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MARINE PLANKTON ECOLOGY

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PREFACE

The word plankton (from Greek πλανκτος = drifting) was introduced by Hensen in 1887 to distinguish all the organisms passively floating in the water. As a result of much progress in oceanography, the study of the plankton has been considerably developed. Systematics has been followed by ecological research; the available data are numerous and important but far from final. Nevertheless, there is a need for them to be collected together for both the plant and animal kingdoms, and their relations to the physical and chemical factors considered in order to allow a logical interpretation of the facts. This work attempts to fulfill this aim and is the result of lectures given to students specializing in biological oceanography. It pre-supposes a general knowledge of marine organisms. It tries to tabulate our present ecological data, and to describe mechanisms and relations rather than to give exhaustive descriptions of particular situations. It is, therefore, less complete as compilation of the phenomena described, and more an attempt to understand planktonic ecology, relying on the most important work. Its aim is to assist the reader to be able to study the ever more numerous specialized investigations, which explore the different aspects of the planktonic ecology and to help him to place each of these in more perspective.

海洋浮游生物生态学

本书首先介绍海洋浮游生物总的概况，随后论述海洋浮游动物、浮游植物的特征、与环境因子之间的相互关系、定量分析方法及海洋浮游生物在整个海洋生态系中的地位等。最后还介绍了海洋浮游动物和浮游植物的主要门类的分类位置，以及研究海洋浮游生物的各种计算公式、常遇到的等值及其相应值等。内容较为全面。另外书中还列举了一些海区的浮游生物生态学研究的情况和研究结果。除可供大专院校生物系、水产系、海洋系师生参阅外，对海洋及水产方面的科研工作者也有参考价值。

全书共14章，目次：①浮游植物：一般特征及分类系统概述，影响光合作用的因子，③—④氮和磷的循环，⑤矽、微量元素和生长因子，⑥浮游植物的定量研究，⑦初级生产力，⑧—⑪浮游动物的门类系统组成、定量研究及分布、垂直分布及昼夜移动、营养、新陈代谢及能量储存，⑫浮游生物的次级生产力，⑬浮游生物在海洋生态系中所占的地位，⑭附录。

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INTRODUCTION

0-1—DEFINITION AND DIVISIONS OF THE PLANKTON

The plankton is defined as the whole of those pelagic organisms which float and drift under the action of water movement. It differs from the nekton, also pelagic, in the absence of self-motility, and stands in contrast to the benthos which consists of the bottom-living organisms or those living near the bottom. As in any classification, such distinctions, between plankton on the one hand and nekton and the benthos on the other, are not always so clearly marked. We shall see later that some organisms, considered as planktonic are able to make rapid vertical migrations which are not dependent on water movement. Indeed, they are very close to the animals which form the micronekton i.e., the small-sized nekton. Other organisms which live near the bottom, or on the bottom itself, have a pelagic phase in their life cycle, so that here distinction between the planktonic and the benthic animals is blurred. Even so, most of the planktonic organisms show relatively little movement in the environment and are usually collected with plankton nets; these consist of large cones of silk or nylon gauze filtering the organisms through their meshes, retaining organisms larger than the pores-size, and concentrating them at the end of the cone in a collector. Exceptions from this method are the collection of elements smaller than the finest gauze by special methods and, on the other hand, the collection of larger organisms by hand on the surface, by diving or by using a pelagic trawl.

The above definition of plankton is very general and includes a wide spectrum of animals. For detailed studies we must use more limited categories which may be defined according to various criteria. The first criterion is that of size. Classical terminology considers those planktonic organisms whose size is greater than several millimeters as macroplankton. The microplankton includes forms larger than 50 μm which is the mesh size of a fine plankton net; and the nanoplankton consists of planktonic organisms passing such nets. Some authors have tried to give more precise definitions; Dussart (1965, 1966), for example, suggested the following classification for fresh water plankton.

Ultramicroplankton: $<2\ \mu m$; nanoplankton: 2–20 μm.
Microplankton: 20–200 μm; macroplankton: 200–2000 μm.
Megaplankton: $<2000\ \mu m = <2$ mm.

There is, however, still no general agreement on the categories to be established by size: a collective effort to standardize the method of collection brought together an international team of planktologists, (Anonymous, 1968) who, on an essentially pragmentic basis, distinguished the following categories of the zooplankton;

Microzooplankton: <200 μm (grouping the nanoplankton and the microplankton).

Small mesozooplankton: mean size >200 μm but < 10 mm and collected on a gauze with 200 μm mesh net.

Large mesozooplankton: organisms collected by 1 mm mesh net.

Macrozooplankton: a range of 2–10 cm and collected as the nekton.

This terminology is, itself, still not precise and it is better to define as closely as possible, the size of the meshes of the nets by which the plankton is collected. We shall indicate these dimensions in parentheses and with an oblique line, thus: (/505 μm) corresponds to plankton collected with a net with mesh width of 505 μm, and (/8-12 μm) to plankton collected by a net which has a pore size ranging between 8 and 12 μm. Later we shall discuss the relation between the mesh size of the gauze and the dimensions of the organisms collected by it (Chapter 9-3). We may draw attention to the works of Sheldon and Sutcliffe (1969) and of Sheldon (1972), concerning the retaining capacity of filters.

The vertical distribution forms another basis for the separation of different-groups. Epiplankton is that plankton living in the epipelagic zone (photic zone) including, in shallow water, animals found at a depth of 20–120 m depending on the region and the conditions; mesoplankton (different from the mesoplankton defined by its size) is that plankton living in the mesopelagic zone, i.e., 100 to 300 m depth, infraplankton that in the infrapelagic zone, 500–600 m, and bathyplankton that in the bathypelagic zone deeper than 600 m.

The shallow water plankton well studied by Zaitsev has a distinctive classification (David, 1967). The pleuston consists of those animals living on the surface of the water, partly in air and partly in water and drifted mainly by the wind (*Velella Physalia, Janthina*), while the neuston consists of the remainder of the shallow fauna and includes the epineuston living above the interface and the hyponeuston living below the interface.

On the basis of its nutrition we may divide the plankton into the plant plankton, or phytoplankton, capable of synthesizing some of its own material by photosynthesis, and the animal plankton or zooplankton feeding on existing material.

Another important distinction is based on biological criteria and divides the plankton into holoplankton and meroplankton. The holoplankton consists of organisms which are planktonic throughout all their life cycle. Most of the Chaetognatha are holoplanktonic since the eggs, larvae, juveniles, and adults are pelagic. *Salpa* has an alternation of generation and since both the sexual and the asexual generations are planktonic *Salpa* is, therefore, included within the holoplankton. On the contrary, most of the hydromedusae are meroplanktonic since they are a part of the life cycle of the Hydrozoa, the larvae of which after hatching from the eggs settle on the sea bottom (or other substrata) and give rise to a benthic polyps which by budding give the medusae. An important fraction of the meroplankton is larval, many of them belonging to benthic or nektonic organisms and are only a short stage in the life cycle as for example the pleuteus larvae of sea urchins and the eggs and larvae of most of the bony fish.

Finally, we must distinguish between the plankton and other floating particles, termed seston, which is made up of the living particles–the plankton–and the non-living particles, the tripton, which consists of dead organisms, organic detritus, and particulate minerals (Reid, 1961).

0-2.—GENERAL CHARACTERISTICS OF THE PLANKTON

Despite the extreme diversity of the plankton it is possible to find some general characteristics which gives it its particular characters. These are essentially its colour and the dimensions. Planktonic animals have a tendency to be transparent and are little coloured, pigmentation being restricted to some organs. This is particularly clear in the hydromedusae, the siphonophora, and *Salpa*. Two exceptions should be mentioned; surface planktonic animals often have a deep blue colour (*Velella*) while those living in deep water are often red or brown.

In general planktonic organisms are rather small, although there are some exceptions such as some medusae which reach a diameter of 1 m, or *Pyrosoma* which reaches a length of several meters. Yet the majority of the organisms have dimensions of the order of centimeters or millimeters, in the case of planktonic animals and 100 or 10 μm in the case of plant plankton.

0-3.—ADAPTATION TO PELAGIC LIFE

The planktonic organisms are necessarily adapted to pelagic life and have to remain in the water and not sink to the bottom; in other words, their sinking velocity must be zero for a perfect adaptation.

According to Stoke's law, the sinking velocity of a spherical particle with a radius, r, is as follows:

$$v = \frac{F}{6\pi\eta r}$$

Where F is the difference between the weight of the organism (density of the body multiplied by its volume) and Archimedes upthrust (density of the medium multiplied by volume of the body) acting on the organisms, and η is the viscosity of the sea water. Stoke's law is strictly appreciable only to spheres below a limited diameter (for quartz spheres it is 60 μm); this limit is higher when the difference of density from the milieu is less (Sverdrup, Johnson and Fleming, 1946). This law may serve as a guide when dealing

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with the physical relations between the plankton and the surrounding sea water. A decrease in F will decrease the sinking velocity and any reduction in the density of the organism relative to sea water will be an advantage to planktonic existence. This may be realised in different ways. In a given group skeletal components may be less resistant and lighter in planktonic species than in the benthic species; there are numerous examples of this in the diatoms, carapaces of crustacean, shells of gastropods. In the Heteropoda we can find a series passing through *Atlantia* and *Carinaria* with shells and ending in the complete disappearance of the shell in *Pterotrachea*. The increase in body tissue water by the development of gelatinous substances is another and frequent method of pelagic adaptation. A comparison of the amount of water in the same group shows this clearly.

Cnidaria:	planktonic form (*Cyanea*)	96.5%
	benthic form (*Anemonia*)	87.2%
Crustacea:	planktonic form (*Calanus*)	85.7%
	benthic form (*Crangon*)	74.5%

Another way of decreasing the weight is to maintain an osmotic equilibrium with the sea water by lighter ions. The monovalent chloride ion (35.5) replaced the divalent sulphate ion (96/2 = 48). Frequently floats are found in planktonic organisms, gas floats in the Siphonophora or oil "floats" in fish larvae and some copepods.

A reduction of the organisms dimensions also decreases its sinking velocity. According to Stoke's law F is proportional to the difference between the density of the body and that of the water and the body volume; so $F = kr^3$, where k is a constant. The previous expression becomes:

$$v = \frac{kr^3}{6\pi\eta r} = \frac{kr^2}{6\pi\eta}$$

As the radius become smaller the sinking velocity is lowered. The small size which, as we have noted, is one of the general characteristics of planktonic organisms, contributes to their improved adaptation to a planktonic existence.

The adaptation to pelagic life is improved by any morphological characteristics which increase the resistance to sinking. More or less flattened forms, which reduces the sinking velocity are found in the plankton, for instance *Sapphirinia* (Copepoda) or phyllosoma larvae (lobsters), while the morphology of medusae is very similar to that of a parachute. Another efficient adaptation is the existence of very long and even exaggerated appendages such as those of *Chaetoceros* (a diatom) or some zoea (larval crustaceans).

When the adaptation is imperfect the organism must have a "complementary adaptation". This involves a waste of energy in motor activities such as undulation of the flagellum in peridinians, the beating of the cilia of the ciliary bands of many larvae or the swimming activity of crustaceans.

We shall return now to Stoke's law. The viscosity of sea water, η, may be markedly modified, particularly by temperature: at 0°C it is 18 millipoise, at 10°C 13 millipoise, and at 20°C 10 millipoise. As a consequence, an organism with given dimensions and density, which is in equilibrium with the water at a given temperature will sink when the temperature rises and eventually have to spend a certain amount of energy to complete its adaptation.

For a spherical organism in equilibrium with sea water at 0° the radius must be decreased by a factor of 0.74, i.e., reduced by a quarter in order to maintain its equilibrium at a temperature of 20°C because of the change in the viscosity of sea water. On the other hand, it is well known that the solution of certain substances such as agar–agar considerably increases its viscosity in water and this may be attained with a small quantity of material. It does not seem that the possibility of this kind of reaction has been considered until recently as affecting plankton, despite the fact that many organisms are known to be able to excrete organic substances. (This is probably an interesting field of research).

Concerning the physical meaning of the viscosity this has to be considered in the light of Margalef's ideas (1957) which emphasise the importance of electrostatic charges. For a detailed study on the flotation of the phytoplankton see the review of Smayda (1970).

CHAPTER 1

THE PHYTOPLANKTON: GENERAL CHARACTERISTICS AND SYSTEMATIC OUTLINE

1-1.—GENERAL

The phytoplankton is defined as the plant plankton, i.e., plankton which is able to photosynthesize materials from water, carbon dioxide, using light energy.

The phytoplankton as well as the benthic algae are the source of the primary production of organic matter in the sea. Light penetration, however, rapidly decreases with depth, and in consequence the benthic algae are restricted to the littoral fringe, while the phytoplankton is distributed over the entire superficial zone of the seas, apart from those regions covered by ice. Even these latter regions are not without plant production. An abundant unicellular algal flora is developed on sea ice (Bunt & Lee, 1970), but according to the definition of plankton these algae do not, strictly, belong to the phytoplankton. With one exception, the phytoplankton consists of microscopic algae, single cells, or cells forming chains, their size ranging from several μm to several hundred μm. The ratio of the external surface to the volume is higher in single or loosely attached cells than in grouped cells. As we have already seen the increase of this area/volume ratio improves the buoyancy but this is not the only way used by planktonic organisms to attain this end. A high surface to volume ratio also increases the surface available for the absorption of nutrients needed for photosynthesis, of importance because the concentrations of nutrients in sea water are very low. However, the aggregation of cells in the multicellular benthic algae does not seem to be a handicap in this respect. Finally, in the present state of our knowledge we can only state the fact of the microscopic nature of the phytoplankton without any possibility of showing that this corresponds to the only possible adaptation of plants to a pelagic life.

There is one exception, namely, *Sargassum* a brown alga from the order Fucales which attains a size of several decimeters; it has small spherical floats. *Sargassum* is abundant in the waters of the central Atlantic, between 20° and 30°N an area known as Sargasso Sea. The floating *Sargassum* does not produce reproductive organs but continues to grow as the older parts decay. These plants are not, therefore, algae torn from the coast by wave action and accumulating in this zone but are true planktonic algae. Another exception has been described by Womersley & Norris (1959), namely, a floating red algae which is present on the coasts of Australia. This algae, of the genus *Antithamnion*, forms spherical floats about 1 cm in diameter and is cast up on the coast in large quantities.

Among the unicellular planktonic algae we shall first consider the diatoms, with numerous species, and often very abundant. Another important group is the order Peridinales, which are flagellated unicellular algae. A certain number of other groups of flagellated algae, mainly coccolithophorids and silicoflagellates, are also found in the phytoplankton population. The Cyanophyceae (may mainly in tropical waters) contribute to the phytoplankton. These different groups will be reviewed using the classification of Parke & Dixon (1968), and summarized in Chapter 14-1.

1-2.—THE DIATOMS

The Bacillariophyceae, more commonly known as diatoms, is a class of algae with numerous species both benthic and planktonic; the latter are the most important group in the economy of the sea. The diatoms are unicellular algae whose hard cell envelope, termed a frustule, is made up of pectic substances associated with silica; cellulose is absent. The frustule is made of two halves, or valves, which form a pill box-like structure similar to the two halves of Petri dish. The valves are laterally prolonged by connective bands (pleura) forming a girdle, and these can move one over the other. There is a large vacuole in the cytoplasm and this often occupies a large part of the cell. The nucleus is of the usual type. The chromatophores (Fig. 1-1, a, g, i, k), yellow or gold-brown, contain chlorophyll (chlorophyll *a* and *c*) and carotenoids, (xanthophylls among which the most abundant is fucoxanthin and carotins); they are generally small and numerous in planktonic diatoms. The products of synthesis are small drops of lipids, and granules of volutin. This latter substance, enigmatic for a long time, is a phosphatic accumulation, in the form of polyphosphates. Diatoms do not produce starch.

Multiplication is by binary fission. The valves separate from each other, mitosis gives rise to two nuclei, the protoplasm divides and the wall which is formed is split into two halves. Each new valve forms a new pill box with the old valve which accompanies it, the older one becoming the outer half of the pill box. The size of the cells must tend to decrease at each division. This phenomenon is not, however, as general as was at one time thought, and in cultures stable dimensions have sometimes been observed; the frustule can probably grow a little. The diminution in size is compensated by means of a special mode of multiplication, namely, auxosporulation, the characteristics of which often presents some sexual phenomenon; the process differs according to the group, but always gives rise to a voluminous cell called an auxospore which secretes a larger frustule (Fig. 1-1, c, i).

There are other methods of reproduction. In microsporulation small biflagellated cells without a silicous membrane, the microspores, are formed; they swim and two fuse to produce a zygote which gives rise to a normal cell. In the formation of endospores protoplasm is concentrated within

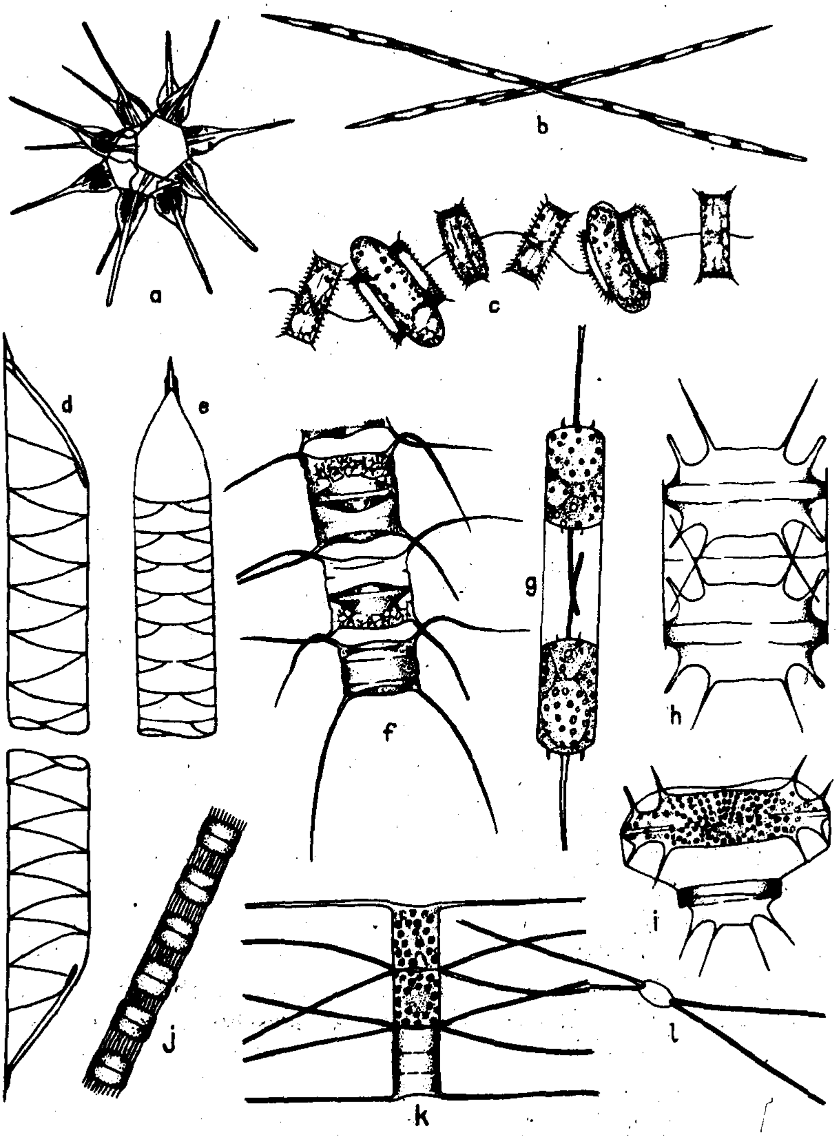

Fig. 1-1.—Planktonic diatoms. a, *Asterionella japonica*, cells in a spiral colony formation showing chromatophores (length of one cell, 50–90 μm); b, *Nitzschia seriata*, cells in chain formation (length of a cell, 90–100 μm); c, *Thalassiosira gravida*, cells in chain formation with two auxospores (diameter, 20–60 μm); d, *Rhizosolenia styliformis*, side view of two extremities of a cell (diameter, 40–100 μm; length, up to 1.5 mm); e, *Rhizosolenia styliformis*, dorsal view of an extremity; f, *Chaetoceros diadema*, with two endospores (diameter of valve, 12–46 μm); g, *Ditylum brightwellii*, cell after division with chromatophores (diameter: 28–46 μm); h, *Biddulphia mobiliensis*, cells beginning to divide (length with spines 60–200 μm); i, *Biddulphia mobiliensis* after forming auxospores showing chromatophores; j, *Skeletonema costatum*, cells in chain formation (diameter, 8–15 μm); k, *Chaetoceros danicum*, cells in chain formation showing chromatophores (diameter of valve, 16–20 μm); l, *Chaetoceros danicum*, cell in valve view (after Hendey, 1967).

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