fastened at one end to a gelatine-like stalk, and their cells are wedge-shaped, narrow at the bottom and widening out towards the top. Others, like *Epithemia*, are convex on the one side and straight on the other, the straight side being the one by which they are attached. And there are others again that consist of more or less highly organised and often ramifying colonies, composed of series of cells, or sheaths of mucilage, within which the cells are able to move past one another.

Attached
forms.

Pelagic forms usually have thinner cell-walls, and the characteristic ornamentations on their silicated valves are not so prominent, though in their case too a high magnifying power will nearly always render them visible. The families that are endowed with locomotion organs are very scantily represented, and even amongst the few that are thus favoured, several species make use of them for quite a different purpose, employing them as organs to secrete mucilage and thus keep the cells united in chains. Most of the pelagic diatoms belong to families that lack organs of locomotion, though by way of compensation various types have highly developed suspension organs, which increase their superficies and consequently their friction against the surrounding water-masses. It is possible, too, that these algæ are able to reduce excess weight by evolving specifically lighter matter, such as fat, within the cells or air-bladders outside them, but this has not yet been properly investigated.

The suspension organs, however, have been most carefully studied, especially by Schütt, who was one of the members of Hensen's Plankton Expedition in 1889, and the different cell-forms, with their numerous contrivances for maintaining a floating existence, may be grouped under four heads:—

(1) *The Bladder Type*.—In these the cell is comparatively large, while the cell-wall and protoplasm are merely thin membranes round a big inner cavity which is filled with a cell-fluid of about the same specific gravity as sea-water. Among diatoms the best instances of this type are species of the genus *Coscinodiscus*, whose structure resembles cylindrical boxes, sometimes fairly flat-shaped, and sometimes more elongated and rounded at the top and bottom. In most forms the cell-wall is quite thin, though it is strengthened by means of a fine mesh-work of more or less regular hexagons. One of the biggest, *Coscinodiscus rex* (*Ethmodiscus rex*, *Antelminellia gigas*), is over a millimetre in diameter, and is quite a common form in the warmer parts of the Atlantic (see Fig. 215). A series of species with stouter structure, and more distinct ornamentations on the cell-wall, occur especially in the deeper water-layers, at about the lowermost limit of plant-life (100 to 200 metres), and belong to a characteristic twilight-flora, of whose existence Schimper became aware during the "Valdivia" Expedition.

Four types of suspension organs.

(2) *The Ribbon Type*.—The surface is enlarged owing to the cell being flattened down into a plane, which is often bent or twisted to a certain extent. Diatoms of this type (see Fig. 216) are scarce. We have, along the coasts especially, a few species with flat cells, which are associated in ribbon-shaped colonies, such as *Fragilaria* and *Climacodium*. The cell-walls of these species are extremely thin, and not of a particularly distinct structure.

(3) *The Hair Type*.—The cells are very much prolonged in one direction, or else they are united in narrow, elongated colonies. Diatoms

Distribution
of diatoms.

furnish many varieties of this type. Sometimes the length axis is situated in the division-plane of the cells, as, for instance, in *Thalassiothrix longissima*, one of the characteristic forms in colder seas; at other times division takes place across the elongated cell, as in the genus *Rhizosolenia*, of which there are many species (see Fig. 217). Hair-shaped cells of this kind create a great deal of friction when horizontal, but would sink rapidly when perpendicular, if it were not for the fact that they are either slightly curved, or else their terminal faces are sloping; so that



FIG. 215.—*COSCINODISCUS REX* ($\frac{60}{1}$).

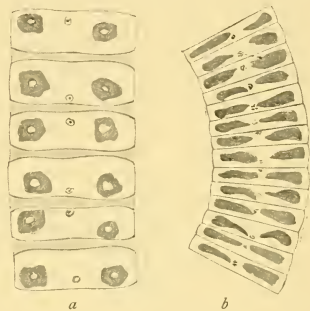


FIG. 216.—PELAGIC DIATOMS OF THE RIBBON-TYPE ($\frac{500}{1}$).
a, Chain of *Navicula vanhöfeni*, the cells connected by a band of mucilage; *b*, part of a chain of *Fragilaria oceanica*.

the resistance of the water soon restores them to an almost horizontal position, and they sink slowly in long spiral sweeps.

(4) *The Branching Type*.—The surface of the cell is enlarged by various kinds of hair-shaped or lamelliform outgrowths. To this type belongs the genus *Chaetoceras* with its numerous species (see Fig. 218).



FIG. 217.—PELAGIC DIATOM OF THE HAIR-TYPE, *RHIZOSOLENIA HEBETATA-SEMISPINIA*.
a, Entire cell ($\frac{200}{1}$); *b*, end of a cell ($\frac{500}{1}$).

Every cell has four long setiform outgrowths, and the cells are besides nearly always associated in chains, so that these setæ radiate in every direction. When the chain is straight and stiff it is frequently furnished with special terminal setæ, which are stiffer than the others, and act as a sort of steering apparatus.

In addition to the actual outgrowths from the cell many diatoms can secrete long filaments of mucilage from special

secretion pores. These filaments act as an effective suspension-apparatus (see Fig. 219). During unfavourable conditions

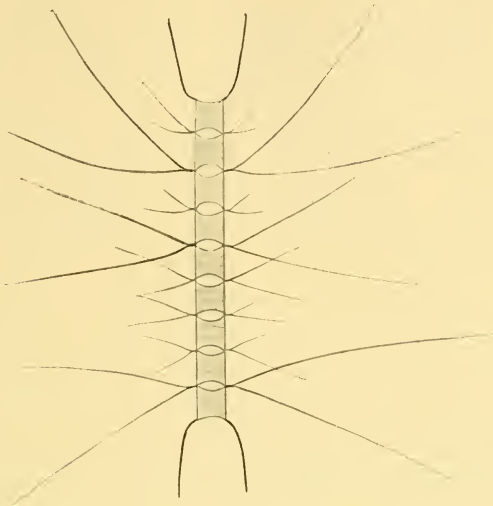


FIG. 218.—CHAIN OF *CHETOCERAS DECIPIENS* ($\frac{1}{4}$ °).

of existence, especially when there are considerable changes in the salinity, sufficient mucilage is secreted to form a protecting

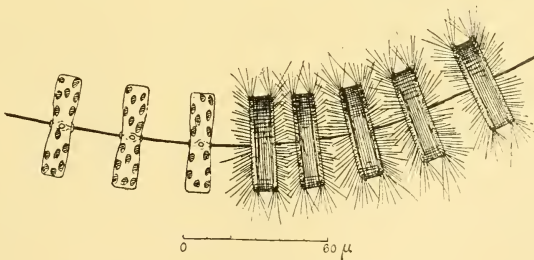


FIG. 219.—CHAIN OF *THALASSIOSIRA GRAVIDA* ($\frac{1}{4}$ °).
Showing on the right five cells with filaments of mucilage. (Mangin.)

sheath round the cells. This I have myself observed in the case of species of *Thalassiosira* on the Norwegian coasts.

Adjustment of their organisms to the conditions of their

floating existence affects the whole structure of these algæ, though it is not always carried out to the same degree in the different genera and species. If we examine into their distribution we shall find that no particular region is distinguished by specially well-equipped species. Genera with the greatest numbers of species have their representatives in both the warmest and the coldest areas of the sea, and no essential difference in the development of their suspension-apparatus is to be found between the species of *Chaetoceras* and *Rhizosolenia* which live near the confines of the polar sea, and their relatives in the tropics. The greatest abundance of forms is to be met with in coastal waters, where, too, the majority of the species have their home. I shall return later on to the special biology of these coast-forms.

Many species of diatoms show variations indicating that within certain limits the algæ can adapt their floating power to the demands made on them. Their tendency to sink increases with a rise of temperature, and decreases with an increase of salinity. It is not alone the specific gravity (density) of sea-water that is here the determining factor; no doubt we must bear specific gravity in mind also, but its variations are comparatively small. Ostwald has shown that the internal friction or viscosity of sea-water is the most important consideration, and this diminishes with an increase of temperature. Other things being equal, sea-water at 25° C. offers only half the resistance that it would at freezing-point. Salinity, on the other hand, is of less account. A rise of 1 per cent in the salinity will produce no more than an increase of 2 to 3 per cent in the internal friction, and as salinity in the open sea is subject to what are after all quite inconsiderable variations, it follows that it is really temperature which indirectly affects the development of the suspension-organs. In areas of the sea where there is a big difference in temperature between summer and winter, we find a number of species with distinct summer and winter forms, that have sometimes even been supposed to belong to totally different species. And the same variation occurs also in species with a wide distribution, the warm-water types corresponding to the summer forms, and the cold-water types to the winter ones. The summer forms have usually thinner cell-walls, and a more slender structure; their excess weight appears to be reduced, though at the same time their surface is comparatively larger. As, however, diatoms vary greatly in their dimensions throughout their life-cycle,

Viscosity
of sea-water.

Summer and
winter forms.

their cells diminishing by being divided and increasing again owing to the formation of auxospores (see Fig. 220), it is

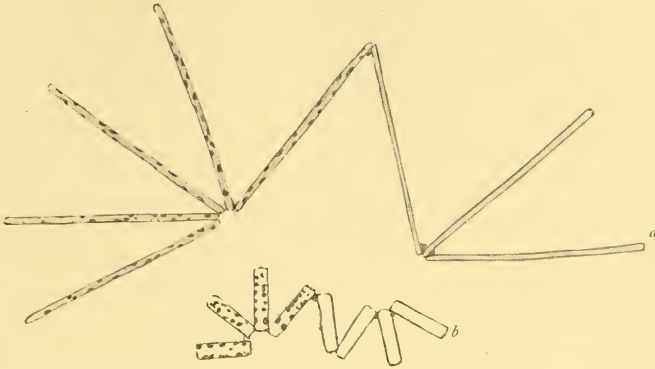


FIG. 220.—COLONIES OF *THALASSIOTHRIX NITZSCHIOIDES* ($\frac{800}{1}$).
a, With long cells shortly after auxospore formation; *b*, with shorter and thicker cells.

difficult to show in the case of many species to what extent variations are due to adaptation and regulation of their floating power, though in the case of some chain-forming species it is

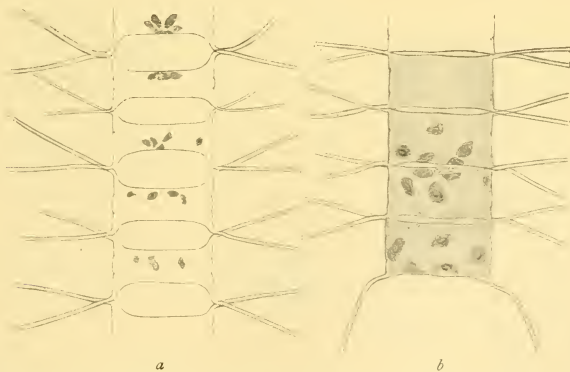


FIG. 221.—PARTS OF TWO CHAINS OF *CHAETOCERAS DECIPIENS* ($\frac{440}{1}$).
a, From the Atlantic off the coast of Spain, April 1910; *b*, from Christiania-Fjord, March 1911.

evident enough. *Chaetoceras decipiens*, one of the commonest species in the northern Atlantic, consists of straight chains of flattened, almost rectangular cells, every one of which is

furnished with four long setæ. Each of these setæ is attached at the root to its fellow from the neighbouring cell, the result being the formation of the chain. The terminal faces of the cells are otherwise separate, so that there are openings between them. In the winter and spring *Chatoceras decipiens* is furnished with thick cell-walls and stout setæ, and the interstices between the cells are quite inconsiderable (see Fig. 221, *b*); but in summer the walls are thin and the setæ extremely fine, and the openings in the chain between the cells then become large, round or oval gaps, which are almost as big as the cells themselves (see Fig. 221, *a*). Corresponding variations occur in other species of *Chatoceras*, and in other diatoms, such as *Biddulphia aurita*. Along the arctic coasts, for instance, *Biddulphia* has a rather gross structure, and is almost cylindrical, with short conical projections at the corners, but off the south of Norway it has a comparatively much larger surface, and the corners develop into long, slender outgrowths.

We find a variation of a different nature in the case of

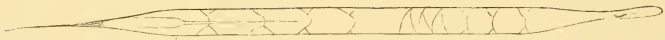


FIG. 222.—CELL OF *RHIZOSOLENIA HEBETATA-SEMISPINA* ($\frac{2200}{100}$).
One end of the cell belongs to the typical arctic *hebetata* (on the right), the other to the Atlantic form *semispina*.

Dimorphism.

Rhizosolenia hebetata. It occurs in two perfectly distinct forms, that were formerly regarded as good species. The first, which belongs to arctic waters, is thick-walled and gross, and is the true *R. hebetata*. The second, *R. semispina*, has thinner walls and is proportionately longer, and it is furnished with a long hair-like point at each end. Its distribution extends over practically the whole Atlantic, though it is chiefly to be found in the neighbourhood of the cold currents. These two "species" can originate from one another reciprocally as the result of one cell-division. During the course of transition a cell may be *hebetata* at the one end and *semispina* at the other (see Fig. 222). Dimorphism of this kind is known, moreover, in the case of other species.

Still, in the open sea conditions of existence are comparatively uniform compared with what we find in coastal waters, where the temperature and salinity vary considerably. Most of the diatoms which belong particularly to the coastal waters have a special adaptation, the so-called resting-spores, which must be regarded as a means of protection against such altered conditions. The contents of the cell can shrink into a denser

Resting-
spores.

mass in the middle, and become enwrapped in a new thick wall of characteristic shape within the old cell-wall, which is discarded as soon as the resting-spore is completely developed (see Fig. 223). The spores have now acquired an increased specific weight, as compared with their original cell, and sink down into deep water, where they may be found months after they have disappeared from the surface-layers. The majority of them, however, rest on the bottom in shallow coastal waters, until conditions of existence again occur which induce them to make a fresh start.

The germination of the resting-spores has not yet been described, though Hensen states that Lohmann has observed the first stages on several occasions. It will be a great advantage when we can follow their development-history through all its stages, and study the conditions of existence that lead to germination. Resting-spores are unknown in the true oceanic species; but, as already stated, they are found in most of the species belonging to coastal seas. not aware of them till quite a short

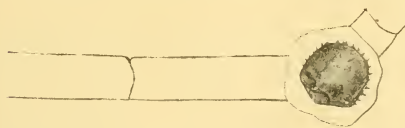


FIG. 224.—*LEPTOCYLINDRUS DANICUS*, WITH RESTING-SPORE ($1\frac{0.0.0}{1}$).

are liberated, and in *Chaetoceras pseudocritum*, in which the resting-spores originate in auxospores.

So far as we are able to ascertain, the auxospores of pelagic diatoms are always formed without any sexual act. There is, however, another kind of organ, the so-called microspores, Microspores.

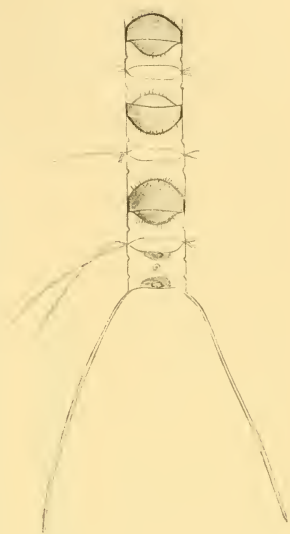


FIG. 223.—CHAIN OF *CHAETOCERAS CONSTRICTUM*, WITH THREE RESTING-SPORES AND ONE NORMAL CELL (THE END-CELL OF THE CHAIN) ($1\frac{1.0}{1}$).

In some cases we were time ago. It is only recently that they have been discovered in *Leptocylindrus danicus* (see Fig. 224), in which the cylindrical cells are broken across in the process of spore-formation, so that the spores

which, according to Bergon's investigations, would seem to be zoospores, and which Karsten assumes to be sexual cells. Karsten has observed the formation of microspores in an antarctic diatom, *Corethron valdiviæ* (see Fig. 225), and in the same microscopic preparations found amalgamations of small cells resembling microspores. We cannot yet, however, consider this conclusively settled. We do not know the life-history of the numerous small spores after they have emerged from the mother-cell. We can only hope that the centrifuge will enable us to study the most diminutive and sensitive cells immediately after capture, and that we shall thus succeed in solving this problem in the biology of diatoms.

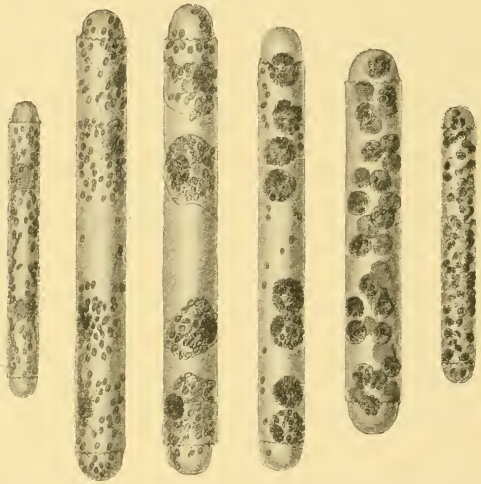


FIG. 225.—MICROSPORE-FORMATION OF *CORETHRON VALDIVIÆ* IN DIFFERENT DEVELOPMENT STAGES (³³²).

Ripe microspores in the cell to the right. (Karsten.)

Peridineæ. Peridineæ are mobile algæ furnished with two cilia. Several species can produce brilliant phosphorescence. Their cells are highly organised, with a distinct difference between the anterior and posterior ends, and between the dorsal and ventral faces. The cell-wall is built up entirely of organised matter, which dissolves soon after the death of the cell. Peridineæ are therefore not noticeable in the deposits of the ocean-bottom, which is one of the reasons why, until quite recently, they were but slightly and imperfectly known. A number of laminae, characteristic in shape and position, compose the cell-wall. On the posterior side there is a characteristic furrow, with a pore for one of the cilia, which can be withdrawn spirally into a sheath (see Fig. 226). The ventral furrow is often protected by curtain-membranes. Another furrow encircles the cell, and

is known as the ring-furrow. It is guarded by projecting borders on the anterior and posterior sides, called ring-borders. It is in this furrow that the second cilium lies and vibrates.

These principal organs appear in a great variety of shapes. The genus *Ceratium* has the anterior end drawn out into a long horn, which is open at the top; its posterior end has also nearly always two horn-like projections, which in most species bend in a forward direction. The species of *Ceratium* are well supplied with brown pigment granules, and they occur in the upper water-layers, where they constitute an essential part of the plant

Ceratium.

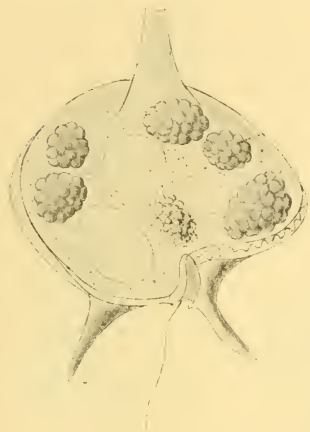


FIG. 226.—*PERIDINIUM DEPRESSUM* ($\frac{37}{7}$).
(Schütt.)

life. The horns must be regarded as suspension-organs, even though the mobility of the cell makes an adaptation of this kind less indispensable. We frequently find them, especially in the species of tropical seas, transformed into very consummate suspension-organs. Sometimes they are decidedly long and hair-shaped, sometimes flattened, and in a few species actually terminate in radiating branches. Kofoid has shown that the species of *Ceratium* can regulate their floating power, and that when, owing to the movement of the water masses, they enter colder or warmer layers of water, they can shed portions of their horns or prolong them at will (see Fig. 227). They have also still another mode of improving their floating power. The cell wall grows in thickness during the whole life of the algæ, and simultaneously ribs and pores are constantly developing; but as soon as the cell gets too heavy, one or even several laminæ peel off from the cell armour, and new extremely thin plates take their place.

Kofoid.

The species of *Ceratium* are also formed by division, and with them, too, the daughter-cells each retain half of the membrane of the mother-cell, the other half being new. This does not, however, take place within the cell-wall of the mother-cell, and there is therefore no gradual diminution in the bulk of the individual. Sometimes the cells hang together in chains,

and it is then quite evident that the direction and shape of the horns may vary considerably from one generation to another.

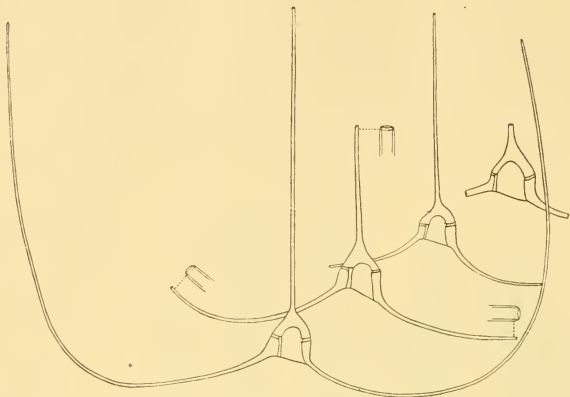


FIG. 227.—*CERATIUM TRICHOCEROS*.

Showing progressive and proportionate reduction of the horns in autotomy ($\frac{1}{16.5}$). (Kofoid.)

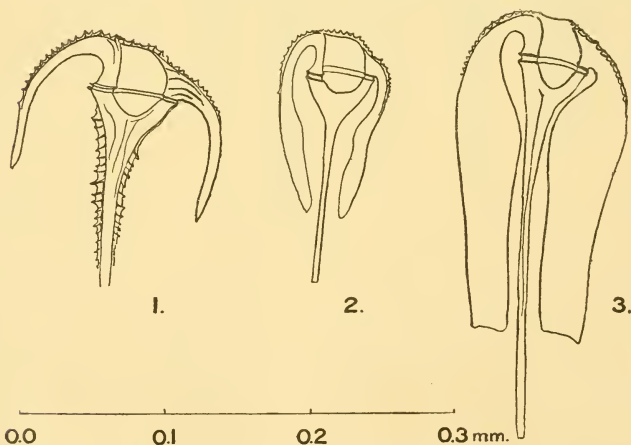


FIG. 228.—*CERATIUM PLATYCORNE*.

1, *Forma compressa*; 2, 3, *forma normalis*.

In other cases, where the cells separate immediately after division, it is more difficult to tell which variations are due to hereditary dissimilarities and which are the result of direct

adaptations from one generation to the other. Still, now and then even this, too, is possible. I found during the Atlantic expedition of the "Michael Sars" that the subtropical *Ceratium platycorne*, both of the posterior horns of which are developed ordinarily into flat wing-like suspension-organs, changed gradually into a form with cylindrical horns belonging to the Gulf Stream in the Norwegian Sea, that I had myself previously described under the name of *Ceratium compressum* (see Fig. 228).

Discontinuous variations have been found as well as continuous ones in the species of *Ceratium*. Lohmann has shown that the ordinary Baltic form, *C. tripos*, can set up an intermediate generation of a totally different type, much smaller and with short, straight horns, corresponding to the forms described under the name of *C. lineatum*. Kofoid has met with similar variations in American species (see Fig. 229). The significance of these development forms has not yet been discovered. Jörgensen, who has recently published a monograph on the genus, is inclined to regard them as degenerate forms that have been produced under abnormal conditions of existence. It seems to me, however, more probable that these

Lohmann.

Jörgensen.

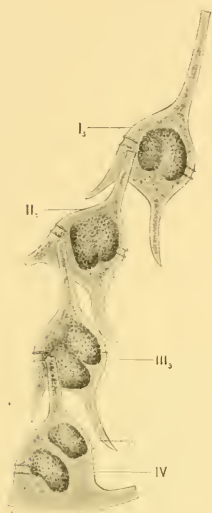


FIG. 229.

CHAIN OF *CERATIUM TRIPOS*.

Only one cell (IV.) shows the character of the type, the others (I.-III.) belonging to the type of *Ceratium californiense* (²⁷⁹). (Kofoid.)

development-cycle of the species of *Ceratium*. It is still questionable whether peridineæ propagate sexually, even though Zederbauer claims to have discovered sexual propagation in the ordinary fresh-water form (*Ceratium hirundinella*). But, *a priori*, it is quite possible that the above described intermediate generation may be a sex-generation. Just as little as these "mutations" do we understand the significance of the gemmation which Apstein has lately described in *Ceratium tripos*, nor do we know what conditions of existence cause gemmation instead of normal cell-division.

Zederbauer.

Apstein.

Another important genus with many species, *Peridinium*, *Peridinium*.

differs in various ways from *Ceratium*, though systematically it is not far removed from it. The cells, however, lack the brown pigment-granules (at any rate, this is so in the case of marine species), and the contents are pale yellow or pink. It is improbable that it can assimilate carbonic acid, and it must therefore somehow or other obtain organic matter for its nourishment. Unfortunately nothing is known regarding its mode of nourishment. These forms do not live so close to the surface as the species of *Ceratium*, but all observations made hitherto indicate that they belong exclusively to parts of the sea to which light penetrates, where they exist along with the other



FIG. 230.

GONYAULAX POLYGRAMMA.

The cell-contents form a zoospore, shed out from the bursting cell-wall ($\frac{1}{4}$). (Schütt.)

algæ. Their cells are much grosser than those of the species of *Ceratium*, and the projections corresponding to the horns of *Ceratium* are short or entirely wanting. The membrane-curtains along the furrows are only slightly developed, and the cell itself is much more globular. The species of *Peridinium*, and some other genera (*Gonyaulax*, *Goniodoma*), have thus at best only imperfect suspension-organs, but the mobility of the cells makes up for this deficiency. The way they are formed, too, is different from what we notice in *Ceratium*. There is no proper cell-division, but the cell changes its contents to one, two, or four naked spores, which are shed out from their original covering (see Fig. 230). Each spore afterwards gradually evolves a new cell-wall for itself, within which it develops as the wall expands, and bands, due to accession of growth, intervene between the laminae composing the structure. This has been demonstrated by Broch. The genus *Peridinium* includes a large number of species distributed throughout all the seas of the world, but the systematic arrangement of the species is extremely difficult, and has not so far been sufficiently investigated. A large amount of material has, however, been brought home by our expedition, and it is to be hoped that we shall now be able to ascertain the characteristics to which we can ascribe chief systematic importance. A good beginning, at all events, has been made by Kofoid and Broch.

The family Dinophysidæ possesses the most remarkable suspension-organs of all the peridineæ. In northern waters its representatives are limited to a number of species all

resembling one another and all belonging to the same genus, namely, *Dinophysis*. The commonest of these, *D. acuta* (see *Dinophysis*. Fig. 231), has a small tongue-shaped mobile cell without particularly well-defined suspension-organs. Its ring-furrow and protecting borders are situated at the forepart of the cell, and its sides are flattened to such an extent that the ventral furrow is on quite a sharp edge, where it is guarded by two membrane-cur-tains. The cell is formed by division, which takes place per-pendicularly to the ring-furrow. Within the cell are several brown chromatophores, showing that *Dinophysis* is one of the peridinea that assimilates carbonic acid.

In warmer waters this funda-

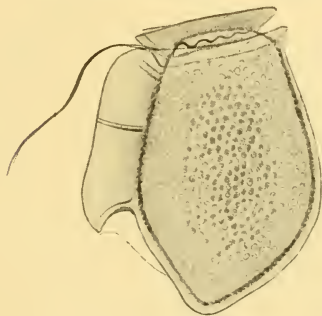


FIG. 231.—*DINOPHYSIS ACUTA*.
From the west coast of Norway ($\frac{600}{100}$).
(Jørgensen.)

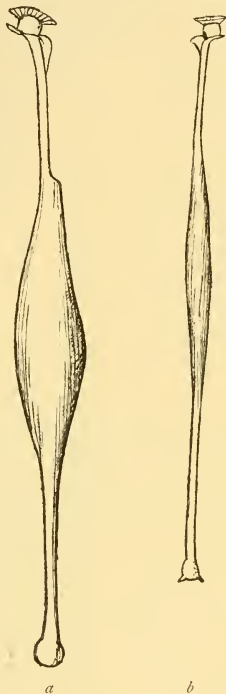


FIG. 232.
a, *Amphisolenia globosa* ;
b, *Amphisolenia tenella*, n.sp. ($\frac{600}{100}$).

mental type shows strange variations. *Amphisolenia* (see Fig. *Amphisolenia*. 232) has its whole cell drawn out to a hair, the ring-furrow is situated right in front on a little head, and the ventral furrow is on a narrow neck with slightly developed membrane-cur-tains like a kind of collar. The cell widens out slightly like a spindle in the middle, and posteriorly ends in a globular knob by way of balance, or in two or three ramifications. *Triposolenia* (see *Triposolenia*. Fig. 233) has a similar anterior structure, but the middle part is

more expanded, and the two bent legs which issue from it do not lie in quite the same plane, with the result that in sinking the cell describes very long sweeps. Besides these we get other genera, where the suspension-organs are not formed by the cell itself, but by the membrane-curtains. In *Ornithocercus splendidus* the ring-borders are transformed into an unmistakable parachute, stiffened by a network of ribs (see Fig. 234, *a*), and in some species, such as *O. steinii* and *O. quadratus*, the membrane-curtains are ventrally or posteriorly most highly developed (see Fig. 234, *b*).

The majority of these more differentiated forms are without chromatophores, but some of them by way of compensation are in almost constant symbiosis with small brown naked cells that are probably immobile stages of brown flagellates. In *Ornithocercus magnificus*, for instance, we find these naked cells in the space between the ring-borders, where they are well protected against harm (see Fig. 235); and in a series of species of the remarkable tropical genus *Histioneis* this home of theirs is expanded posteriorly into a cavity which may be of considerable dimensions as compared with the cell. In

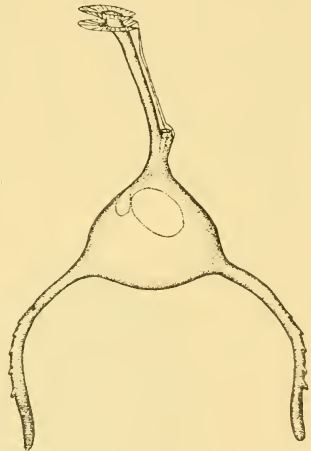


FIG. 233.—*TRIPOSOLENIA BICORNIS* ($\frac{3}{4}$ °).
(Kofoid.)

Citharistes the cavity takes up the whole of what should be the central portion of the cell, and the cell-membranes are merely the outer skin like the shell of a guitar (see Fig. 236).

A remarkable subdivision of the peridineæ is the genus *Pyrocystis*, which Sir John Murray discovered during the "Challenger" Expedition. *Pyrocystis noctiluca* (see Fig. 237) has large globular cells with a thin layer of protoplasm along the cell-wall, a denser mass round the nucleus, and brown pigment granules. Murray stated that the genus was abundant in all tropical and subtropical waters, where the temperature exceeds 68° F., and where the salinity at the surface is not lowered by the presence of coast or river water. The cells have no organs of motion, but belong to the most brilliantly phos-

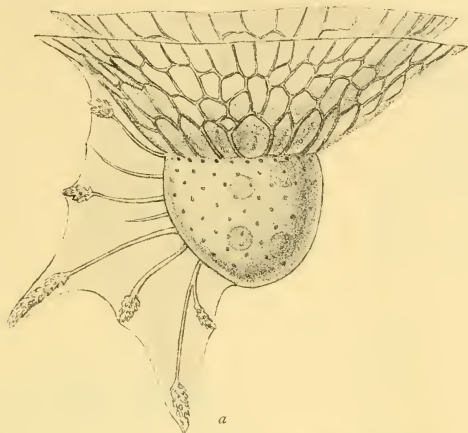
Ornithocercus.

Histioneis.

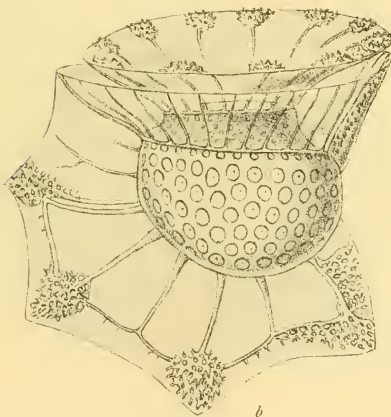
Citharistes.

Pyrocystis.

phorescent of the algæ; biologically they are of the "bladder-type." Other species are elongated (see Fig. 238), straight, or crescent-shaped. Within their cells they form big zoo-



a



b

FIG. 234.

a, *Ornithocercus splendidus* ($\frac{31}{1}^0$); b, *Ornithocercus steinii* ($\frac{30}{1}^0$). (G. Murray and Whitting.)

spores, built up exactly like the peridineæ type with a ring-furrow and two cilia, for which reason the species of *Pyrocystis* are included among the peridineæ, though their fully-developed cells are really of a quite different type.

Besides these highly-organised forms, which I have given as instances, the peridineæ include many with a far more simple structure. There are, especially in the samples collected by



FIG. 235.
ORNITHOCERCUS MAGNIFICUS.
With brown flagellate cells in the space between the ring-borders ($\frac{4.5}{1.0}$). (Schütt.)

means of the centrifuge, numerous series of small forms, both coloured and colourless, and often with very poorly developed cell-walls. These, too, have already got or will shortly be given names, although many of them are probably nothing more than development-stages of the larger forms. We can recognise the whole series by their characteristic ring-furrow, so that we are seldom left in doubt as to the classification of even the simplest types. Still a good deal remains to be done before we can claim a thorough acquaintance with their development-history and systematic arrangement.

The third series of pelagic algæ consists of brown flagellates, the chief place amongst which is occupied by calcareous flagellates or coccolithophoridæ (see Fig. 239). Their cells are

Coccolitho-
phoridæ.

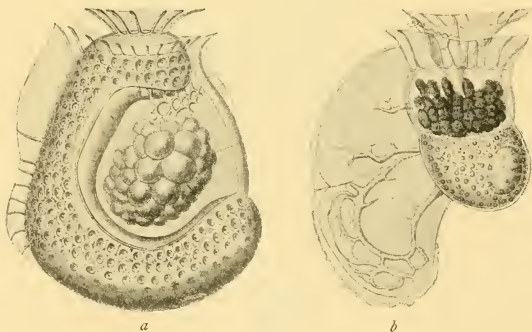


FIG. 236.
a, *Citharistes apsteini* ($\frac{7.5}{1.5}$); *b*, *Histioneis gubernans* ($\frac{6.75}{1.5}$), both with cells of brown flagellates in special chambers. (Schütt.)

generally nearly globular, with one or two cilia and one or two brown chromatophores, and they are protected by remarkable shields of lime which unite into a complete defensive covering, though sometimes with a big opening in front. The cell does not

always occupy the whole internal space, but lies sometimes, as it were, at the bottom of a hollow hemisphere or up at the mouth-opening in a conical sac. The shields of lime can be dissolved by the weakest acids, and the cell then remains as an insignificant mass with undefined boundaries. Still, these shields are very characteristic, and have been found in such enormous quantities in the deposits on the ocean-bottom that they aroused the attention of scientists long before the algæ themselves were known. The commonest forms (*Coccolithophora*, *Pontosphaera*) have an almost globular lime-covering, and are therefore without special suspension-organs, though their surface is big in proportion to their bulk, if we consider their extraordinarily minute dimensions (5 to 20 μ

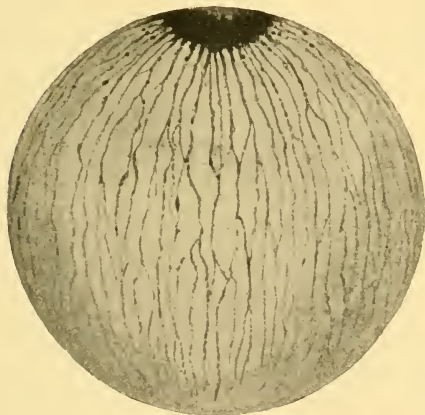


FIG. 237.—*PYROCYSTIS NOCTILUCA*. (From Chun.)

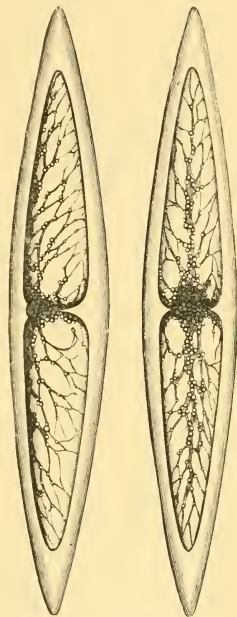


FIG. 238.
PYROCYSTIS FUSIFORMIS ($1\frac{1}{2}^{\circ}$).
(From "Challenger" Narrative.)

in diameter). But in forms like *Rhabdosphaera* the calcareous shields have each a more or less large spike in the middle. In *Discosphaera* we find trumpet-shaped spines, in *Scyphosphaera* barrel-shaped outgrowths, and during the "Michael Sars" Expedition I succeeded in discovering even stranger forms. *Ophiaster* has a tuft of slightly spiral flexible calcareous filaments. *Michaelsarsia* carries in the front of its cell a sort of parachute or pappus of hollow jointed calcareous tubes arranged in a

wreath. *Calciosolenia murrayi* resembles, to some extent, the shape and structure of *Rhizosolenia*, as the shields of lime are not rounded like those of most other species, but rhomboid and spirally bent, so that between them they form a cylindrical tube, pointed at either end, and furnished at the extremities with one or two fine calcareous setæ.

Notwithstanding their small dimensions these microscopic



FIG. 239.—DIFFERENT TYPES OF COCCOLITHOPHORIDÆ.
(1900).

1, *Michaelsarsia elegans*; 2, *Ophiaster formosus*; 3, *Rhabdosphaera claviger*; 4, *Syracosphaera prolongata*; 5, *Calciosolenia murrayi*; 6, 7, *Coccolithophora leptopora*; 8, *Pontosphaera huxleyi*.

calcareous algæ occupy a very important place in the economy of the sea, and their shields of lime, which may be met with in geological deposits dating from as far back as the Cambrian period, show that they have retained their shape practically unaltered through immeasurable ages. They are almost entirely oceanic, and mostly belong to the warmer seas. In coastal waters, where the salinity is lower, they are scarcer, but the commonest species, the little *Pontosphaera huxleyi*, has been found even in the Baltic, and

there were such immense quantities of it in the inner parts of the Christiania fjord during the hot summer of 1911 (5 to 6 million cells per litre) that the calcareous cells with their strong refraction gave the sea quite a milky appearance.

The naked flagellates in the sea are still only imperfectly known, though, no doubt, the part they play is quite a considerable one. In coastal waters they occur sometimes in such abundance that we have actually been able, even with our present defective methods, to discover and describe a number of species. In the open sea we are best acquainted with the passive and

usually almost globular development-stages that live in symbiosis with various animals, and, in particular, with radiolaria. Of these radiolaria, which would seem from Brandt's investigations to derive special benefit from the assimilation-products of algæ, we occasionally get the colony-forming species and Acanthometridæ in such myriads among the surface-layers, that they contribute a very large proportion of the organic substance produced. I have previously stated that the brown algæ also regularly associate with a whole series of Dinophysidæ. Another family of brown flagellates includes the species of *Phaeocystis*, which form large colonies visible to the naked eye, and enveloped in a loose slime (see Fig. 240). In cold waters these have actually been known to occur in sufficient numbers to stop up the meshes of silk nets, and render them ineffective in working.¹

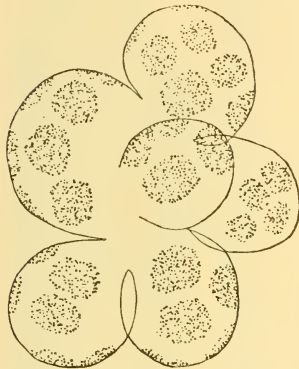


FIG. 240.—*PHÆOCYSTIS POUCHETI*.
(Lagerheim.)

It is the brown algæ that, properly speaking, characterise the plant-world of the sea. Still there are two other important series, the cyanophyceæ and the chlorophyceæ, which preponderate in fresh water, and are, no doubt, represented in salt water also, though by only a few species.

The Cyanophyceæ are chiefly to be met with in warmer seas, if we except the brackish water forms that may be found along the coasts

of North Europe in the height of the summer. The genus *Trichodesmium* appears as clusters of threads, composed of brownish-yellow or red cells, which are either parallel to one another, or twisted together, or matted and tangled, and radiating in all directions. Wille, who described these forms collected by the German Plankton Expedition in 1889, showed that all the types may belong to the same species, *Trichodesmium thiebaulti*, under different development-forms. The clusters may be seen sometimes when they collect near the surface in calm weather, and resemble yellowish-brown snowflakes. Like the different kinds of fresh-water forms, they can raise themselves in the water by means of vacuoles that, according to Klebahn, contain air. When abundant they sometimes

¹ See Summary of Results Chall. Exp., p. 499, 1895.

cover the surface in one unbroken layer, a phenomenon which Ærsted observed in 1849, and which led him even then to look upon microscopic plants as the basis of production in the sea. Besides the species of *Trichodesmium* we have another genus, *Katagnymene*, with spiral series of cells in sheaths of slime. Mention must also be made of the remarkable little alga, *Richelia intracellularis*, described by Johs. Schmidt, which lives in cells belonging to various species of *Rhizosolenia* (see Fig. 241). These diatoms appear to have no difficulty in accommodating their guest, which apparently reproduces itself within the cell, and is thus transferred to new generations of the hospitable plant. The riddle is, how did it originally manage to get in? Most likely this happened at a stage when the *Rhizosolenia* had not yet developed the silicated cell-wall of the hermetically sealed chamber with which we are acquainted.

The green colour which predominates in plants on land is practically only to be found at sea in the globular *Halosphæra viridis* (see Fig. 241). This has been described by Schmitz from Naples, where the people call it "punti verdi," that is to say, green spots. It is or may be lighter than sea-water, so that it floats quite close to the surface. On the other hand, Hensen's expedition found it at profound depths, even at 1000 metres, away down near the limit of the penetration of sunlight, but if this denotes anything in its life-history, it must be at any rate in a state of resting. *Halosphæra* is reproduced by zoospores, though we do not know how they proceed to form the small globular cells that little by little grow up to the normal size. The cell-wall is so firm and thick that its outer part is burst at last in the course of growth and discarded, and the inner elastic parts are thus enabled to expand. Cleve has also observed thick-walled

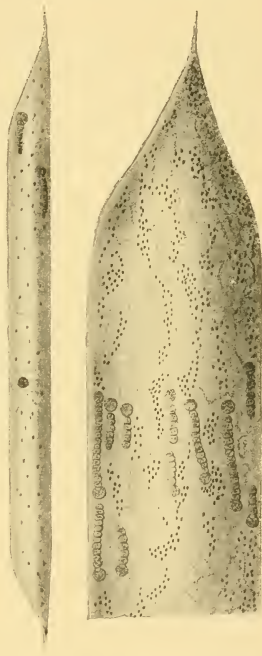


FIG. 241.—CHAINS OF *RICHELIA INTRACELLULARIS* WITHIN THE CELLS OF *RHIZOLENIA STYLIFORMIS*. (Karsten.)

resting - cells. *Halosphæra* occurs over the whole Atlantic Ocean, and follows the Gulf Stream to its farthest ramifications in the north near the coasts of Norway and Spitzbergen. In the North Sea there are quantities, especially in the winter, and they form their zoospores in May, and thereby commence their new generation.

Just as *Halosphæra* differs from all the rest of the pelagic algæ in having a pure green colour, so, too, it has its own special mode of reproduction. The other forms, whose development-history we know, are reproduced by division, and this goes on incessantly, the rate of increase depending upon different conditions of existence. *Halosphæra* does not undergo division, but continues to grow for a comparatively lengthy period, and then finally transforms all its contents, as has just been stated, into a great number of zoospores.

In addition to *Halosphæra viridis* there are one or two similar species that have been described, but they do not call for any particular discussion.



FIG. 242.—*HALOSPHERA VIRIDIS*,
THROWING OFF ITS OLD CELL-
WALL ($\frac{7}{10}$).

In the foregoing I have sketched the most important types of pelagic algæ and their biology, but the picture would not be complete if I omitted to describe the drifting species of seaweed. These do not really belong

Floating sea-
weeds.

to the open sea. They grow along the coasts in the littoral zone, and their gas-filled bladders assist them in maintaining their position whatever be the state of the tide. The violence of the waves finally tears them loose, and then these same gas-bladders keep them for a long time floating on the surface. These patches of seaweed are to be met with in every coastal sea, the chief kinds along the coasts of North Europe being *Fucus vesiculosus* and *Ascophyllum nodosum*, and in the Mediterranean species of *Cystosira*. They may also drift right out into oceanic waters, and in the Sargasso Sea we have an immense eddy where the patches of weed often collect in enormous quantities. The prevailing weed is *Sargassum bacciferum*, but one frequently gets patches of *Ascophyllum nodosum* as well, the whole being derived from the coasts of Central America. The Sargasso weed is easily recognisable, owing to its

berry-like bladders on special small side branches (see Fig. 243).

One cannot help being struck by the fact that the drifting Sargasso weeds are destitute of the ordinary organs of reproduction. This seems to be invariably the case with attached algæ that have been torn loose from their support. They continue to grow vegetatively, but are deprived of all power of forming new reproduction organs, until they can attach themselves afresh. The same holds good, too, with those strange



FIG. 243.—BRANCH OF *SARGASSUM BACCIFERUM*.
(From Kerner.)

broken-off masses of algæ that one finds drifting about along the bottom in bays, the constant movement of the water-masses preventing them from attaching themselves to the soft mud or sand. The Sargasso weed continues to grow as it drifts, but the gas-bladders are not formed in the same proportion as on the ordinary branches, the result being that one finds newly detached patches close up to the surface, whereas the older patches with a greater specific weight have sunk lower down. These last have, moreover, thinner branches and a lighter olive-brown colour. Finally, the power of floating ceases altogether, and the patches sink into deep water and perish. Their disappearance is, however, quite imperceptible, since fresh patches of weed are constantly arriving from the coast.

It is quite usual to find smaller algæ fastened to the Sargasso weed, and there is, besides, a characteristic animal-life amidst its branches, but none of these organisms properly belong to the ocean, notwithstanding their being found there so invariably.

This is true also of the attached algæ, which develop upon driftwood, vessels, and other large objects. They show that germs of littoral organisms abound in the open sea, and are far more numerous than our random samples would seem to indicate. In May 1904, when cruising in the Norwegian Sea, in lat. 67° N., where the bottlenose whales are annually shot, we came across some wadding from a whaler's gun drifting in the sea, the lower side of which was thickly overgrown with attached forms of littoral diatoms.

Castracane, after examining the first big collection of pelagic diatoms from all the seas of the world made by the "Challenger" Expedition, came to the conclusion that there was no essential difference between the flora of the different areas. In this, no doubt, he was right to a certain extent, since many species are very widely distributed; still a closer study has shown us that there are definite marine areas and conditions of existence in which they develop in vast numbers, whereas in other localities they occur perhaps in such small quantities that only their skeletons in the bottom-samples furnish evidence that they have actually been present. Besides, we often find that species with a wide distribution have different forms in the different areas, though we have not yet the means of deciding whether these forms diverge from the main type by virtue of hereditary characteristics, or whether they merge into one another through constant modifications. But in any case these forms are characteristic of the flora of a given locality, and any one who examines plankton-samples will become aware that it is nearly always possible to determine the area from which they have come. During the German Plankton Expedition under Hensen in 1889, Schütt convinced himself that the different currents had their characteristic flora, and he was at a loss to understand how it is that local boundaries of distribution can continue, seeing that the currents are ever carrying off the microscopic plant-life from one part of the ocean to another, and it might consequently be expected that all differences would be obliterated.

Schütt has also given a good description of the character of the plant-life in different parts of the Atlantic, but the honour of being the first to systematically investigate the distribution of all the different species, and the influence exerted upon them by ocean currents, must be assigned to the Swedish biologist Cleve. A chemist by profession, he had for many years made a

Geographical
distribution
of the pelagic
algæ.

Schütt.

Cleve.

special study of diatoms before he commenced co-operating about 1890 with the well-known hydrographers, Otto Pettersson and Gustaf Ekman. They commenced their labours in the Skagerrack, that remarkable little sea where so many different water-masses meet and pass each other; and it very soon became clear that different currents might each possess synchronously its own particular flora, and therefore there was the possibility of ascertaining where the water-masses came from, by determining their flora.¹ All that was requisite was to know the distribution of the different species in contiguous parts of the sea. The investigations were accordingly extended, and samples were collected by ordinary steamers in the North Sea, the Norwegian Sea, and the Northern Atlantic, in addition to the collections that were gradually formed chiefly through the efforts of Swedish, Norwegian, and Scottish scientific expeditions. Cleve also studied the annual changes in the plankton, and had weekly collections made at selected stations on the Swedish coast. The scope of his investigations was further enlarged, for his unique knowledge of forms enabled him to determine, not merely all pelagic plants, but also little by little, a whole series of animal-families which proved no less useful than the algæ as "guiding forms" to determine the character and origin of the plankton.

Cleve believed that he could distinguish a series of plankton-types characteristic of defined marine areas. Particular species were therefore assigned by him to one or other of these main types. But whereas outside the Skagerrack each of the plankton-types had its own characteristic distribution, within this sea the same types were found to predominate, each in its own characteristic season. From February to April there were the same species that we have learnt to connect with the coasts of Greenland and Spitzbergen in the Polar Sea, and from May to June there was a plankton resembling that of the Western Baltic. During the course of summer and autumn there were, first of all, species like those belonging to the southern part of the North Sea, and afterwards Atlantic and more northerly forms. Cleve was led to conclude that these changes in the Skagerrack were due to the fact that it is supplied during the course of the year

¹ "While passing through the Japan Stream the tow-net observations indicated water from two different sources. When in the colder streams there were very many more small diatoms, *Noctiluca*, and Hydromedusæ than in the warmer streams, where the same pelagic animals that were obtained all the way from the Admiralty Islands prevailed. Many similar instances occurred during the cruise, where the approach to land or the presence of shore water was indicated by the contents of the tow-nets" (Narrative of the Cruise, Chall. Exp., vol. i. p. 750, 1885; see also Summary of Results Chall. Exp., pp. 893 and 895, 1895).

in regular rotation with water-masses from the marine areas to which these plankton-types belong.

Subsequent investigations have shown that Cleve's view, which he endeavoured to apply even more widely, was pre-conceived. His eagerness to discover how far the distribution of particular species depended on sea currents, made him apt to forget that algæ are living organisms which are incessantly in process of formation. Accordingly, when the conditions of existence in the flowing water-masses gradually alter, it is the new conditions of existence that decide the character of the flora, since the species best qualified to endure them will very soon get the upper hand over the others. When, therefore, in a sea like the Skagerrack we find northern and southern forms alternating during the course of the year, we are not compelled to assume that the flora is being periodically recruited from different areas. The periodic alterations in the conditions of existence, and particularly in temperature and sunlight, which in our latitudes follow the course of the seasons, sufficiently explain why at one time northerly species predominate and thrive in low temperatures, and why southern forms succeed them and benefit by the warmth which they find necessary for their proper development. Of course it is absolutely essential that germs should be present ready to develop whenever the conditions of existence become favourable. A certain proportion of these, no doubt, may be introduced by currents from elsewhere, but there is nothing to prevent them from remaining in a particular area, even though the water-masses are in constant motion. Recent hydrographical researches have shown us that eddies are far more common than was at one time believed. Even in areas where huge masses of water are constantly streaming in one direction, which one might naturally suppose would carry away with them all germs belonging to a local flora, these eddies act as a retaining factor, preventing any complete replacement till germs sufficient to maintain the local flora have been transferred to the supplanting water-masses. In coastal seas, moreover, many of the species are able to evolve resting bottom-stages, which lie waiting to reproduce the local flora, as soon as the conditions of existence are congenial.

Still Cleve's investigations have been of great value, and his plankton-types provide us with a biological division of species which is yet in the main quite serviceable. All that we have to say by way of qualification is that Cleve looked upon his types as representing communities of species limited

to definite marine areas, whereas in reality the areas of distribution of the different species encroach so upon each other, that a division of this kind is hardly practicable. This is true, not merely of the altering flora of ocean-currents, but also of the attached flora along the coasts and on land. Unless the areas are exceedingly remote from one another, the forms common to the areas usually exceed those peculiar to each area. Cleve's types, on the contrary, have no species in common, and therefore do not record the species in any definite area, but merely group them in accordance with their conditions of existence. If we adopt his principles we can certainly obtain a biological division of the species that is satisfactory in the main; but when we come to details it will, in some cases, be difficult to decide whether a species is to be assigned to this or to that type.

Biogeographically, the pelagic algæ may be divided, firstly according to the latitudes in which they are distributed, which is generally tantamount to saying according to their need of warmth and light, and secondly according to their occurrence along the coasts or in the open sea. This latter classification gives us the most distinct boundaries, and we will therefore consider it first. There is a whole series of species which unmistakably belong to coastal waters, and occur there in myriads at definite seasons of the year. Out in the ocean we do not find them, except when salinities or other physical properties indicate that they must have drifted from the coast. These have been termed neritic on the suggestion of Haeckel. Opposed to them are the oceanic species, which belong to the ocean and float over profound depths, from which occasionally they are swept by the currents into coastal seas and there usually perish.

Haeckel.

Neritic
species.

It is possible to imagine various reasons why the neritic species keep in the vicinity of the coasts. Some may derive benefit from the low or fluctuating salinities, which enable them to outstrip the more easily affected forms. Others, perhaps, require the abundant supply of nourishment from the land in order to grow and multiply as fast as such organisms should do. There may be other species, again, whose development-history makes it necessary for them to remain on the bottom at one stage of their existence, like the hydroid medusæ and all pelagic young-stages of littoral animals. Most of the neritic algæ have a bottom-stage, in so far as they form resting-spores

that sink to the bottom in the shallow coastal seas, where they rest until conditions of development become favourable again. This has been observed by many naturalists since Schütt first noticed in the Western Baltic that a species which begins to form resting-spores disappears shortly afterwards from the surface-layers. He showed, too, that the resting-spores sink down to the bottom, and, although their germination has not been carefully studied, we may be sure, all the same, that it does take place; further, when we subsequently find the same species once more in abundance, we have every reason for surmising that the resting-spores on the bottom were the principal source from which these forms have been derived.

Resting-spores.

Ability to form resting-spores must be of the utmost importance for the existence of the species in coastal waters. The chief difference between coastal seas and the ocean, so far as hydrographical conditions are concerned, lies in the extreme and rapid changes in such fundamental conditions of existence as salinity and temperature in coastal waters. Resting-spores, therefore, must be the means by which many species continue in coastal seas, notwithstanding the fact that there conditions of existence are only favourable for a limited portion of the year. The arctic diatoms, for instance, which are sometimes to be found in the plankton of the Skagerrack, are very easily affected by a rise in temperature, but their development takes place during the winter months from February to April, when the temperature is at its minimum. In the summer they are not to be seen, but their resting-spores are then most probably on the bottom. In the same way a whole series of warmth-loving species pass through the winter as resting-spores, and are to be found along our shores only in the warmest months of summer and autumn.

The neritic species may often be met with a long way out at sea, still continuing to increase, though they are seldom in any great quantity. One of the few instances that I know of, where we regularly find an immense production of neritic diatoms in the open sea, is in the Gulf Stream north of Shetland and the Faroe Islands during May. I made this discovery as long ago as 1895, and it has often been confirmed since then during the international investigations. When the snows begin to melt in the spring, the surface-layers of water are carried far away out from the land, and the neritic algæ are taken with them. I shall presently show that it just happens to be in the spring that conditions of nourishment favourable

Neritic diatoms in the open sea.

to an abundant plant-life exist in the Northern Atlantic, and the somewhat exacting neritic species benefit accordingly. This explanation, at any rate, seems to me the most reasonable one.

Another well-known instance is in the Polar Seas during the summer. Close to the melting polar ice, where it meets the warmer water-masses, a rich flora of neritic diatoms sometimes develops, while littoral species form a brown layer over the floes and broken lumps floating between them. Blessing, who took part in Nansen's expedition during 1893-1896, has given a good description of this latter phenomenon. We must look upon the Polar Seas as coastal waters in the biological sense. They have the extreme variations of temperature and salinity, and probably also the abundant supply of nourishment, that we would expect to find in a coastal sea. The resting-spores are enclosed in the ice, as I was able to show after examining the material collected by Nansen.

In the warmer parts of the Atlantic there are neritic diatoms nearly everywhere, but never in any great quantity, except where rivers enter the sea in the tropical regions. As a rule, too, they are smaller and weaker in structure than those we meet with in coastal waters under similar conditions of temperature. The cell-walls are very often only slightly silicated, and the form itself is so indistinct that it is difficult to distinguish species, which in their properly developed condition have unmistakable characters. It is not easy to tell whether this degeneration is merely a sign of insufficient nourishment, or whether other causes are also responsible. Certainly in one case want of nourishment is not entirely to blame. Out in the water-masses of the Atlantic to the south of Iceland we get a community of neritic diatoms that occur especially in the spring and autumn. Most of them are species of *Chaetoceras*. The prevailing forms have been long ago determined, and are undoubtedly *C. schüttii* and *C. lacinosum*. Still they are so dwarfed in structure, and so much the reverse of typical, that one might very well say that they were separate species (see Fig. 244). During this last expedition of ours we succeeded in finding this diatom-flora again, though in smaller quantities, in the Gulf Stream off the east coast of North America, so that it is practically certain that the neritic diatoms of the Atlantic south of Iceland are derived from the American coastal sea. As they are borne passively northwards towards

the shores of Iceland, they commence to develop at a great rate, with the result that the plankton in those parts frequently yields abundant though monotonously uniform samples of these degenerate forms. The altered conditions of existence, which obviously must have supervened, have thus resulted in an extensive production of algæ, though without investing them with their normal robust appearance. The strings of cells are of much smaller diameter than usual, so that the formation of auxospores cannot have taken place at the stage that is usual elsewhere. Wesenberg-Lund has told us that pelagic

Wesenberg-
Lund.

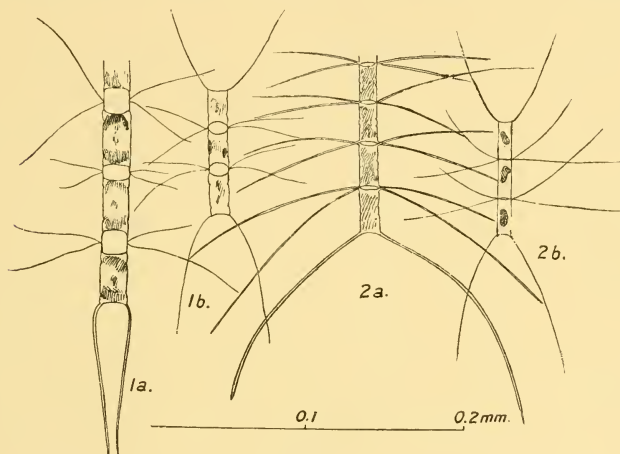


FIG. 244.

1a, *Chatoceras lacinosum*; 1b, forma pelagica; 2a, *C. schüttii*; 2b, forma oceanica.

fresh-water diatoms, such as *Asterionella gracillima* and *Fragilaria crotonensis*, keep on reducing their dimensions in the Danish lakes for months, sometimes even for over a year, and then suddenly return to their maximum measurements, and that this is undoubtedly due to the formation of auxospores. All are not, however, affected alike by such a change, and the species occur thereafter in two different sizes, making it necessary to express the measurements of their cell-dimensions by means of divergent curves. This goes on uninterruptedly, moreover, and the smallest forms diminish and seem to degenerate more and more, until in Wesenberg-Lund's opinion they lose all power of regaining their normal

dimensions and of reproducing their kind. The degenerate forms of neritic diatoms met with in the open sea appear to me to lack the stimulus which in some unknown manner leads to the formation of auxospores; consequently their ultimate extinction is only a matter of time, even though they may continue reproduction through a whole succession of generations. This is, of course, merely an unsupported surmise, for the few random investigations we have hitherto made do not afford sufficient material to settle questions of this nature at all definitely; but my idea is that the hypothetical views of an author are of more value than the enumeration of solitary facts that have no apparent connection.

Resting-spores
in the open
sea.

When the neritic diatoms evolve resting-spores out in the open sea, which occurrence we have been able to observe on more than one occasion, it might be supposed that the spores would be destroyed after sinking down to profound depths. This is not, however, necessarily always the case, since they appear to sink slowly, and remain within the region of light for weeks if not for months. The spores after leaving their cells are so minute that they are rarely caught in silk nets, so that little has been done as yet to throw light upon this question. But now that we have adopted the centrifuge-method it is possible to collect them, and we discovered numbers of resting-spores of species of *Chatoceras* in our centrifuge-samples from the Atlantic. In a litre of sea-water from Station 87 (lat. $46^{\circ} 48' N.$, long. $27^{\circ} 46' W.$), from a depth of 100 metres, I secured altogether 1160 resting-spores belonging to three different species of *Chatoceras*, though the forms themselves were not present at that time in a vegetative state either in the surface-layers or deeper down. Most probably what we got were representatives from the last remnants of the diatom-masses that throng the surface-layers there during the spring.

Distribution.

Neritic species include a very large number of diatoms—a class by far the most characteristic in coastal seas. In the majority of these neritic diatoms we have now been able to prove the existence of resting-spores. The peridineæ, on the other hand, are mainly oceanic, especially the species of *Ceratium*. One of the best-known neritic peridineæ is the comparatively low species *Prorocentrum micans*; but there are probably, too, whole series of small forms, as yet imperfectly known, which prefer the neighbourhood of the coasts. The coccolithophoridæ, again, are undoubtedly oceanic, whereas most of the naked flagellates are most likely domiciled in

shallower waters. *Halosphæra* is oceanic, and so also are the species of *Trichodesmium*; but there are several blue-green species that are brackish-water forms, and they must of course be accounted neritic (*Anabaena baltica*, *Nodularia spumigena*, *Aphanizomenon flos-aquæ*).

Several of the neritic algæ practically only occur locally. *Detonula cystifera*, for instance, appears in the Limfjord in Denmark and along the south coast of Norway, while *Lithodesmium undulatum*, *Coscinodiscus granii*, *Navicula membranacea*, and *Streptotheca thamensis* belong to the English Channel and to the southern portion of the North Sea. I could mention additional examples, but the greater number of them are far more widely distributed. It has been found possible to allocate all the species along the coasts of the Northern Atlantic to three comprehensive main groups, namely, the arctic, temperate, and tropical. This is perhaps rather an arbitrary arrangement, as these groups encroach to a very great extent upon one another; so that we get northern forms a long way south in the winter, and in the autumn the southern forms extend northwards. Further researches, too, might result in a stricter classification, while it is known that there are species which, biologically speaking, unite the groups, and might with equal reason be assigned to the one or to the other.

(1) *Arctic neritic species* are mainly those which Cleve termed Sira-plankton, and consist principally of diatoms. The characteristic forms are the species of *Thalassiosira* from which this name was derived. They are composed of long strings of short cylindrical cells united by a central thread of slime. *Thalassiosira hyalina* has its southernmost limit off the north of Norway, while *T. gravida* and *T. nordenskiöldii* occur in winter as far south as Central Europe. A series of species belonging to the genera *Fragilaria*, *Achnantes*, *Navicula* and *Amphiprora* are also distinctly arctic forms, and are characterised by having their cells bound together like ribbons. These include *Fragilaria oceanica*, *F. islandica* and *F. cylindrus*, *Achnantes tæniata*, *Navicula septentrionalis*, *N. vanhoeffenii* and *N. granii*, and *Amphiprora hyperborea*. The usually predominant genus *Chaetoceras* is only represented by two purely arctic species, namely, *Chaetoceras furcellatum* and *C. mitra*. We must likewise add the well-known *Biddulphia aurita*. Besides these diatoms, there are the peridinean *Gonyaulax triacantha*, and the brown flagellate *Phæocystis poucheti*, with its naked cells in large slimy round or lobate colonies.

(2) *Temperate neritic species* are even more numerous. The warmth-loving species fall under Cleve's designation of Didymus-plankton, with *Chaetoceras didymum* as the most characteristic form. It is, however, a better arrangement, perhaps, to associate with them a series of other species with a slightly more northerly character, that cannot be really

Arctic neritic species.

Temperate neritic species.

called arctic. Here, too, diatoms predominate, and *Chaetoceras* takes first place. The commonest forms include :—

(a) Northerly : *Chaetoceras teres*, *C. constrictum*, *C. diadema*, *C. debile*, *C. crinitum*, *C. pseudocrinitum*, *C. scolopendra*, *C. sociale*, *C. simile*, *Rhizosolenia setigera*, *Thalassiosira decipiens*, *Coscinosira polychorda*, *Leptocylindrus danicus*.

(b) Southerly : *Chaetoceras weissflogii*, *C. contortum*, *C. didymum*, *C. lacinosum*, *C. schüttii*, *C. curvisetum*, *C. cinctum*, *C. anastomosans*, *C. radians*, *Lauderia annulata*, *Cerataulina bergonii*, *Biddulphia mobiliensis* and *B. regia*, *Eucampia zodiacus*, *Ditylum brightwellii*, *Guinardia flaccida*, *Asterionella japonica*, the peridinean *Prorocentrum micans*, and the brown flagellate *Phaeocystis globosa*.

(3) *Tropical neritic species* have had far less study devoted to them ; still we may denote by this term a whole series of species that have their northernmost limit on the coasts of the Mediterranean. Of these we may mention :—

Chaetoceras furca, *C. diversum*, *C. femur*, *Hemiaulus hauckii* and *H. heibergii*, *Detonula schröderi*, *Asterionella notata*, *Rhizosolenia cylindrus*.

The neritic flora off the coasts of the Atlantic in the southern hemisphere has also been comparatively little studied as yet. Still we are justified in saying that the neritic diatoms of the antarctic, from the ice barrier northwards, differ in the main from species belonging to the northern hemisphere. The difference indeed is so great, that hardly a single species is common to both arctic and antarctic waters. The investigations of Cleve, Karsten, and Van Heurck show that the following neritic diatoms may be considered characteristic of the antarctic :—*Chaetoceras radiculum*, *Mølleria antarctica*, *Eucampia balaustium*, *Fragilaria antarctica*, *Thalassiosira antarctica*, and probably several others whose biology is as yet only slightly known.

Oceanic plankton algæ are much more widely distributed than neritic algæ, and it would almost seem from our material that each species may be met with in all the seas of the world, wherever there are favourable conditions of existence. The diatoms are apt to occur irregularly. Sometimes we find enormous quantities of them, and at other times they may be so scarce that it is difficult to detect them. The peridineæ are more evenly distributed, and this is true especially of the species of *Ceratium*, which are fairly abundant and hardly ever absent from oceanic-samples, unless perhaps in arctic waters. They may well be used as guiding forms to express the character of the plankton. It is possible that the different

Tropical
neritic species.

Neritic dia-
atoms in the
Antarctic.

Oceanic
species.

species and varieties of the genera *Peridinium* and *Gonyaulax* might be employed with equal advantage, but they are more difficult to determine, and so little studied as yet that the determinations of Hensen and Karsten are unserviceable. Owing to so little being known about their distribution, I have decided to ignore them for the present.

The oceanic species may also be divided into three main groups:—

(1) *Arctic forms*, corresponding to Cleve's Tricho-plankton and Chæto-plankton. Most of them occur also in antarctic waters. Arctic oceanic species.

Diatoms: *Thalassiothrix longissima*, *Coscinodiscus subbulliens*, *Chæto-ceras criophilum*, *C. boreale*, *C. convolutum*, *C. atlanticum*, *C. decipiens*, *Rhizosolenia hebetata* (*semispina*), *Nitzschia seriata*.

Peridineæ: *Ceratium arcticum*, *C. longipes*, *Dinophysis granulata*.

(2) *Temperate-Atlantic forms*, corresponding to Cleve's Styli-plankton and Tripos-plankton. The latter of these two designations comprises a small community of species, which are less exacting as regards salinity, and are therefore produced in quantities along the coasts of North Europe. Temperate oceanic species.

Diatoms: *Rhizosolenia styliiformis*, *R. acuminata*, *R. alata*, *Coscinodiscus radiatus*, *C. centralis*, *C. stellaris*, *Chæto-ceras densum*, *C. dichæta*, *Corethron criophilum*, *Dactyliosolen antarcticus*, *Thalassiosira subtilis*, *Coscinosira æstrupi*, *Asteromphalus heptactis*, *Bacteriastrum delicatulum*, *B. elongatum*.

Peridineæ: *Ceratium tripos*, *C. bucephalum*, *C. azoricum*, *C. macroceros*, *C. intermedium*, *C. lamellicorne*, *C. reticulatum*, *C. fusus*, *C. furca*, *C. lineatum*, *Dinophysis acuta*, *D. hastata*, *D. homunculus*.

Coccolithophoridae: *Coccolithophora pelagica*, *Pontosphaera huxleyi*.

Chlorophyceæ: *Halosphaera viridis*.

(3) *Tropical-Atlantic forms*, corresponding to Cleve's Desmo-plankton, and comprising a series of species, especially peridineæ and coccolithophoridae. Cleve's guiding form is the blue-green alga *Trichodesmium thiebaultii*. The following are some of the commonest:— Tropical oceanic species.

Diatoms: *Coscinodiscus rex*, *Planktoniella sol*, *Gossleriella tropica* (see Fig. 245), *Rhizosolenia castracanei*, *Chæto-ceras coarctatum*, *Asterolampra marylandica*, *A. rotula*.

Peridineæ: species of *Ceratium* of all groups (*prælongum*, *cephalotum*, *gravidum*, *candelabrum*, *pennatum*, *extensum*, *palmatum*, *massiliense*, *carriense*, and several others), species of *Oxytoxum* and *Podolampas*, *Ceratocorys horrida*, species of *Phalacroma*, *Dinophysis schütti* and *D. uracantha*, species of *Amphisolenia* and *Triposolenia*, *Ornithocercus magnificus*, *O. quadratus*, *O. steinii* and *O. splendidus*, *Pyrocystis noctiluca* and *P. fusiformis*.

Coccolithophoridae: *Coccolithophora leptopora*, species of *Syracosphaera*, *Calciosolenia murrayi*, *Michaelsarsia elegans*, and many others.

The boundaries of the areas populated by these communities of species are as variable as the limits of distribution for the

species themselves. Our investigations at different seasons, both in coastal waters and in the North Atlantic, have shown us that the flora of each locality is constantly changing. One species succeeds another as month follows month, and different societies predominate in the same locality at different seasons.

Along the west coast of Norway, for instance, we find a flora during the winter, from December to February, scanty in numbers, but consisting of many species, and mainly composed of true Atlantic forms (Styli-plankton), which reach their northernmost limits in the dark months of the year. About March or April the temperature attains its minimum, and great quantities

Flora of west
coast of
Norway.

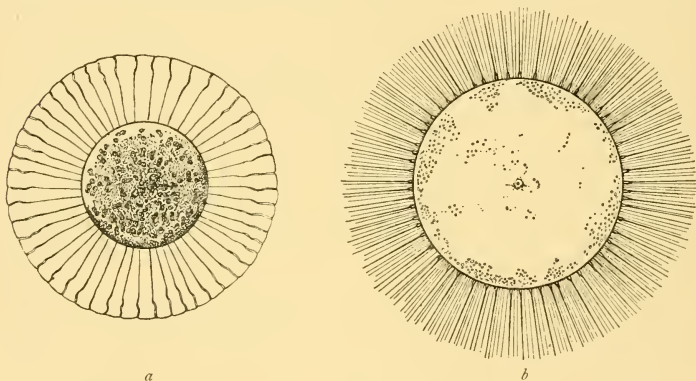


FIG. 245.

a, *Planktoniella sol*, and *b*, *Gossleriella tropica*, from the Atlantic. (Schütt.)

of diatoms are then produced, which are mainly arctic. Sometimes these are almost entirely neritic, and sometimes there is a considerable addition of oceanic species. As often as not it is the species of *Thalassiosira* and *Coscinodiscus* which first appear, and then comes *Chaetoceras*, *C. debile* being usually the form found on the west coast, *C. constrictum* preferring the Skagerrack. In May the predominant form is generally *Leptocylindrus danicus*. We next get a period in June when the prevailing forms are oceanic, *Ceratium longipes* at that time attaining its maximum development and characterising the flora. In August the warmth-loving peridineæ begin to be more and more numerous, *Ceratium fusus*, *C. furca*, and *C. tripos* being then much in evidence, and continuing to increase until October. Finally, in November we get a comparatively

large amount of southern neritic species (*Didymus*-plankton), made up to a great extent of forms of distinctly foreign origin. As the dark months of winter approach, however, their numbers rapidly decline.

In the open sea, too, our investigations appear to indicate that the southern forms reach farthest north in the autumn, say about November, while during the months of spring, from April to May, northern forms extend very far south. We have not as yet made investigations at different seasons in the tropical parts of the Atlantic; consequently we cannot say whether there is an annual cycle of plant-development in a region where the conditions of existence seem to vary so little. It would be an excellent thing if researches of this nature could be undertaken.

Flora of the
open sea.

Supposing that the ocean-currents do exercise a direct influence upon the character of the plankton in the tropics, it is fair to imagine that it must be in the direction of periodicity. Lohmann has put forward the suggestion that the changes in pelagic animal life near the coasts of South Europe are connected with a cyclic movement of the water-masses. When these reach their northernmost point the conditions of existence will affect the organisms, so that the water-masses that pass through this region in the winter are likely to have a different fauna from that of the water passing through in summer. Elsewhere it is very difficult to tell what changes in the plankton are due to the direct influence of ocean-currents, and what changes are the result of altered conditions of existence partly due to ocean-currents and partly to other causes. It has often been observed, not only by Cleve and Hensen, but also during previous researches made by the "Michael Sars" and during the "Challenger" and "Valdivia" Expeditions, that the plankton changes its character the moment one passes the boundary between two currents. Thus an examination of the plankton may serve as a check on purely hydrographical investigations, which aim at ascertaining the boundaries of currents by means of observations of their temperatures and salinities. Perhaps the best guiding forms are the species of *Ceratium*, and strangely enough it is very often the species that systematically are the nearest related, which replace each other as we pass from one area to another. Many of them are so closely related that it is only for the sake of convenience that we regard them as distinct species, and there is always the possibility that they may be able to pass directly from one form into the other, even if we cannot actually prove

Ocean-
currents and
the plankton.

that they do so. There is a series of closely related species, for instance, grouped round *Ceratium macroceros*. *Ceratium arcticum* is the farthest outpost in the direction of the polar sea, and shows the greatest variation. Its three horns are extremely divergent; the centre one, which points forward, is slightly bent, and so also are the other two. Near the southern limit of the species there are more and more instances, in a series of transition forms, where the two posterior horns bend forward, till we get to *Ceratium longipes*, the characteristic form of the Norwegian Sea and North Sea during the first half

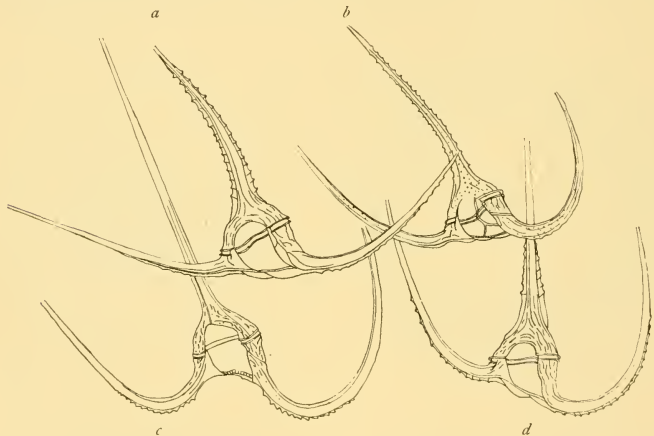


FIG. 246.—SPECIES OF *CERATIUM* BELONGING TO THE TYPE OF *C. MACROCEROS*, NORTHERN SPECIES.

a, *C. arcticum*; b, *C. longipes*; c, *C. macroceros*; d, *C. intermedium* (1 $\frac{1}{2}$!). (Jørgensen.)

of summer. In this case, the posterior horns are bent quite forward, so that their extremities are parallel with the frontal horn. In the Gulf Stream we get *C. intermedium*, which has a straight frontal horn, like the other members of this type, and all three of its horns are much longer and more slender than those of the two northern species. At the eastern limit, where fresh water from the Baltic and the coasts of North Europe reduces the salinity, and where, too, the high summer temperatures diminish the viscosity of the surface-layers, there is a species with an even better suspension-apparatus, namely *C. macroceros* (see Fig. 246). Its frontal horn is particularly long and thin, and the posterior horns first bend a little backwards, and then

sweep round to the front, sometimes in a direction parallel to the frontal horn, and sometimes with a moderate amount of divergence. We have already mentioned that *C. arcticum* and *C. longipes* belong to the Tricho-plankton and that *C. intermedium* and *C. macroceros* are Styli-plankton. We have finally a whole series of variations belonging to the tropical Desmo-plankton, namely *C. vultur*, *C. pavillardii*, *C. trichoceros*, and *C. tenue*, which we reproduce from Jørgensen's excellent mono-

graph (see Fig. 247), and many others. They illustrate the different tendencies to variation. In similar fashion there are series of variations which group themselves round the other main types of the genus.

Guiding forms like these are of very great assistance in defining the boundaries of adjacent currents which have a different biological character. But

we need to exercise the utmost care in drawing conclusions as to

the origin of ocean-currents from the composition of their pelagic flora, and it must not by any means be taken for granted that areas where the same species occur are necessarily united by a continuous stream connection. We have repeatedly made discoveries which go to indicate that most plankton-species of any consequence are to be found scattered about here and there outside their proper domain, so that these stray individuals might easily originate an abundant flora whenever conditions of existence became favourable.



FIG. 247.—SPECIES OF *CERATIUM* BELONGING TO THE TYPE OF *C. MACROCEROS*, TROPICAL SPECIES.

a, *C. pavillardii* ($\frac{2}{1}^4$); *b*, *C. trichoceros* ($\frac{2}{1}^4$); *c*, *C. vultur*, var. *japonica* ($\frac{2}{1}^4$); *d*, *C. tenue*, var. *buceros* ($\frac{2}{1}^0$). (Jørgensen.)

Cleve, who looked upon the dispersal of organisms by currents as the chief factor in affecting the character of the plankton, was at first of opinion that he could fix the north-western boundaries of the Gulf Stream by noting the distribution of *Rhizosolenia styliiformis*, the guiding form in his Styli-plankton. But he, too, found that its area of distribution extends northwards in the course of spring and summer, and that the swarms of *Rhizosolenia* actually outdistanced the speed of the current. The wider distribution of the algæ was evidently, therefore, due not alone to the increased volume of the current, but also to a rapid propagation produced by summer warmth outside the influence of the current, the algæ apparently having been already present in this area in small quantities.

I may further instance the close agreement between oceanic species in arctic and antarctic waters. *Thalassiothrix longissima* and *Rhizosolenia semispina* (*hebetata*) are the two most characteristic forms among algæ along both the polar boundaries of the Atlantic, though they have also been found in small quantities at various localities in the tropics. I personally came across them on several occasions during the "Michael Sars" Expedition, and it requires, in my opinion, no special theories to account for this "bipolarity." There is quite sufficient connection between the two oceans to enable a few germs which are exceptionally tenacious of life to pass from the one to the other, and this would amply explain the agreement. Characteristically enough there is no similar agreement between arctic and antarctic waters when we come to the neritic forms, and this is probably because they are less adapted to travel over such immense distances. It may be, too, that their tendency to evolve resting-spores is an obstacle to long passive wanderings.

As a means of determining the direction and velocity of currents pelagic algæ will be found of very little use. Their continued existence during the progress of the current must always depend upon their persistence in reproduction, and this again is dependent upon conditions of existence and competition with other species. It is not mere coincidence that the microscopic flora of the warm Atlantic extends farthest north during the dark winter months, when no other species are much inclined to develop, and there is therefore no competition of any consequence, the character of the flora consequently remaining for a long time unaltered. Large animals, such as medusæ and salpæ, or the larvæ of bottom-animals like *Phoronis*, will be found far better indicators of the currents. Ostenfeld

Bipolarity of
oceanic
diatoms.

has, however, encountered one solitary case where plankton algæ could be employed for this purpose. *Biddulphia sinensis* (Fig. 248), a neritic diatom from the coasts of the Indian Ocean, was met with in the North Sea for the first time in 1903, to begin with in the southern parts, and then gradually farther and farther north, until at last it was discovered on the west coast of Norway at Bergen. Its travelling rate corresponds to the values which have been otherwise obtained for the velocities of the current along the coasts of Denmark and Norway. Latterly, it has found a fixed distribution-centre in the north-eastern corner of the North Sea, whence it extends

still farther northwards every autumn. The velocity of the current could hardly be determined from the observations of these last few years, as there is always the possibility that this diatom has more than one centre of distribution, but its annual wanderings clearly indicate the direction of the current.

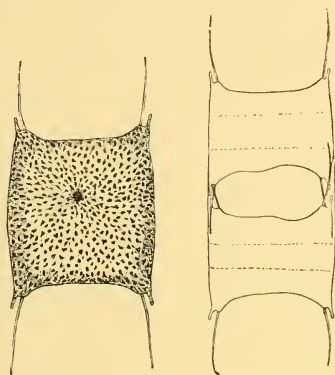


FIG. 248.—*BIDDULPHIA SINENSIS* ($\frac{1}{2}$ °).
(Ostenfeld.)

tion of the different species. We have been particularly successful in our study of the coccolithophoridæ, owing to the improved methods we were able to adopt. I shall deal separately with their distribution in what follows, and at the same time give some particulars of their quantitative occurrence. Part of the material is still incompletely examined. The difficult species of *Peridinium* in particular, and of a few other genera, will require a separate monograph for their special treatment; we have secured immense numbers of these forms. In other respects our observations practically confirm the views regarding the distribution of species that we owe chiefly to Cleve.

I shall now give a preliminary description of the character of the plankton along our route, founded upon an examination of

A large quantity of plankton algæ has been collected during the "Michael Sars" Expedition along the whole route, and will contribute valuable information regarding the distribu-

Phytoplankton collected during the "Michael Sars" Expedition.

material from representative stations, and upon observations of the living organisms on board ship.

The coast
banks of
North Europe.
(Stations 1-10,
9th-20th
April.)

All our first stations about the middle of April, with the exception of Stations 1 and 5, that were close in to land and had a less abundant flora, had an extremely plentiful diatom-plankton, such as we only get in the waters of North Europe during the spring. Our experiments with the closing-net, which, thanks to the fine calm weather, were made with the utmost exactitude at Stations 3 and 10, showed that by far the larger number were to be found between the surface and a depth of 100 metres, though even at a depth of 100 to 150 metres there were still quite considerable quantities. The character of the flora was mainly northern, especially in the case of the oceanic species. Among the principal forms we got *Rhizosolenia hebetata* forma *semispina* and *Nitzschia seriata*. Neritic diatoms were also numerous, and some had resting-spores. They are of a distinctly southern character compared with the species which occur, for instance, along the coasts of the North Sea; further, they belong to a local flora, which does not seem to have any direct connection with the North Sea. On the whole, these neritic diatoms are so small in their dimensions that they show signs of an "oceanic degeneration."

Besides them, there was an addition of subtropical species, especially in the deeper layers, and especially at the southernmost stations, Nos. 9 and 10, consisting of both diatoms and peridineæ, not in any great quantity, but still occurring regularly. These are the northernmost outposts of the Desmoplankton, including such species as *Planktoniella sol*, *Ceratium gibberum*, *Dinophysis schüttii*, and *D. uracantha*.¹

The coast
banks of South
Europe and
North Africa.
(Stations 11-
41, 21st April-
22nd May.)

Throughout the stretch of sea along the coasts of South Europe and North Africa our investigations were carried on comparatively close to the coast, and the plankton was generally found to be poor both in quality and quantity as soon as we stood at all far out from the land. It was then composed

¹ As representing this area, I here give a list of species from Station 7, depth 0-20 metres :—
Oceanic diatoms : *Chetoceras decipiens*, *C. densum*, *C. convolutum*, *C. peruvianum*, *C. atlanticum*, *C. dichata*, *Coscinodiscus centralis*, *C. marginatus*, *Euodia cuneiformis*, *Thalassiosira subtilis*, *Asteromphalus heptactis*, *Rhizosolenia alata*, *R. semispina*, *R. stollerfothii*, *R. shrubsolei*, *R. acuminata*, *R. amputata*, *Dactyliosolen antarcticus*, *Nitzschia seriata*, *Thalassiothrix longissima*.

Neritic diatoms : *Chetoceras diadema*, *C. schüttii*, *C. contortum*, *C. coronatum*, *C. scolopendra*, *Bacteriastrum varians*, *Eucampia zodiacus*, *Thalassiothrix nitzschioides*, *Cerataulina bergonii*, *Dactyliosolen tenuis*, *Thalassiosira decipiens*, *T. excentrica*, *T. nordenskiöldii*.

Peridineæ : *Ceratium tripos* forma *atlantica*, *C. lamellicorne* forma *compressa*, *C. azoricum*, *C. furca*, *C. arietinum*, and several others.

Coccolithophoridae : *Distephanus speculum*, *Coccolithophora pelagica*.

of oceanic species, that we subsequently met with in the central parts of the ocean, though there was not more than a mere selection of the very commonest forms. It was here that we first became aware of the immense contrast between the scanty plant life and the teeming animal life. Sir John Murray and I examined the stomach contents of the salpæ abounding in the Strait of Gibraltar, and could see that they lived almost entirely on small forms like coccolithophoridæ and tiny peridineæ, which were too diminutive for our silk nets to capture. Radiolaria, however, both Acanthometridæ and colony-forming species, in symbiosis with brown flagellates, were present sometimes in such quantities that their assimilation of carbonic acid played no small part in proportion to that of the scanty plant plankton. Close in to the shore, on the other hand, there was abundance of plankton, and we got quantities of neritic diatoms off Lisbon, in the Strait of Gibraltar, and at several places on the coast of Morocco down to Cape Bojador. Different species predominated in the different samples, but *Lauderia annulata* was the commonest form everywhere.

No one accustomed to the plankton algæ of northern waters, with their numerous dark-brown chromatophores, could fail to be struck by the fact that the species never had more than a few small chromatophores, and thus had a pale appearance. In the diatoms the strong light frequently had the effect of making the chromatophores group themselves in the centre of the cell, or in *Lauderia annulata* at the terminal faces where the cells in the chain touch each other. This was invariably the case in plankton near the surface, though deeper down the position of the chromatophores might be normal.¹

On this cruise we made acquaintance with the tropical Atlantic plankton in all its abundance. For a northerner it was most fascinating to study the many strange forms, especially of peridineæ. Every fresh batch disclosed species that were new or rare, or else remarkable stages of development. The

The Central Atlantic from the Canaries to the Azores, and from the Azores to the Newfoundland Bank.

(Stations 44-69, 28th May-29th June.)

¹ The following list is from a sample pumped up from the surface, off the south coast of Portugal, on 24th April 1910:—

Diatoms: *Lauderia annulata* (the prevailing form, found with auxospores), *Thalassiosira subtilis*, *T. gravida*, *Stephanopyxis turris*, *Paralia sulcata*, *Coscinodiscus concinnus*, *Leptocylindrus danicus*, *Rhizosolenia alata*, *R. shrubsolei*, *R. styliformis*, *R. stollerfothii*, *R. delicatula*, *R. robusta*, *Chatoceras densum*, *C. schüttii*, *C. didymum*, *C. curvisetum*, *C. decipiens*, *C. lorenzianum*, *C. diversum*, *Eucampia zodiacus*, *Hemiaulus hauckii*, *Biddulphia mobilensis*, *Bacteriastrium varians*, *Nitzschia seriata*.

Peridineæ: *Ceratium lineatum*, *C. macroceros*, *C. fusus*, *C. furca*, *C. candelabrum*, species of *Peridinium*, *Gonyaulax spinifera*, *Diplopsalis lenticula*, *Dinophysis acuminata*, *D. rotundata*, *D. acuta*; *Coccolithophora pelagica*.

multitude of species was surprising, though none of them was very numerously represented. Every day one might sit and examine some unique microscopical form, which might be lost only too easily, and consequently had to be drawn there and then. And whereas in the north there are large quantities of every species, so that it is easy to investigate them in all their stages of development and variation, this multiplicity of forms in the tropics renders it incomparably harder to find out what stages of development belong to the same species, or how the boundaries between the different species are to be fixed.

The various stations did not differ much from one another, if we except Station 59, near Fayal in the Azores, where there were numbers of neritic diatoms, and Station 66, close to the Newfoundland Bank, where there was an addition of arctic forms. On the whole, the multiplicity of species increased as we went westwards. Possibly considerable differences may be revealed when the material has been completely treated, but all the species occur too sparsely in these samples to justify one in drawing conclusions from negative results.¹

The Tropical Atlantic flora much resembles the plankton flora of the Indian Ocean observed by Karsten. In the Pacific there would seem, according to Kofoid, to be an even greater multiplicity of species, but I found several of the new species obtained by him during the "Albatross" Expedition, and it is probable that more and more of these rare Pacific species will gradually be found within Atlantic waters also.

In conclusion, it should be stated that, as far as quantity is concerned, the smallest plankton organisms, Lohmann's Nanno-plankton, play a far more important rôle than the whole of the other species caught in our silk nets, which will be subsequently discussed in their proper order.

¹ To show the character of the flora I append a list of species found at Station 64, lat. 34° 44' N., long. 47° 52' W., in a closing-net sample from a depth of 200 metres to the surface:—

Diatoms: *Coscinodiscus rex*, *C. lineatus*, *Euodia cuneiformis*, *Planktoniella sol*, *Gosslerella tropica*, *Thalassiosira subtilis*, *Asterolampra marylandica*, *Rhizosolenia castracanei*, *R. acuminata*, *R. styliformis*, *Bacteriastrum elongatum*, *Hemiaulus* sp., *Chatoceras dicheta*, *C. tetrastichon*, *C. peruvianum*, *C. coarctatum*, *C. jurca*.

Peridineæ: *Ceratium pentagonum*, *C. teres*, *C. candelabrum*, *C. gravidum*, *C. fusus*, *C. extensum*, *C. pennatum*, *C. gibberum*, *C. buceros*, *C. platycorne*, *C. azoricum*, *C. tenue*, *C. pavillardi*, *C. karsteni*, *C. declinatum*, *C. gracile*, *C. arietinum*, *C. macroceros*, *C. massiliense*, *C. arcuatum*, *C. carriense*, *C. reticulatum*, *C. trichoceros*, *C. palmatum*, *C. limulus*, *C. pulchellum*, species of *Peridinium*, *Diplopsalis lenticula*, *Blepharocysta splendor maris*, *Ceratocorys horrida*, *Goniodoma polyedricum*, *G. fimbriatum*, *Gonyaulax polygramma*, *G. joliffei*, *G. pacifica*, *G. fragilis*, *G. mitra*, *Protoceratium reticulatum*, *Podolampas elegans*, *P. palmipes*, *P. bipes*, *Oxytoxum scolopax*, *O. reticulatum*, *O. cristatum*, *O. milneri*, *O. tessellatum*, *Dinophysis uracantha*, *D. schiittii*, *D. schröderi*, *Phalacrocoma argus*, *P. doryphorum*, *P. cuneus*, *P. rudgei*, *Amphisolenia palmata*, and another new species, *Ornithocercus quadratus*, *O. magnificus*, *O. steinii*, *O. splendidus*, *Pyrocystis lunula*, *P. noctiluca*, *Hexasterias problematica*.

Cyanophyceæ: *Trichodesmium thiebaulti*.

The plankton of the cold water on the Newfoundland Bank was very poor in species, *Ceratium arcticum* and *Peridinium parallelum* being the commonest forms. There were, besides, a few diatoms, such as *Chaetoceras atlanticum*, *C. criophilum*, and *Rhizosolenia semispina*, all well-known species in the Norwegian Sea. In the harbour of St. John's, on the other hand, we found the plankton quite abundant, consisting of northern forms, both neritic and oceanic: the species of *Chaetoceras* (*decipiens*, *debile*) predominated.

The New-
foundland
Bank.
(Stations 70-
79, 30th June
-10th July.)

Our northern section across the Atlantic contributed largely to our knowledge of the distribution of species, since it showed

The northern
Atlantic
section.
(Stations 81-
92, 12th-24th
July.)

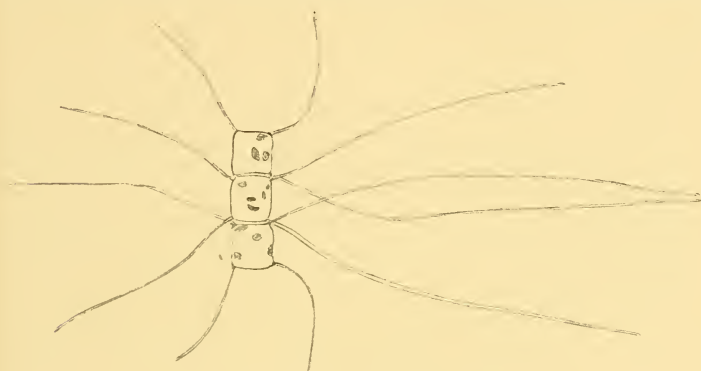


FIG. 249.—*CHAETOCERAS PERPUSILLUM* ($\frac{800}{1}$).

us that a great many tropical forms are still to be found in lat. 45–50° N. These particular waters had been very little studied previously, and it was extremely interesting to follow all this Atlantic flora on its passive journey northwards. On the whole, its character remains unchanged, though of course the number of species becomes considerably reduced. During the first half of the section, on the western side of the mid-Atlantic ridge, there were a few small degenerate neritic diatoms belonging to the species which occur in the Atlantic water-masses south of Iceland: namely *Chaetoceras schüttii*, *C. lacinosum*, and others. It seems unquestionable that they are derived from the American coast, and follow the current as far as Iceland. At Station 85 I also came across a remarkable little *Chaetoceras*, that Cleve found in 1897 in the Skagerrack and named *Chaetoceras perpusillum*

(Fig. 249), which had not been met with subsequently. The whole structure of this diatom shows that it, too, is most probably a neritic form, and it must therefore have a wider distribution than was commonly supposed.¹

As we neared the coast banks of Europe we found the number of species growing distinctly less, though on the other hand the quantity of the plankton increased.

The plants of the sea like those of the land build up all the organic substance which forms the chemical foundation of life. If we wish to know clearly when and how and under what conditions vigorous production takes place, or what prevents the development of an exuberant plant-life, we must first acquire the means of estimating the amount of vegetation in the different parts of the sea.

Hensen was the first to take up this problem, the solution of which depends on three assumptions: (1) it is absolutely essential to have apparatus that can capture all the organisms living in a specified quantity of water, (2) the plankton must be supposed to be uniformly distributed in the sea, so that the catch represents a reasonably extensive area; and (3) a scientific examination of the catch must supply a really correct picture of the amount of plants and their capacity of production.

The apparatus employed by Hensen and his assistants consisted of extremely fine straining-cloth, with meshes 0.04 to 0.05 mm. in diameter. He made the mouth of his net small in proportion to the filtering silk surface, to ensure as far as possible the immediate filtering of all water that came in through the opening, his object in this being to ascertain approximately how much water was filtered, when the net was drawn through the sea for a calculated distance. Experiments showed that in

¹ As illustrating a haul on this section I append a list of the species found in the closing net at Station 81 (lat. 48° 2' N., long. 39° 55' W.), from a depth of 50 metres to the surface:—

Diatoms: *Coscinodiscus excentricus*, *Euodia cuneiformis*, *Planctoniella sol*, *Coscinosira æstrupi*, *Thalassiosira subtilis*, *Corethron criophilum*, *Rhizosolenia styliformis*, *R. shrubsolei*, *R. fragillima*, *R. alata*, *R. semispina*, *Bacteriastrum delicatulum*, *B. elongatum*, *Chatoceras atlanticum*, *C. boreale*, *C. mediterraneum*, *C. peruvianum*, *C. criophilum*, *C. decipiens*, *C. contortum*, *C. schüttii*, *C. curvisetum*, *C. lacinosum*, *C. furcellatum* (a resting-spore), *Thalassiothrix longissima*, *T. nitzschioides*, *Nitzschia seriata*.

Peridineæ: *Ceratium lineatum*, *C. candelabrum*, *C. pentagonum*, *C. gravidum*, *C. fusus*, *C. pennatum*, *C. tripos*, *C. asoricum*, *C. gibberum*, *C. platycorne*, *C. arcticum*, *C. intermedium*, *C. macroceros*, *Protoceratium reticulatum*, *Peridinium oceanicum*, *P. depressum*, *P. divergens*, *P. conicum*, *P. ovatum*, *P. tristylum*, and some others, *Diplopsalis lenticula*, *Pyrophacus horologium*, *Goniidoma polyedricum*, *Gonyaulax polygramma*, *Podolampas elegans*, *P. palmipes*, *Oxytoxum scolopax*, *O. diploconus*, *Ptychodiscus carinatus*, *Dinophysis acuta*, *D. schüttii*, *D. rotundata*.

Flagellates: *Phæocystis poucheti*.

Silicoflagellates: *Dictyocha fibula*.

Chlorophyceæ: *Halosphaera viridis*.

Cyanophyceæ: *Trichodesmium thiebaulti*.

Law of production of organic substance in the sea.

Hensen.

Hensen's net.

practise his net could not filter the whole of the water which ought to pass through; it was possible, however, to work out a coefficient for each size of net, namely a fraction indicating what proportion of the total quantity of water had actually been filtered. Hensen trusted chiefly to vertical hauls, since he was anxious to know definitely the exact distance through which the net had passed. He lowered his apparatus open, but with a heavy weight attached, so that it went down end-first and therefore caught nothing until hauling in began. Initial investigations aimed at ascertaining the total quantity of plankton in the photic zone, and accordingly the net was drawn in one haul from a depth of 200 metres right up to the surface, or from the bottom to the surface in water shallower than 200 metres, the idea being to find out the quantity of plankton in a column of water of known depth 1 metre square.

It is not, however, sufficient merely to compare the total quantity of plankton present in different localities; it may be just as important to know what there is at different depths, not only because we have to consider the effect of light, let us say, upon plant production, but because there may be layers of water, such as we find especially in coastal areas, totally distinct in hydrographical characters, and with different conditions of existence. Hensen made vertical hauls from different depths, and had recourse to subtraction when estimating the plankton of the deeper layers, but since that time closing-nets have been introduced, and we are able now to get samples from any layer we wish to study. C. G. Joh. Petersen constructed a closing-apparatus to go with Hensen's vertical net, and Nansen also designed a vertical closing net which was invariably used by the "Michael Sars," and found to be handy and reliable. Provided only the bag be long enough in proportion to the opening, it will act successfully from a quantitative point of view, though we did not employ it much for this purpose, as we had better methods of our own for estimating quantity. Otto Pettersson obtained his estimates of quantity by attaching silk nets to a large current-meter, which recorded the velocity of the current, and thus indirectly supplied approximate figures denoting the amount of water filtered. A series of very interesting determinations, from samples secured in this way, has been described by Broch.

Petersen's
closing
apparatus.

Nansen's
closing net.

Pettersson's
method of
attaching nets
to current-
meter.

Broch.

The net-method was found unreliable as time went on. In the first place, it does not fairly represent the total quantity of plankton, since many of the smaller forms pass altogether, or to

a very great extent, through the meshes; and, secondly, the meshes become gradually clogged with the slimy little algæ, or animals, so that the coefficient of filtration does not remain constant. Even during the course of a single haul we occasionally noticed that everything worked well to begin with, but that the cloth became more and more stopped up, until at last filtration ceased entirely. In other words, it is sometimes impossible to tell how much water has been filtered, and consequently the catch is practically valueless from a quantitative point of view.

An endeavour was made to overcome this last difficulty by filtering a quantity of water, previously measured, either through silk nets, or through an even less porous filter-material, such as taffeta, or hardened filter-paper, or sand, an additional advantage being that by this means the very smallest organisms could be retained. Water-samples were secured by water-bottles or by pumps. Lohmann, who did much to perfect the pump-method, was not only able to get his water-samples from any depth desired, but could obtain samples representing a column of water from the surface down to a specified level. The pump was made to work in connection with a long, flexible hose, the mouth of which was lowered as far down as considered necessary, and then drawn gradually up towards the surface as pumping proceeded. The pumped-up water thus represented proportionally the whole distance through which the hose passed before reaching the surface. These samples were afterwards filtered by Lohmann, and the results compared with catches obtained by vertical hauls with the silk nets.

The methods of capture had thus been greatly improved, and it was possible to obtain the smallest organisms, but for practical reasons it was necessary to limit the quantity of water filtered on each occasion. This forced us to turn our attention to the second question, namely the regularity with which organisms are distributed in the sea. Fortunately, the researches of Hensen and his assistants, as well as those of Lohmann and myself, have all gone to show that the distribution of the pelagic plants, at any rate, is extremely regular. The samples from adjacent localities with similar life-conditions have yielded very concordant results. I do not consider it any exception to this statement that in tropical waters dense masses of *Trichodesmium* sometimes collect as water-bloom in certain areas and not in others, or that diatoms near the edge of the polar ice occur in more or less local swarms, for I consider it more than probable that these irregularities

Filtering
method.

Lohmann's
pump method.

Distribution of
pelagic plants
extremely
regular.

arise because the conditions of existence vary in closely adjoining areas. Lohmann has found that at certain seasons 10 to 15 c.c. of sea-water amply suffice to give a representative sample of the total plankton, but it is evident that only the commonest organisms floating in the sea in any locality do occur so densely and regularly that we can be sure of securing them, or even of catching enough for ascertaining their comparative frequency, in a water-sample consisting of only a few litres of water or less. The more scattered or mobile the individuals are, the larger masses of water must we examine to get a knowledge of the quantity present in any locality.

It follows, therefore, that we must abandon all thought of a universal method. Fine silk nets give us complete collections of the larger Ceratia and diatoms, but are of no use for the smallest species, for which we are obliged to have recourse to more delicate methods of filtration, and to the centrifuge. The larger forms, too, will be found in our silk nets in sufficient quantities, if they are at all abundant, but where they are scarcer than, say, fifty specimens to the litre, the centrifuge cannot be depended on. Besides amongst these larger organisms some species are so scanty that even a vertical haul with the big net yields insufficient material, so we have been compelled to adopt the special methods described in this volume.

Various methods have been employed for estimating the quantity of plankton on the basis of catches made. We can allow the whole sample to sink to the bottom of a measuring glass, and appraise its volume, or we can weigh it while the organisms are saturated with water or spirit, or we can weigh the dry substance. Such determinations of volume and weight give us our first rough idea of the variations in the quantity of plankton, but there are many sources of error which it is unnecessary to discuss here. The worst fault is that measurements of this kind group into a whole the most diverse values, such as plants and animals, producers and consumers, one-celled organisms that are constantly reproducing themselves, and multicellular animals with a longer duration of life, or, again, organisms with slow and others with rapid metabolism. If we want to know a little about the conditions of development of organisms, we must have a method of investigation that allows us to trace the growth and retrogradation of each of the different species by itself, and counting then becomes the only method possible, as Hensen has continually asserted. Counting is a method that requires much time, and also absolute accuracy in

No universal method of estimating quantity of plankton.

Determinations of volume and weight.

Counting necessary.

determining the species whose development we desire to trace; consequently most of those who endeavour to work at these interesting questions will be forced to confine themselves to definite problems, and content themselves with tracing the growth of a limited number of species. No doubt a man like Lohmann may be able to know all the species within certain limits, and may actually calculate by counting what each of them contributes to the total plankton volume, but speaking generally a "universal method" that will give us the total quantity of all the plants and animals of the sea in curves and tables is unattainable.

During the "Michael Sars" Expedition our quantitative investigations yielded really remarkable results. Lohmann had succeeded by means of a centrifuge in determining the quantity of plankton in quite small samples of Baltic water, and we felt confident, therefore, that this excellent method ought also to prove serviceable in the open sea. We very soon found, however, that the algæ there

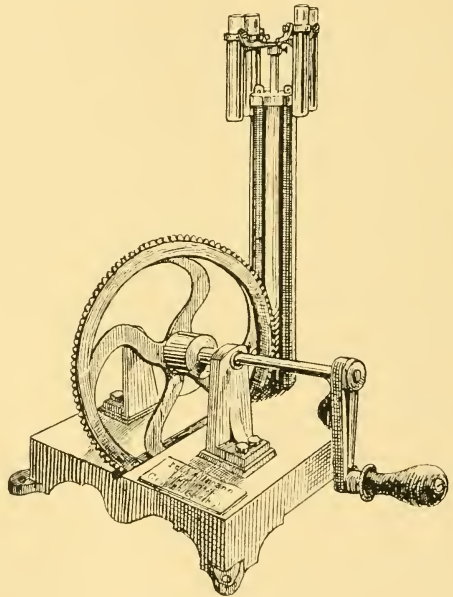


FIG. 250.—LOHMANN'S HAND-CENTRIFUGE.

were too scarce for our little hand-centrifuge (Fig. 250) to be of much utility; there was so little to be found at the bottom of the centrifuge glasses (Fig. 251) that we obtained a hopelessly inadequate idea of the plant life, whereas in the stomachs of salpæ we might, perhaps, get a quite abundant flora of small forms. Fortunately, we had taken with us a big centrifuge to be worked by steam (see Fig. 91, p. 105), and in its six glasses we could centrifuge at one time as much

Quantitative investigations on board the "Michael Sars."

Centrifuge.

as 1200 c.c. of sea-water. It made 700 to 800 revolutions per minute, and after eight minutes the plants were all collected at the bottom of the glasses. Our next proceeding was to pour away the clear water, and after rinsing the deposit, to put it in a smaller glass with a tapering bottom, where it was subjected to the action of a small hand-centrifuge. In this way we collected all the contents of, say, 300 c.c. of sea-water in one drop, which we examined in a counting chamber beneath the microscope, and noted carefully each single organism. As a rule we had to centrifuge the whole 300 c.c., but, if the plankton was very abundant, 150 c.c. or even 100 c.c. might suffice. Examination with the microscope is always more difficult when the organisms in the counting chamber lie close together.

These investigations were carried out all the way from the Canaries to Newfoundland, and thence to the Irish coast banks, and resulted in our discovering that the smallest organisms which pass right through the silk nets are far more abundant than the others in the open sea, while the larger diatoms and peridineæ would appear to be so scanty that the total of all their species together only amounts to about ten per litre. Despite this fact, however, we found in the samples taken with our nets that there were at least fifty species of these larger forms at every station, so that as far as species go the flora is exceedingly rich.

Smallest organisms the most abundant in the open sea.

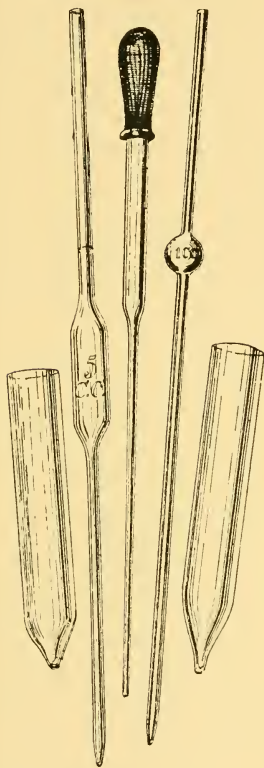


FIG. 251. — CENTRIFUGE GLASSES AND PIPETTES FOR USE WITH LOHMANN'S HAND-CENTRIFUGE.

We were also able in this way to determine the occurrence of algæ at different depths. Samples from the surface, and from 20, 50, 75, and 100 metres were taken regularly, and we also examined samples now and then from still greater depths. We found, invariably, however, that the plant life

Amount of plant life at different depths.

below 100 metres was extremely scanty. The maximum in the ocean nearly always lay at about 50 metres, which is what Lohmann also found in the case of the Mediterranean coccolithophoridæ. At the surface there was less than down in the 20 to 50 metres zone, though the plankton nearly always approached its maximum value as soon as we reached a depth of 10 to 20 metres. At 75 metres the quantity diminished to about half of that found at 50 metres, and at 100 metres it had dwindled to at most a fifth. These were the values on our southern section. On the northern crossing the quantity of plankton fell away even more rapidly as we went deeper down; at Station 92, where there was a slight admixture of coast-water near the surface, and the lighter surface layer was separated from the pure Atlantic water somewhere between 25 and 40 metres, there were upwards of 250,000 plant cells per litre in the surface layer; whereas at 50 metres the plankton was less abundant than at any of our previous stations, and only amounted to 2213 cells per litre.

These results quite bear out the most valuable investigations so far made regarding the vertical distribution of algæ in the ocean, namely Schimper's observations in the Antarctic during the "Valdivia" Expedition. He found that the entire production was practically limited to the uppermost 200 metres, that the bulk was to be found above 100 metres, and that the maximum lay between 20 and 80 metres, or to be more precise, between 40 and 60 metres. We were able to confirm this, after comparing the volume of the samples taken with nets on those few occasions when there was a sufficiently large quantity of plankton at our stations to make such volume-measurements of any real value. There was, however, a different vertical distribution everywhere along the coasts where diatoms abounded, for then the exuberant plant production was limited to the surface layer, which was mixed with fresh water from the land.

As illustrating our investigations at a station in the warmest part of the Atlantic, I give particulars of what I found at Station 64 (lat. 34° 44' N., long. 47° 52' W.) in water-samples from 50 metres (150 c.c.) and 75 metres (300 c.c.). The figures denote the number of individuals per litre.

Schimper's
observations
in the Ant-
arctic.

Number of
individual
plant-cells at
50 and 75
metres at
Station 64.

	Cells per litre.	
	50 m.	75 m.
Coccolithophoridae :—		
<i>Pontosphaera huxleyi</i> , Lohm.	300	173
<i>Syracosphaera echinata</i> , n.sp.	287	123
„ <i>spinosa</i> , Lohm.	193	33
„ <i>ampulla</i> , n.sp.	93	40
„ <i>laevis</i> , n.sp.	147	83
„ <i>blastula</i> , n.sp.	3
„ <i>pulchra</i> , Lohm.	160	100
„ <i>robusta</i> , Lohm.	80	67
<i>Calyptosphaera oblonga</i> , Lohm.	593	370
<i>Coccolithophora leptopora</i> , Murr. and Blackm.	33	7
„ <i>pelagica</i> , Wallich	73	53
„ <i>wallichii</i> , Lohm.	7	...
„ <i>lineata</i> , n.sp.	7	...
<i>Rhabdosphaera styliiger</i> , Lohm.	33	37
„ <i>claviger</i> , Murr. and Blackm.	7
<i>Discosphaera tubifer</i> , Murr. and Blackm.	107	93
<i>Scyphosphaera apsteini</i> , Lohm.	23
<i>Calciosolenia murrayi</i> , n.sp.	7	13
<i>Ophiaster formosus</i> , n.sp.	7
Undetermined coccolithophoridae ¹	887	497
Total coccolithophoridae	3007	1729
Pterospermataceae :—		
<i>Pterosperma disculus</i> , n.sp.	20
Peridineae :—		
<i>Protodinium</i>	1853	1007
<i>Amphidinium gracile</i>	33	37
<i>Oxytoxum scolopax</i>	7	3
„ <i>hjorti</i> , n.sp.	3
<i>Dinophysis</i> , sp.	7	...
<i>Exuviaella</i> , sp.	3
Other peridineae	300	350
Total peridineae	2200	1403
Diatoms :—		
<i>Nitzschia seriata</i>	3
„ sp.	7	33
<i>Rhizosolenia calcar avis</i>	14	43
<i>Thalassiothrix frauenfeldi</i>	7
Silicoflagellates :—		
<i>Dictyocha fibula</i>	43	93
Other plant-cells	447	377
Total plant-cells	5718	3708

I have previously given a list from this station of the species found in a vertical haul with the silk net. The number of

¹ Mainly young stages, which could not be determined with certainty; to a great extent they belong no doubt to *Coccolithophora leptopora*.

Plankton less abundant in the open sea than in coastal waters.

species is very considerable, yet the total quantity of individuals is surprisingly small compared with what we might find, for instance, off the coasts of Europe. In the Skagerrack one often gets plant-cells in tens of thousands or even hundreds of thousands in every litre of sea-water from the upper layer, and, what is more, they are much larger and more nutritive than the stunted forms which make up the bulk of this ocean plankton.

It cannot be denied that our investigations are as yet too incomplete to justify us in framing laws for plant production in the ocean. Still the great expeditions which have made researches in the open sea have given us a general conception of the conditions prevailing over wide stretches of water at certain seasons; on the other hand, careful investigations of the variations in the plankton throughout the year have been carried out at a number of coast stations, while our international researches have resulted in a great deal of material being collected at all seasons from the North Sea and adjoining areas. Though these investigations have not all been devoted to studying quantity, they have nevertheless enabled us to form some idea of the annual variations.

Plankton less abundant in tropical than in temperate seas.

One thing at any rate we may learn even from this incomplete material. The development of the plankton is much more irregular than it would be if merely such simple factors as warmth and light controlled production. It is not in the warmest waters that the greatest amount of organic substance is to be found. On the contrary we get larger masses of plants in temperate seas than we have ever yet come across in tropical or subtropical areas,¹ at any rate so far as the open ocean is concerned. Even when we come as far north as the coast of Norway we find that it is not in the hottest months of summer that the plankton attains its maximum, but in the early part of the spring or the end of autumn. Now it is certainly true that the quantity of vegetable matter present at any given moment is no direct measure of production. According to the law of Van 't Hoff, metabolism always takes place quicker *ceteris paribus* at a high temperature than at a low temperature, and a plant-cell in the tropics may perhaps produce more organic matter than a similar cell would do in the North Sea in the same space of time. The small tropical plants may

Van 't Hoff. Metabolism more rapid in warm water than in cold water.

¹ The "Challenger" met with diatoms in the Arafura Sea in as great abundance as in the Antarctic regions, but neritic in character (see lists of species in Summary of Results, Chall. Exp., pp. 515 and 733).

pass more rapidly through their life-cycle, and their numbers may be more drawn upon by the abundant animal life; consequently considerable additions to their apparent total may be necessary, if we wish to estimate properly the importance of plant life in the tropics, as compared with that in higher latitudes. We must remember, moreover, when dealing with observations made in coastal waters all the year round, that the different species have a natural periodicity that may be connected with unknown internal factors in their cycle of life, as well as with the influence of currents which at one time carry the surface-layers away from the coast and at another time towards it. All the same there are many irregularities which cannot be explained as being solely the result of the actual physical conditions of existence. Besides light and warmth we might perhaps be apt to think of salinity, which, in the course of its variations, influences both the density and the osmotic tension of the sea-water. Though we are aware that a low or greatly varying salinity is injurious to many pelagic organisms, there are others which thrive remarkably well and multiply exceedingly under such conditions, as for instance the diatom *Skeletonema costatum* and the peridinean *Ceratium tripos* forma *subsalsa*. Results, in fact, are often the reverse of what one might expect. The flora of brackish-water bays, which is poor in species, may develop into even greater masses than we find synchronously in the open sea, where no osmotic changes have disturbed the vital activity of the numerous species belonging to the community of oceanic algæ.

We cannot get away from the view, which was first confidently put forward by Brandt, that certain indispensable nutritive substances occur so sparsely that, according to Liebig's minimum law, they act as factors which limit production. Liebig found that the growth of plants on land depends on the amount of the requisite nutritive substances present, the determining substance being the one of which at any moment there is least in proportion to the needs of the plant. As long as a particular nutritive substance occurs "in minimum," plant production will be proportionate to the available quantities of it, even though there be a superabundance of all other essentials.

If this law is made to include all necessary conditions of life, it will be found to apply universally to all organisms both on land and in the sea, in which case that condition of existence, whether it be physical or chemical, which occurs "in minimum," will be the factor of limitation. We must remember, however, that produc-

tion at a given moment need not necessarily be proportionate to the conditions of existence prevailing. There may be after-effects of a previous set of conditions. Indeed it is possible to point to places totally destitute of vegetation, owing to former unfavourable circumstances having destroyed all germs, while new germs have not yet found their way there. Still this is the only reservation we need to make, when asserting the universality of this natural law.

The necessary nutritive substances which are most likely to occur "in minimum" in the sea are nitrogen, phosphoric acid, and, in the case of diatoms, silicic acid; all others occur even to superfluity. Brandt in his works on metabolism in the sea discusses at some length the importance of nitrogen, phosphoric acid, and silicic acid, and his assistants at Kiel have carried out a number of tests to ascertain the extent to which these substances are present in sea-water. Not only the nitrogenous compounds (organic compounds, ammonia, and nitrates), but also phosphoric acid and silicic acid, occur in extremely minute quantities, so that it is particularly difficult to get accurate values representing them. We have therefore, unfortunately, no proper conception as yet of the way in which these substances vary in different parts of the sea. According to Raben's latest investigations the total quantity of combined nitrogen (ammonia, nitrates, and nitrites) in true North Sea water varies between 0.110 mg. and 0.314 mg. per litre, of which 0.047 to 0.124 mg. is saline ammonia, the whole being reckoned as free nitrogen. Even if we assume that the quantity of nitrogen in the Atlantic is considerably less, these values are high compared with the quantity of nitrogen to be found combined in the cells of the plankton-algæ. It seems, therefore, hardly possible that the nitrogenous compounds are entirely consumed by the algæ. It is, however, quite conceivable that the variations in the total quantity of nitrogen, or in the quality of such compounds as are easiest to absorb, may hasten or retard the augmentation of the algæ. The same is the case with silicic acid, which Raben found to vary between 0.30 mg. and 1.03 mg. per litre in thirty samples from the North Sea. The quantity of phosphoric acid, according to Raben's investigations, is as a rule below 1 mg. per litre, though it slightly exceeds the quantity of nitrogen.

Brandt starts by discussing the occurrence of nitrogenous compounds in the sea. He calculates that large quantities of combined nitrogen are carried out from the land by the

rivers, as organic nitrogenous compounds, ammoniacal salts, and nitrates. The result would be a constant increase, until at last the sea became poisoned, were it not that it is continually being absorbed by living organisms, or else being restored in some form or other to the atmosphere. We now know that there is very little combined nitrogen in the sea, so that it must evidently be used up as fast as it arrives. The consumers of nitrogen are first and foremost the seaweeds growing along the coasts, and the floating algæ of the open sea, but besides them there are also bacteria, which exist in all sea-water, as shown by Fischer. Their competition with the algæ for the nitrogenous compounds is not of any great consequence, so long as they do not interfere with the circulation of nitrogen otherwise than by disintegrating organic compounds so as to form ammonia, or by binding ammonia and nitrates in their cells as albumen.

Fischer.

From the bacteria-life of the soil, however, we are acquainted with another kind of nitrogenous metamorphosis produced by bacteria. There are nitrifying species which oxidise ammonia into nitrites and nitrates, without requiring organic substance to enable them to live; there are further whole series of other species which can reduce nitrites and nitrates, and give off nitrogen in a free state. Their action drives out of the natural circulation larger or smaller quantities of this valuable nutritive substance, scarce enough already, which all plants generally utilise to the uttermost. How great the loss is, as compared with the metamorphosis in other respects, and under what conditions it takes place, are questions that require our most careful attention before considering anything else.

Nitrifying and
denitrifying
bacteria.

Baur, and others after him, succeeded in finding several kinds of these denitrifying bacteria in the sea, where they appeared to be widely distributed. It was found, too, that they produced free nitrogen with greater rapidity when the temperature was high (20° to 30° C.) than when it was low. Brandt, accordingly, put forward the hypothesis, that to the activity of these bacteria is due the fact that the abundance of plant life does not increase as we approach the tropics, but on the contrary very often decreases. This theory has now for some years been considered the only explanation of the irregular distribution of the plankton, but recent researches have shown that it is untenable.

Baur.

The denitrifying bacteria require organic substance for their existence. If they are to give off free nitrogen, they must have

nitrites, though denitrification is as little a vital necessity for them as alcoholic fermentation is for the fermentation fungi. Feeding them with sugar and ammoniacal salts will result in their multiplying to an unlimited number of generations, without exhibiting their power of denitrification. They can attack nitrates whenever met with, utilise their oxygen, and give off nitrogen, but denitrification is not of any particular importance, provided the bacteria find sufficient free oxygen in their surroundings. It is only when this fails that they attack nitrates to any great extent. Given the requisite quantity of oxygen they will enter the regular circulation, and no nitrogen worth mentioning will be produced even where denitrifying bacteria are living and multiplying.

This is the case at any rate in the soil, where denitrification is of no importance, unless nitrates are brought into contact with considerable quantities of easily disintegrated organic substance. In the sea the quantity of organic substance is generally so small that a cubic centimetre of salt-water from the open sea rarely contains more than 50 to 100 living bacteria cells, while the nitrogenous compounds occur for the most part as ammonia or inorganic compounds, and not as nitrates or nitrites. It is more than likely that nitrates are not formed to any great extent in sea-water. Nitrifying bacteria are met with occasionally in the mud along the coasts, but they have not been proved to exist in the open sea; in any case they have not the same importance there that they possess on land, where numbers of them are present in every single gram of cultivated earth. So it is probable that the small quantities of nitrates and nitrites in the sea-water are brought either from the land, or in a minor degree from the atmosphere as the result of electrical discharges. Most of the combined nitrogen of the sea occurs as organic compounds or as saline ammonia, neither of which can be reduced by denitrification. Supposing then that denitrification does play any noticeable part, it will only be in more or less enclosed bays and fjords, where there is a comparatively large amount of organic substance, a plentiful supply of nitrates from land, and so little circulation that there may be a lack of oxygen. In the open sea it is negligible.

Nathansohn.

We must look for other conditions to explain the apparent irregularities in the distribution of the plankton. Nathansohn was the first to notice that vertical currents are bound to exercise considerable influence. If it be true that one or

several of the necessary nutritive substances may be present in such small quantities as to act as factors that limit the development of the vegetation, then the more or less considerable exchange taking place between the illumined surface-layers and the vast water-masses of the deep is certain to produce a great effect. All the forms of animal life inhabiting the sea below 200 metres live solely upon organic substances which are due to plants in the surface layers; that is to say, they either feed directly upon the plant-cells which sink downwards, or upon the inanimate remains or excrements of the animals living up above, or else upon other animals which, in their younger stages, have inhabited the surface-layers and fed on the plants they found there. A large proportion of the produce of the surface-layers must thus be continually descending into the deep sea, and these nutritive substances are therefore withdrawn from their regular circulation in the photic zone. Down in deep water, no doubt, the destructive metabolism of animals will set free these nutritive substances, so that eventually carbonic acid and ammonia will be produced; still these gases can only regain the photic zone by very slow degrees if diffusion is their sole means of conveyance. If, however, whole masses of water are brought up from the deep sea to the surface, the nutritive substances contained in them will once more enter into circulation, and cause an abundant plant life to develop. Nathansohn has pointed out that marine areas where such ascending currents occur, and where the surface-layers are replaced by water from the deeper layers, are well known to be extremely prolific, not merely in plankton, but also in larger organisms. In anticyclonic systems like that of the Sargasso Sea, on the other hand, where, conformably to the laws of ocean-currents, the water-masses cannot ascend from the deep sea, but where the surface-layers sink downwards, the plankton is much less plentiful than in any other similar area where investigations have been made. Our researches in the Atlantic during the summer of 1910 have done a great deal to settle this question. I shall first of all, however, refer to a series of investigations which bring quite another light to bear upon the question, and show what difficulties we have to face.

Ascending
currents.

In 1907 Professor Nathansohn and I commenced to study the Christiania fjord, and subsequently I continued these investigations alone. My previous observations had taught me that the pelagic algæ in this fjord attain their maximum between

Pelagic algae
of Christiania
fjord.

March and May, and that they occur in rather smaller quantities from June to August. From September to October there is again a maximum, but from then onwards they decrease rapidly and reach their minimum between December and January. It is not surprising that the plankton is scanty during the dark period of the year, but the unmistakable secondary minimum in the summer months must be due to some special cause, which it should be possible to discover by studying carefully the whole year round the variations in quantity and the fluctuations in the outward conditions of existence. It struck me that the factors at work might be analogous to those which cause the differences in production met with in different regions of the great oceans.

Method of
estimating the
quantity of
plankton.

To ascertain the quantity of plankton present we employed the method introduced by Sedgwick and Rafter for drinking-water tests in North America, which has been described by Whipple. A litre of water is filtered through a fine grade of sand, and the algæ that collect on its surface are rinsed off. To the rinsed-off water containing the algæ, filtered water is added until the whole comes to exactly 10 c.c. We then transfer 1 c.c. of this with a pipette to a counting-chamber 5 cm. long, 2 cm. broad, and 1 mm. high, which exactly holds it. For examination we use a microscope which magnifies to 40 or 50 times the natural size. A thorough knowledge of the species is requisite to enable us to enumerate them correctly. When counting species represented by many individuals we require a micrometer, with a larger or smaller number of millimetre squares marked off by lines, placed in the eyepiece of the microscope.

We soon found that our task was more difficult than we had at first imagined. The quantity of plankton fluctuated greatly in the course of short periods of time, yet the variations could not be ascribed directly to conditions of existence, since these remained fairly constant. The temperature in the surface-layers rose steadily during March to May from 1.5° C. to 6.3° C., the quantity of chlorine was about 16 per thousand, and according to Nathansohn the quantity of free ammonia in filtered samples of sea-water was between 0.0175 mg. and 0.031 mg. per litre, and of ammonia in organic combined form between 0.105 mg. and 0.217 mg. per litre. Of nitrates and nitrites he only found infinitesimal quantities up to 0.009 mg., set down as ammonia. *Chaetoceras constrictum*, one of the commonest diatoms in the spring plankton of the Christiania fjord, furnished the following

figures, denoting the number of living cells in every litre of surface-water near Dröbak :—

1907.	27/III.	30/III.	2/IV.	9/IV.	15/IV.	20/IV.	4/V.	6/V.	1/VI.	19/VI.
<i>Chaetoceras constrictum</i>	20,850	45,850	12,750	59,730	760	44,425	192,500	95,480	1280	0

A quite satisfactory explanation presented itself, however, for the variations turned out to be closely connected with the direction of the winds and currents. The outflowing current in the surface-layers might reduce the quantity of plankton to a mere fraction of the normal amount in the course of a day or two, while the inflowing current might perhaps double the quantity in a few hours. The current exerts so great an influence because the abundant plant life is limited to a thin surface-layer which is sharply differentiated both in salinity and temperature from the water-masses below. On 28th March 1907, for instance, the temperature from the surface down to 20 metres was 2.6° – 3.6° C., and the quantity of chlorine worked out at 16.74–17.62 per thousand; from 40 metres down to the bottom at 80 metres the temperature was 6.2° C., and the quantity of chlorine was 18.73 per thousand. The outflowing current carries the surface-layers with their algæ out of the fjord, and the infertile deep water may be sucked up to perhaps 5 metres below the surface. The inflowing current, on the other hand, heaps up the fertile surface-waters. We found, on examining the plankton at different depths, that the bulk of the plants was limited to a very thin surface layer, say 5 metres in depth, after the current had set outwards, whereas subsequent to the inflow of the current they were as abundant down to 30 or 35 metres as at the surface.

At a place like this it was difficult to trace any regular connection between the local conditions of existence and the development of plankton-algæ, in view of the fact that currents caused variations of even greater extent than those actually due to conditions of existence. We had therefore to conduct our investigations on other lines. Supposing it were possible to determine the rate of growth of the algæ we should get a better measure of production, and probably also of the influence due to vital conditions, than variations in the total amount could give us. The number of individuals at any given moment depends not merely upon the rate at which production has

taken place, but also upon how many have perished or been carried away; and the causes bringing about diminution, which we may perhaps term factors of loss, may vary without being in any way directly connected with the conditions of existence of the plankton. There is one genus, at any rate, whose rate of augmentation can be approximately determined. The species of *Ceratium* only divide their cells at night, so that if we make our investigations early in the morning we can tell which cells have been divided during the night and which remain entire. In a sample of surface-water on 10th September 1907 we found 300 whole cells and 161 half cells of *Ceratium tripos*, the latter consisting of 79 anterior parts and 82 posterior parts. The number of cells, then, had in twenty-four hours increased from $300 + \frac{161}{2} = 380.5$ on 9th September to $300 + 161 = 461$ on 10th September. The addition is accordingly $\frac{161}{2} = 80.5$ individuals, and the percentage of the total amount on 9th September works out at $\frac{100 \times 80.5}{380.5} = 21.2$ per cent.

This was the plan we adopted for calculating the augmentation of the species of *Ceratium* at Dröbak during the whole of their vegetation period in 1907, and we also recorded the average number per litre at different depths during the whole year.¹ The following tables show our chief results:—

¹ Similar investigations in the case of *Ceratium tripos* were carefully carried out during 1908–1909 by Apstein in the Baltic. The values he obtained for percentages of augmentation on the whole accord as nearly with mine as might be expected.

NUMBER OF CELLS PER LITRE OF SURFACE-WATER AT DRÖBAK.

Date, 1907-8.	15/iv.	4/v.	1/vi.	19/vi.	6/vii.	20/vii.	1/viii.	15/viii.	30/viii.	10/ix.	23/ix.	7/x.	28/x.	3/xi.	17/xi.	1/xii.	22/xii.	3/i.	9/ii.
<i>Ceratium tripos</i>	60	22	20	840	333	172	343	573	337	1098	837	1433	13860	2149	899	2345	379	30	19
<i>Ceratium fuscus</i>	...	66	180	...	111	234	305	246	581	1610	1553	8747	10230	506	83	30	17	6	...
<i>Ceratium fuscum</i>	...	22	16	55	400	72	58	350	443	1750	4460	536	24	12	21	18	...
<i>Ceratium longipes</i>	260	330	260	60	2	...	10	12	408	3000	440	661	1406	125	21	...

PERCENTAGE OF AUGMENTATION AT THE SAME PLACE.

Date, 1907.	6/vii.	19/vii.	25/vii.	5/viii.	22/viii.	31/viii.	10/ix.	23/ix.	6/x.	13/x.	20/x.	3/xi.	17/xi.
<i>Ceratium tripos</i>	6.5	13	8.3	12.9	23.8	28.8	21.2	13.7	8.7	5.8	2.6	2.1	0.3
<i>Ceratium fuscus</i>	10	27	38.6	15.2	9.6	10.7	3.1	1.6	2.4	...
<i>Ceratium fuscum</i>	30.7	22.1	37.4	21.8	14.2	6.1	5.8
Temperature	14.0	16.0	15.5	15.8	15.1	13.9	13.0	12.4	11.5	11.6	11.3	7.95	5.7

The figures in the tables clearly indicate that, though the rate of increase is highest in August, the number of cells of *Ceratium* in the fjord makes no great advance before October. Throughout the whole summer the number continues at about the same level, in spite of a comparatively rapid production. This affords a further indication that in the Christiania fjord variations in the current and other factors of loss exert a greater influence than the variations in the conditions of existence which affect rate of increase.

The fact that we find in the Christiania fjord, and assuredly also in many other places along the coasts of North Europe, that the plankton is less abundant in the summer months than in spring, does not necessarily imply any unfavourable change in the conditions of existence due to summer. It may be caused by the melting of the snow in spring, and by the river water all through the summer driving the surface-water and its plant-life away from the coast, so that the production near land barely replaces the loss. In the autumn it would seem as if the prevalent sea-winds heap the surface-layers together along the coast, and thereby accumulate large quantities of plankton.

What effect these movements of the surface-water have upon the occurrence of the plankton we are as yet unable to say definitely, but they must be taken into consideration. We were obliged, therefore, to abandon our original intention, which was to ascertain the importance of such conditions of existence as dissolved nutritive substances, and particularly nitrogenous compounds.

I made a series of cultivation experiments, however, under conditions of existence resembling the natural conditions as nearly as possible. Stopped glass bottles holding two and a half litres were kept just floating at the surface, by being filled with about two litres of sea-water; the amount of plankton present was carefully checked in advance, and then one bottle was left in its original state, while in the other two small quantities of chloride of ammonium or calcium nitrate were placed. After an interval of 3 or 4 days the plankton in all the bottles was once more examined, and it was generally found that most of the species had augmented best when nitrogenous nutriment had been added. The addition had naturally to be made with the utmost care, since anything over 0.5 mg. per litre generally had a poisonous effect. The following table shows the result of one of these experiments :—

NUMBER OF CELLS PER LITRE.

	Before experiment on 21/VIII.	Three Days Later (24/VIII).	
		In Original State.	With addition of 0.5 mg. NH ₄ Cl per litre.
<i>Ceratium tripos</i> .	583	640	696
„ <i>fuscus</i> .	543	649	833
„ <i>furca</i> .	155	149	196
<i>Prorocentrum micans</i>	1052	548	1464
<i>Dinophysis acuminata</i>	219	107	226
„ <i>rotundata</i>	33	30	42
<i>Rhizosolenia alata</i> .	157	232	345
<i>Cerataulina bergonii</i>	2840	3381	7214

Experiments with pure cultures of different plankton-diatoms, made by Allen and Nelson at Plymouth, show that they do not thrive without a regular supply of nitrogenous compounds. The plan of working which they adopted may also be employed with advantage when we wish to ascertain what concentration of dissolved nitrogenous compounds induces the plankton-algæ to augment most rapidly. This is the first thing to find out if we desire to know whether a want of dissolved nutritive substances is the limiting factor of production. It is quite possible that augmentation diminishes from lack of nitrogen long before the total amount of this essential has been fully consumed; yet augmentation must not fall below a certain minimum if the species is to hold its own, because of the larger or smaller number of individuals that are constantly perishing. Questions like these can only be settled by experiment, so that the cultivation method of Allen and Nelson is bound to be of great assistance to us eventually. But in the meantime our comparative investigations over large areas of the sea are also of considerable value.

Allen and
Nelson.

I have already stated that plant life in the Christiania fjord was limited to a very thin surface-layer, which, owing to its lesser density, was differentiated from the deeper infertile water-masses, and this was practically the case along all the coasts where plankton-algæ were plentiful. Out in the open sea, on the other hand, where there are not such marked differences in salinity, temperature, and density be-

Plankton
extends
deeper, but
is less
abundant, in
the open sea
than in
coastal areas.

tween the surface water and the deep water, the pelagic algæ extended deeper; at 50 metres, for instance, the quantity was still near the maximum, and even as deep as 100 metres or more the number was considerable. This, at any rate, was what we found in the case of the diatoms that abounded at our first stations off the Irish coast-banks and in the Bay of Biscay, and this too was what Schimper discovered in the Antarctic. It is also a regular rule that plankton is far more plentiful along the coasts than in the open sea, and, judging from investigations hitherto made, the proportion between what is produced in a typical coastal area and what is developed in typical oceanic water-masses would be more accurately expressed by 100 : 1 than by 2 : 1. For this the best explanation which I can give is that the open sea generally suffers from a want of one or more nutritive substances required by the plants, for though these are brought down to the sea in comparatively large quantities by the rivers, they are almost entirely consumed by the plant life of the coastal areas.

This is why the abundant plant life of the coastal seas is confined to the surface-layers, since the water-masses lying below remain separated, and consequently cut off from the plentiful supply of nutritive substances which regulate the augmentation of plants. But out in the open sea there is another important source of nutriment to be taken into account. Nathansohn has pointed out that pelagic animals are constantly taking nutritive matter down into deep water, and that for the time being it is accordingly withdrawn from the plants, even though the metabolism of the animals and the action of bacteria liberate it once more in inorganic form. These nutritive substances may rise to the surface-layers again by diffusion, but the process will require a long time. They may also accompany the ascending water-masses where off-shore winds bring about up-welling, in cyclonic current systems, and where the surface-layers, becoming chilled, sink and make room for warmer layers from below. Wherever vertical circulation takes place, and it is assisted in its action by storms and waves, the temperature and salinity will be extremely uniform from the surface down to a depth where the water-masses have such a high salinity that their greater density sets a limit to circulation. Conversely uniformity in temperature and salinity may be taken as a sign that vertical circulation has just taken place. This was the condition of affairs at our stations to the south-west of Ireland (see Fig. 252), where we

found abundance of plankton in April 1910, algæ being present in large quantities as deep down as they have been known to occur, that is to say as far down as sufficient light penetrates. We can appreciate the difference between these conditions and the conditions in coastal areas like the Christiania fjord, if we remember that the nutritive substances in the first case may rise up from the deep water, while in the second they are derived from the surface through the admixture of fresh water.

Vertical circulation is regulated by differences in temperature at the surface, due to summer and winter, which are sufficient to increase the density of the upper layers till it equals the density lower down, and if circulation is to have any effect in the open sea, the surface-layers must be able to sink to a depth of at least 200 to 300 metres. The greater the difference in temperature between summer and winter, the more effective will vertical circulation generally be.

Assuming, then, that our view is correct, namely that plant production in the sea is mainly regulated by the amount of dissolved nutritive substances, we must expect to find plankton produced in abundance in coastal areas to which large rivers convey nourishment from the land, and in oceanic areas where vertical circulation takes place on a large scale, or where ascending currents bring up the deeper water-masses. Where vertical circulation is the controlling influence, the greatest profusion will be at seasons when the temperature of the surface reaches its minimum; that is to say, generally in winter, or in higher latitudes in the early months of spring. It would be possible to test the truth of this theory if we could

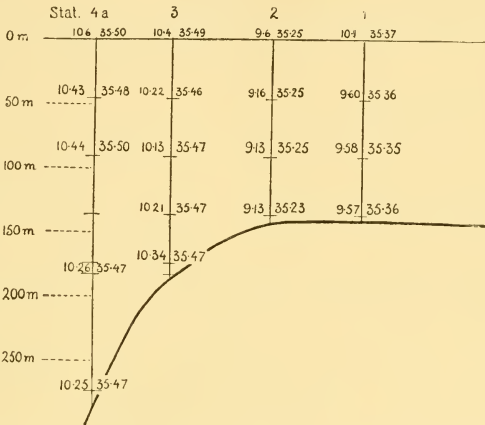


FIG. 252.—HYDROGRAPHICAL SECTION OFF THE IRISH COAST (April 1910).

Temperature and salinity nearly uniform from the surface down to a depth of 250 metres.

carry out systematic quantitative plankton investigations all through the winter, in combination with hydrographical researches, in parts of the Atlantic like the sea round the Azores, where the plankton is known to be scanty during the summer, but where during the course of winter vertical circulation might be expected to create different conditions of existence.

Whipple.

In this connection it should be mentioned that the influence of vertical circulation upon the production of plankton-algæ in fresh water has long been known to biologists. It has been pointed out by Whipple, who showed that the maxima of diatoms in particular coincide with the seasons when vertical circulation takes place, namely autumn and spring. And in the sea, too, it seems that diatoms, with their power of rapid augmentation, are the first to respond to improved conditions of nourishment.

Which of the essential nutritive substances are the chief limiting factors in the sea, it is impossible to say as yet. Probably, however, nitrogen is the most important, and next to it, perhaps, more especially in the case of diatoms, we may put silicic acid. Brandt and Nathansohn have both discussed the occurrence of these substances, but we need further and more conclusive information than what we now possess. Nathansohn has likewise considered the possibility of carbonic acid occurring "in minimum." This seems paradoxical, of course, since there are comparatively large quantities of it in sea-water. Still the greater part is combined in the form of carbonates, and only a very small portion is set free by dissociation at any given moment, so as to become available for the plants. How much there is in this form will depend on the alkalinity of the sea-water and on the temperature. When the free carbonic acid is used up by the plants, fresh quantities will gradually be absorbed from the atmosphere, though this may take place so slowly that there need not necessarily be any equilibrium between the carbonic acid tension in the atmosphere and at the surface of the sea. It is accordingly quite conceivable that the shortage may for a time be considerable enough to stop the algæ from assimilating carbonic acid. When the temperature is high the quantity of free carbonic acid in the sea-water will *ceteris paribus* be less than when it is low, and this also may help to explain the relatively poor production in warm seas. Variations in the tension of carbonic acid, however, have not as yet been sufficiently studied.

The organic substances built up by pelagic algæ unquestion-

ably form the chief basis, and in the open sea practically the sole basis, of nutriment for all the pelagic animal life, as well as, through their pelagic forms, for the fauna of the sea-bottom. It is not, however, quite so certain that all the different algæ are equally useful as food to the animals which live on plant stuffs. Brandt's chemical studies of plankton organisms have distinctly shown that nutritive value does not necessarily correspond to volume. Diatoms, with their long silicated setæ, or with big bladder-shaped cells that merely enclose a thin layer of protoplasm along the inner side of the wall, have little nutritive value compared to the majority of the peridineæ, in which most of the cell-chambers are full of protoplasm. The dry substance of diatoms, according to Brandt's analyses of plankton samples, chiefly *Chaetoceras*, contains 10 to 11.5 per cent albumen, 2.5 per cent fatty matter, 21.5 per cent carbohydrates, and as much as 64.5 to 66 per cent ash, 50 to 58.5 per cent of this last being silicic acid. Another sample, largely consisting of *Ceratium tripos*, had a totally different composition, the dry substance containing 13 per cent albumen, 1.3 to 1.5 per cent fatty matter, 80.5 to 80.7 per cent carbohydrates (half of which was chitin), and not more than 5 per cent ash.

Chemical
composition
of plankton
samples.

We are still without systematic studies of the nutriment of plankton animals, and consequently do not know for certain whether some families of plants are preferred to others. The contents of the intestinal canals of salpæ make it evident that these animals at any rate collect all the different small organisms to be found in their neighbourhood. In warmer waters the greater part of their stomach-contents consists of coccolithophoridæ and other tiny forms, but we find besides representatives of all the plankton-algæ. Small peridineæ, for instance, like *Gonyaulax polygramma*, are seldom wanting. In fact, Stein, the well-known specialist on protozoa, who had no plankton-catches to aid him in his researches, got the best part of his material from the stomachs of salpæ, and was thus able to write his valuable initiatory monograph on peridineæ. And this, too, was the plan adopted at first for studying diatoms, so that our knowledge of pelagic genera like *Asteromphalus* and *Asterolampra* is largely due to the examination of the stomachs of salpæ. During the cruise I invariably examined the stomach-contents of salpæ, and obtained thereby plenty of small forms, coccolithophoridæ especially, for comparison with the material in the centrifuge samples. As we approached the coast of Europe, however, the contents took on another character, for at Station

Food of *Salpa*.

97 most of the forms were diatoms, and to a great extent consisted of *Rhizosolenia alata*. Generally speaking we discovered that salpæ do not trouble to make any selection. Lohmann's studies of *Appendicularia* have shown us that these animals get their nutriment by means of a filter apparatus, which allows only the minutest organisms, coccolithophoridæ in particular, and small peridineæ, to enter the digestive canal.

Food of
*Appendicu-
laria*.

Food of
Copepods.

The chief consumers of plants in the sea are undoubtedly copepods. Their conditions of nutriment, however, have so far been principally studied by means of their excrements, which sink down in the shape of small elongated lumps, and are often brought up in numbers by the silk nets. Still, in these excrementa all the softer components have been digested, and the shells that can be identified do not necessarily always belong to species which are an indispensable part of their nutriment. Undoubtedly the calcareous shields of coccolithophoridæ occur too frequently for their presence to be ascribed to chance, indicating, moreover, that the digestive juices of copepods cannot have an acid reaction. In addition we very often meet with more or less bent and distorted coverings of peridineæ, and in northern waters the excrements contain stiffer forms like the little *Dinophysis granulata* in a practically unchanged condition. In localities where diatoms predominate, the excrements consist largely of bent and broken bits of species like *Rhizosolenia semispina* and *R. alata*. Even if Hensen's view be right that diatoms supply far less nutriment comparatively than the other classes of plants in the plankton, it is at any rate quite certain that the animals do feed on them, and especially when they are plentiful. In the Norwegian Sea I have several times observed that where diatoms abounded there might perhaps be only a few copepods and other plankton animals; still the copepods were there, and in large numbers too, just below the diatom zone, and their excrements consisted to a great extent of the silicious coverings of diatoms.

Proportion of
plants and
animals in
the plankton.

Hensen noticed that the plants in the sea are often so scanty that it is hard to understand how all the animals get enough nourishment, and this is even more difficult to comprehend when we consider that the plants have directly or indirectly to support every single animal from the surface right down to the bottom. In many cases, perhaps, the plants may be more abundant than a cursory examination would seem to indicate; and the most diminutive forms, which are still practically unknown to us, undoubtedly exist in sufficiently

large numbers to play a momentous part in the general economy. Still careful study distinctly reveals the fact that the plants of the sea are in striking disproportion to the animals. The most reliable results so far obtained are those due to Lohmann's researches in Kiel Bay. He studied the quantities of all the plankton organisms for a whole year with great thoroughness, and calculated the volume of the various groups in the plankton of the different water-masses at all seasons. To us his most interesting discovery is that the plants on an average made up 56 per cent and the animals 44 per cent of the total plankton. In the winter months the plants were easily outnumbered by the animals, and from December to February they formed scarcely a third of the total plankton. In the summer, on the other hand, they predominated, and made up sometimes even as much as three-quarters of the whole. Plants which are reproduced by division must necessarily decrease rapidly whenever vigorous augmentation ceases, if animals are constantly consuming numbers of them.

The life-cycle of animals, with its growth-period in youth and propagation in maturity, is more complicated than that of plants, and gives them a better chance of withstanding unfavourable conditions of existence. A lower temperature necessarily reduces their intensity of breathing, and thus diminishes their consumption of nourishment, and it may be also that they can go without feeding for a comparatively long time, during which they live upon reserve matter that they have accumulated at more favourable seasons. Damas made some interesting studies of the life-cycle of the larger copepods, and found that propagation may require a higher temperature than what is necessary for conserving vital energy, and that therefore these forms can delay their propagation until the conditions of existence become more favourable, so that the young animals may have the rich nutriment required for their growth. *Calanus finmarchicus*, the commonest large copepod of the Norwegian Sea, abounds wherever the temperature is over 2° C., in both its half-grown and full-grown stages, but propagation does not begin till the temperature rises to 4° C., either owing to warmer water-masses arriving from the south, or to heating at the surface from the atmosphere.

Life-cycle of animals.

Lohmann has endeavoured to calculate the relation between the augmentation of the algæ and their consumption by animals throughout the year in Kiel Bay. He assumes that there is a daily accession of 30 per cent to the volume of the algæ, and

Relation between production and consumption of algæ.

that this can be consumed by the animals without harm to the plant aggregate. He further assumes that copepods and other multicellular animals require per day a quantity of nutriment equal to a tenth of their own volume, whereas protozoa need half their own volume. In view of what I have previously stated regarding the variations in the rate of production of *Ceratium*, I have no hesitation in declaring that the augmentation of the algæ varies within wide limits, and the same is undoubtedly also the case with the nutriment-requirements of the animals. Still I am quite ready to concede that Lohmann's assumptions may apply to the average conditions. The following table compiled by him, and showing values in cubic millimetres of plankton per 100 litres of sea-water, will doubtless be of interest:—

	Daily Augmentation of Producers available for Nutriment.	Daily Nutriment-requirement of Animals.	Surplus or Deficiency.
August	35	6	+ 29
September	27	8	+ 19
October	14	5.5	+ 8.5
November	9	4.5	+ 4.5
December	3.5	2.5	+ 1.0
January	3	1.8	+ 1.2
February	1	1.8	- 0.8
March	3	2.4	+ 0.6
April	13	2.0	+ 11
May	14	5.5	+ 8.5
June	20	4.0	+ 16
July	17	4.5	+ 12.5
August	16	4.3	+ 11.7

According to this table the surplus plant substance is not large, and in February there was actually a deficiency. It is possible, too, that Lohmann's assumptions are on the optimistic side, and that he has put the production-capacity of the plants too high, and the nutriment requirements of the animals too low.

Pütter, after studying the quantities of oxygen consumed by different marine animals, both benthonic and pelagic, considers that the augmentation of the plant aggregate by no means suffices as nutriment for the animals. If his view is correct, there must, of course, be other sources of nutriment, both to replace the loss of organic substance which the animals incur by

breathing, and also to supply building material for their growth and propagation. Pütter has endeavoured to find out whether organic matter dissolved in the sea-water does not provide this. He investigated its amount, and got surprisingly high values. Improved methods have enabled Raben to check his experiments; in water from Kiel there were 10.9 to 13.9 milligrams, or on an average 12.25 milligrams, of organic combined carbon per litre of sea-water, and at a station in the Baltic 3 milligrams. These are really high values, if we compare them with the quantities of organic substance we are able to point to in the form of living organisms. Lohmann's studies show that the total amount of the organic combined carbon in the plankton at Laboe in Kiel Bay varied during the year between 12.7 mg. and 189.8 mg. per 1000 litres of sea-water. According to Raben's investigations at a place close by, the mean value of organic combined carbon in dissolved form is 12,250 mg. per 1000 litres, or in other words about sixty times as much.

Too little is known, unfortunately, about the occurrence of organic matter, and there are many difficulties to be overcome before we can look for conclusive results. Perhaps the most discouraging thing is that even the best filters allow a good many organisms to pass through them. The water-samples to be examined ought possibly to be freed from all suspended insoluble matter by means of the centrifuge, but even this method will not always give entirely satisfactory results, since some of the algæ (cyanophyceæ, *Halosphaera*) are lighter than sea-water, while the nimbler animals will swim up from the bottom before one can separate the clear water from the deposit. Pütter's hypothesis, however, certainly deserves to be further tested. If it be really true that in the salt-water of the open sea there is organic substance in sufficient quantities to be compared with what is combined in plants and animals, then this substance must be due to the production of plants. We will accordingly be forced to conclude that the pelagic algæ distribute to their surroundings through their surface comparatively large quantities of organic substance, and that their production is thus in actual fact much more considerable than we are led to believe, when we merely measure what they store up in their cells during growth and augmentation. Even if it seems strange biologically that they should evince such want of economy in regard to valuable nutritive matter, it would be unwise to reject the hypothesis, and the best plan is to await the results of continued investigations. Some

biologists favour the theory and others oppose it; some of them have published the results of special studies, particularly of the nutrition-processes of animals, all of which have been of service to the cause of science, though they have not succeeded in deciding this question.

Lohmann and C. G. J. Petersen have maintained that organic detritus may be of intrinsic importance for the nutriment of animals, as well as plants, and they have demonstrated that organic detritus from the land is present in fairly large quantities in waters like the Baltic or off the coasts of Denmark. We have reason, therefore, to expect extremely interesting results from the work of the Danish biologists on organic detritus in the water and in the deposits at the bottom of the sea. But out in the open sea this detritus is only met with in inconsiderable quantities, as our centrifuge-samples showed us on board the "Michael Sars." I do not, of course, include inanimate organic substances, such as excrements or the empty chitin-coverings of copepods, which form a part of the circulation of nutritive substances through the pelagic organisms. Organic fragments, not actually derived from pelagic organisms, either do not occur at all in the open sea, or, if they do, are not worth taking into consideration.

H. H. G.