CHAPTER 1

DISTRIBUTIONS OF PLANKTON AND NUTRIENTS

1.1. TAXONOMIC, ENVIRONMENTAL AND SIZE SPECIFIC GROUPS OF PLANKTON

Organisms which are unable to maintain their distribution against the movement of water masses are referred to as 'plankton'. Included in this group are bacterioplankton (bacteria), phytoplankton (plants) and zooplankton (animals). Generally all plankton are very small and, in many cases, microscopic. However, relatively large animals, such as the jellyfish, are also included in the definition of plankton. Some plankters, including both plants and animals, are motile but their motility is weak in comparison with the prevailing movement of the water. Animals, such as fishes, which can maintain their position and move against local currents are known as 'nekton'. However, the division between plankton and nekton is not precise and some small fish, especially fish larvae, may be a part of the plankton community, while some large zooplankton, such as euphausiids, might also be thought of as 'micronekton'.

The biomass or weight of plankton or nekton per unit volume or area of water is referred to as the 'standing stock'; typical units used for standing-stock measurements are $\mu g/l$, mg/m^3, g/m^2, kg/hectare, etc., where the weight should be specified as referring to wet weight, dry weight, or carbon. The productivity of organisms is defined in terms of 'primary productivity', 'secondary productivity' and 'tertiary productivity'; units are the same as in standing-stock measurements when expressed per unit time (e.g. per hour, day or year). Ideally, primary productivity represents the autotrophic fixation of carbon dioxide by photosynthesis; secondary productivity represents the production of herbivorous animals and tertiary productivity represents the production of carnivorous animals feeding off the herbivore population. However, these definitions are not precise since some plants may utilize growth factors, such as vitamins (auxotrophic growth), and others are capable of taking up organic substrates as a source of energy (heterotrophic growth). Thus the particulate material grazed by secondary producers may be derived from a variety of processes and include phytoplankton and bacterioplankton. Similarly many filter-feeding zooplankton which might be nominally classed as herbivores may at times feed upon other small animals, such as Protozoa; thus the boundaries between components in the aquatic biosphere are difficult to define with the same precision as is used in chemistry or physics. Biological associations are better considered *in toto* as an ecosystem in which various components react with each other to a greater or lesser degree. Components of an ecosystem can be defined in terms of their taxonomy or chemistry; interactions between components can then be expressed quantitatively by empirical equations. Thus a phytoplankton standing stock may be described as consisting of 10^6 cells per litre of a species, *Skeletonema costatum,* or as being represented by a cholorophyll *a* concentration of 1 mg/m^3, or in a trophic sense as a ration for zooplankton, such as is represented in Chapter 4. Attempts to synthesize these various components of biological production in the sea have given rise to a variety of mathematical models. Walsh (1976) has reviewed the many types of models involved; he points out, however, that no model is a perfect representation of the real world. It is in fact impossible to know all the states of biological variables in an ecosystem.

However, where the ecosystem is sufficiently restricted in time and space it is possible to create an acceptable simulation of major events. For example, the upwelling ecosystem is relatively simple in the sense that it is possible both to formulate the principal biological interactions and at the same time to test the ecosystem model using fast, well-equipped research vessels and aerial coverage. More detailed discussions of biological modelling are given by Steele (1974) and by Platt *et al.* (1981).

The lowest forms of life found in the ocean are unicellular organisms; either prokaryotes (lacking a nuclear membrane) or eukaryotes (with a distinct nucleus). For detailed definitions of these two groups the reader is referred to Broda (1978). The marine prokaryotes include the bacteria and the blue-green algae while all other phytoplankton are eukaryotes. Thus in function both eukaryotes and prokaryotes can be either autotrophic or heterotrophic. In practice, however, the role of unicellular eukaryotes in the sea includes most of the autotrophic production by phytoplankton, some heterotrophic (and often phagocytic) production, particularly by certain flagellates, and production by unicellular animals (protozoa) — collectively this whole group may be referred to as the kingdom, Protistae (i.e. Protists). In contrast the ecological function of the unicellular prokaryotes is most apparent in the many activities of the heterotrophic and chemoautotrophic bacterioplankton, with the blue-green algae generally playing a minor role (in the total ecology of the sea) as autotrophic photosynthetic organisms. However, the latter have one notable function in oligotrophic waters which is their ability to fix nitrogen.

The numbers of bacterioplankton in the sea generally are maximal at the sea surface where they are associated with a high concentration of organic material making up part of the neuston (Sieburth, 1971; Tsyban, 1971). Values of 10^8 bacteria/ml may be encountered in the sea surface film while below the sea surface values of 10^5–10^6/ml would be more common in the euphotic zone. Bacteria in the ocean depths decrease by several orders of magnitude ($< 10^4$/ml) except in immediate association with sediments rich in organic material, or near hydrothermal vents. Generally, those bacteria suspended in the water column will be aerobes but microhabitats inside detrital particles, including fecal pellets, allow for the presence of anaerobic bacteria in otherwise oxygenated water columns. In the presence of hydrogen sulphide layers (e.g. the Black Sea or at hydrothermal vents), chemotrophic bacteria are present in large numbers (for recent reviews see Sieburth, 1979; Jannasch and Wirsen, 1979).

According to Wood (1965) the principal genera of bacteria represented in the oceans are the *Micrococcus, Sarcina, Vibrio, Bacillus, Bacterium, Pseudomonas, Corynebacterium, Spirillum, Mycoplana, Norcardia and Streptomyces.* Among these genera are various morphological differences including coccoid, rod and spiral forms. A large number of the most common bacteria are motile and gram negative. The bacterioplankton do not usually contribute significantly to the total biomass of particulate organic matter but in association with detritus (see Section 2.4) they may form an appreciable organic reserve during times of low phytoplankton density. Their role in the oceans is more important in recycling elements and organic material back into the food chain (see Chapter 5). MacLeod (1965) has discussed the specific identity of marine bacteria as compared with bacteria from a terrestrial origin. His findings showed that marine bacteria have special requirements for inorganic ions which include a highly specific need for Na^+ and a partial need for halide ions which could be satisfied by either bromine or chlorine ions. Mg^{2+} and Ca^{2+} were also required, usually at concentrations higher than are normally needed for terrestrial bacteria. Oliver (1982) has devised a flow chart for the identification of marine bacteria. Based in part on Bergey's *Manual of Determinative Bacteriology,* the scheme involves a relatively short series of tests that can be employed to identify major taxa of motile and non-motile gram negative rods.

The taxonomy of phytoplankton has been in a state of revision for some time but it is believed that Table 1 represents the most recent revisions in the various class names. Of the thirteen classes represented in Table 1, four are the most important with respect to the total standing stock of

TABLE 1. REPRESENTATION OF ALGAL CLASSES IN MARINE PHYTOPLANKTON (Prepared by F. J. R. Taylor, Department of Oceanography, University of British Columbia)

Taxonomic class	Common name	Area(s) of predominance	Notes
CYANOPHYCEAE	Cyanobacteria/ blue-green algae	tropical (filamentous) cosmopolitan (coccoid)	Chiefly *Trichodesmium* (= *Oscillatoria*); N_2 fixer. Chiefly *Synechocystis,* minute (2 μm or less).
RHODOPHYCEAE	Red algae	v. rare, coastal	*Rhodosorus*; abundant benthic forms.
BACILLARIOPHYCEAE	Diatoms	all waters, esp. coastal	Major microplanktonic primary producers.
CRYPTOPHYCEAE	Cryptomonads*	cosmopolitan, mainly coastal	Much neglected, but often important, nanoplankters.
DINOPHYCEAE	Dinoflagellates*	all waters, esp. tropics	Autotrophs or heterotrophs; common red tide producers.
CHRYSOPHYCEAE	Chrysomonads* Silicoflagellates*	rare, coastal occasionally abundant	Important in fresh water, except for silico flagellates.
HAPTOPHYCEAE = PRYMNESIOPHYCEAE	Coccolithophorids* & prymnesiomonads*	oceanic (coccolith.) coastal (prymnesio)	Some (coccolithophorids) with $CaCO_3$ scales, others (e.g. *Chrysochromulina, Prymnesium*) without.
RAPHIDIOPHYCEAE	Chloromonads*	rare, but occasionally abundant, brackish	Some fish-killers (*Chattonella*).
XANTHOPHYCEAE	Yellow-green algae/ heterochlorids*	v. rare	A few coccoids; others are mostly benthic or f.w.
EUSTIGMATOPHYCEAE	–	v. rare	A few coccoids; others are mostly benthic f.w.
EUGLENOPHYCEAE	Euglenoids*	coastal	Occasionally common, e.g. *Eutreptiella.*
PRASINOPHYCEAE	Prasinomonads*	all waters	Flagellates are coastal, often tide pools (e.g. *Pyramimomas) 'phycoma' (cyst) phase pelagic (Halosphaera, Pterospema). Micromonas* is an important nanoplankter.
CHLOROPHYCEAE	Green algae, volvocaleans*	v. rare, coastal	Mostly f.w. or benthic.

*Also classified as phytoflagellates of the protozoa.

phytoplankton in the ocean. These are the Bacillariophyceae, Dinophyceae, Haptophyceae and Cryptophyceae. Of these, diatoms and dinoflagellates are found extensively throughout the world oceans both in coastal and oceanic waters; the coccolithophorids are found more abundantly in oceanic waters while the cryptomonads are often numerous in coastal waters. Rarer classes of algae, including such organisms as the silicoflagellates, the prasinomonads, euglenoids and chloromonads have sometimes been found to be abundant in coastal waters. The blue-green algae may be abundant at times in tropical water (e.g. *Trichodesmium* blooms in the Red Sea) while Jeffrey and Hallegraeff (1980) have shown that in warm core ocean waters a prasinophyte, *Micromonas,* probably accounts for small persistent occurrences of chlorophyll *b* in photosynthetic pigment extracts. Similarly Johnson and Sieburth (1979 and references cited) have reported on the occurrence of small (*ca.* 1 μm diameter) cyanobacteria (blue-green algae) in open ocean waters at concentrations of 10^3–10^4/ml. Thus while the largest part of the primary productivity in the oceans is confined to a few classes of algae, it is probable that most other classes of algae in Table 1 are present as minor components which may occasionally form blooms under local conditions. In addition some of the colourless phytoplankton flagellates (e.g. dinoflagellates such as the genus *Noctiluca*) or microflagellates (e.g. see Haas and Webb, 1979 and references cited) may represent secondary production due to their ability to consume either phytoplankton or bacteria. In addition, a number of classes of algae occur as symbionts in animals; these are known collectively as the 'zooxanthellae'.

The zooplankton include members of the animal kingdom (Metozoans) as well as of the kingdom Protistae (Protists). The classification of both kingdoms is a subject of continual revision. For example, the former animal phylum Protozoa, may now be regarded as a sub-kingdom of the Protists;

or, among higher animals, the phylum Ctenophora may be included by some authors as part of the phylum Coelenterata. For purposes of this text, the phyla represented have been taken from a more detailed summary by Newell and Newell (1963).

Phylum	*Some representatives among the zooplankton*
Protozoa (also regarded as a sub-kingdom)	Oligotrich and tintinnid ciliates; Radiolaria; Foraminifera
Coelenterata	Hydrozoa, Scyphozoa (Jellyfish)
Ctenophora	Ctenophores
Chaetognatha	Arrow worms
Annelida	Polychaete worms
Arthropoda (Class Crustacea)	Copepods, cladocerans, mysids, euphausiids, ostracods, cumaceans, amphipods, isopods
Sub-phylum Urochordata	Salps and appendicularians
Mollusca	Heteropods, Pteropods

In addition to the above, there are many large invertebrates having larval planktonic stages (e.g. polychaetes, crustaceans, gastropods, lamellibranchs and echinoderms). Among vertebrates (Phylum: Chordata, Sub-Phylum: Vertebrata) fish eggs and larvae both occur as members of the plankton. Important commercial species which have a planktonic state include the herring, anchovy, tuna, and bottom feeders, such as cod and plaice. From among the types of zooplankton listed above, by far the most abundant group are the Crustacea, and of these, the copepods are the most predominant.

Biogeographical distributions of plankton have been based on the very early recognition that specific environmental factors, such as light, temperature, salinity, and nutrient requirements, to some extent determined the occurrence and succession of species. Smayda (1958 and 1963) has reviewed a number of the terms used to describe plankton from similar environments. Plankton with a tolerance to a wide range of temperatures is described as 'eurythermal', while a narrow range of temperature tolerance is described as 'stenothermal'; similarly salinity (euryhaline and stenohaline), pH (euryionic and stenoionic), and light (euryphotic and stenophotic). A further classification of light response has been used to obtain a vertical separation of plankton communities into those inhabiting the 'euphotic' zone (where the net rate of photosynthesis is positive) as opposed to the 'disphotic' and 'aphotic' zones, where there is enough light for biological detection and where no further light can be detected, respectively (see Chapter 3). Unfortunately, these words usually lack precise quantitative description but some knowledge of their meaning may be useful in reading other publications.

The terms 'oceanic' and 'neritic' have been used quite extensively in describing plankton associated with the oceans and with coastal waters, respectively. The classification may be particularly useful in reporting taxonomic data collected from commercial vessels, such as with a Hardy recorder as illustrated in Fig. 1. From this figure it is easy to see that certain 'indicator species' belong to each region. Over large areas of ocean there may be several oceanic groups. Bary (1959 and 1963) defined such plankton distributions in terms of their temperature and salinity tolerances (called T–S–P diagrams). He emphasized that the importance of such diagrams was in showing the distribution of plankton in certain water bodies rather than the exact geographical location of the samples. Fager and McGowan (1963) used an 'affinity index' to show relationships between groups of species. Their index was defined as

$$\frac{J}{\sqrt{N_A N_B}} - \frac{1}{2\sqrt{N_B}}$$

where J was the number of joint occurrences of species; N_A and N_B were the total number of occurrences of species A and B respectively, where $N_A < N_B$. Pairs of species for which the index was arbitrarily $> 0{\cdot}5$ were considered to show affinity. North Pacific plankton were classified into six groups and showed interrelationships between groups as illustrated in Fig. 2. Perhaps the most important aspect of all such groupings is that the

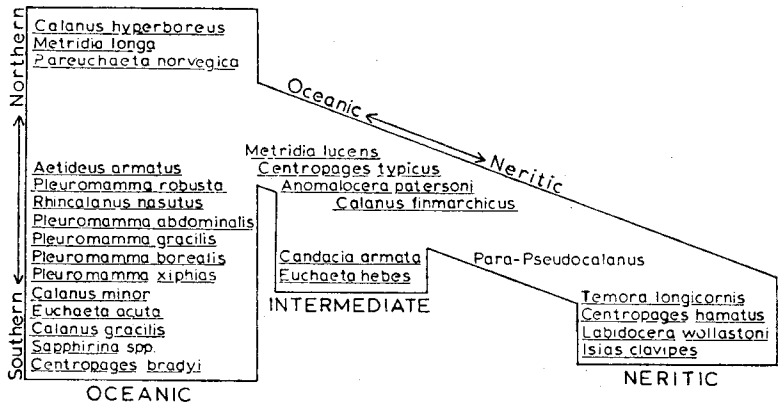

FIG. 1. Distribution series of copepods in the North Sea and the north-eastern Atlantic arranged in such a way that the distribution of each organism is most similar to those of the neighbouring organisms in the list (redrawn from Colebrook *et al.*, 1961).

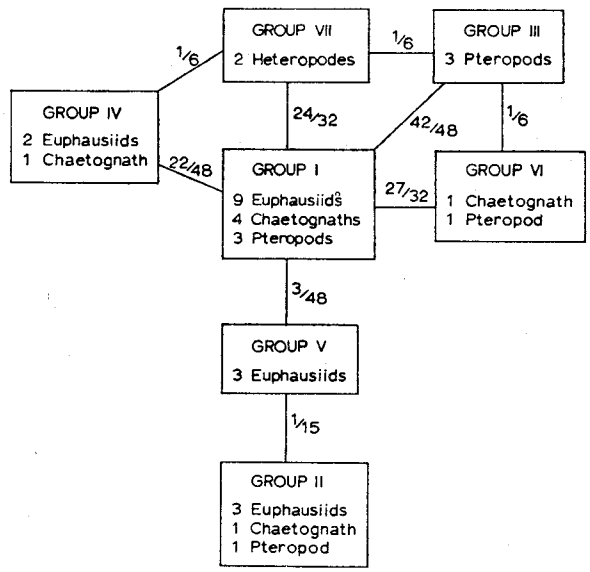

FIG. 2 Composition of zooplankton groups in the north Pacific. Fractions are the ratios of the number of observed species-pair connections between groups to the maximum number of possible connections; for example, there are six possible intergroup species pairs between group IV and VII but only one of these showed affinity at the 'significance' level used (redrawn from Fager and McGowan, 1963).

occurrence of species in another group (or changes in the between groups associations) may indicate changes in the ocean and coastal environments, such as might occur from a shift in the direction of a current. However, Fager and McGowan (1963) found that many of the usually measured properties of water (e.g. temperature, thermocline depth, etc.) were not closely correlated with differences in zooplankton abundance. From this it was concluded that the organisms reacted to a more complex interaction of known properties or to some environmental factors yet to be elucidated.

Phytoplankton species which produce resting spores or have a sedentary phase are known as

'meroplankton' as opposed to 'holoplankton' (Smayda, 1958). However, these terms were originally used to refer to zooplankton and in this sense 'meroplankton' refers to organisms which are only temporarily members of the plankton community (e.g. some bivalve larvae) while 'holoplankton' refers to a permanent member of the plankton community (e.g. most calanoid copepods). A general classification of plankton abundance based on availability of nutrients is used in describing waters as 'eutrophic', 'mesotrophic', and 'oligotrophic', in decreasing order of plankton abundance (see Hutchinson, 1969, for a further discussion of these terms). Plankton may be grouped by the depth zone in which they are found in the 'pelagic' or open-sea environment. These zones have received a number of different classifications but the simplest approximate definitions appear to be 'epipelagic' (0 to 150 m), 'mesopelagic' (150 to 1000 m), 'bathypelagic' (1000 to 4000 m), and 'abyssopelagic' (4000 to 6000 m) (see Hedgpeth, 1957, for further definitions). Plankton (or other particulate matter) produced within a designated ecosystem is referred to as 'autochthonous' while 'allochthonous' material is imported into the ecosystem. A large number of other groupings have been employed by systematists in describing plankton communities. In some cases these terms lack universal usage because of the specificity of their original definition; others have acquired common scientific usage while lacking a precise definition (e.g. see Smayda, 1958). Geographically it has been popular to refer to species as coming from warm or cold regions of the hydrosphere. These regions are not defined by latitude since warm or cold currents may cross such imaginary lines (e.g. the Gulf Stream). McGowan (1971) defines up to twelve subregions of the hydrosphere in describing the distribution of many zooplankton. In general, however, the principal regions may be considered as follows:

Tropical	(> 25°C water all the year)
Subtropical	(*ca.* 15–30°C)
Subpolar	(*ca.* 5–15°C)
Polar	(*ca.* 0–5°C)

The combination of subpolar and subtropical waters also encompasses a region in which authors refer to 'temperate' species.

From the point of view of food-chain studies one of the most useful groupings for plankton and larger organisms is to consider all particulate material on a single size scale. The most recent effort aimed at providing a universal size scale for plankton and nekton is based on an earlier grade scale by Sheldon and Parsons (1967). The scale which has now been proposed by Sieburth *et al.* (1978) is shown in Fig. 3. While definitions of the

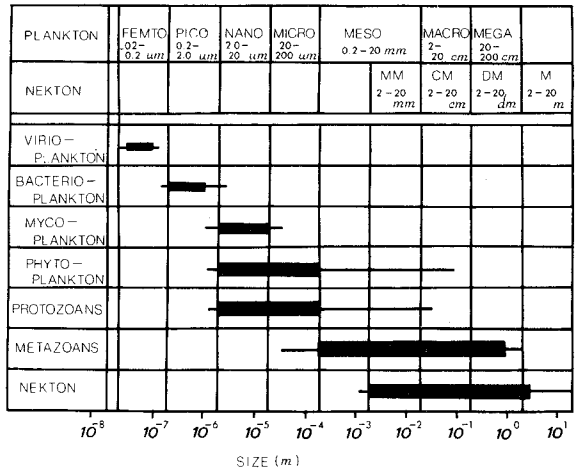

FIG. 3. A proposed size classification scheme for components of the pelagic ecosystem modified from Sieburth *et al.* (1978).

smaller size groupings given in Fig. 3 were originally based on microscopic measurements, or passage through filters of different pore size, it should be noted that neither of these earlier techniques are precise, although they may have considerable practical application, particularly under field conditions. A more precise approach to the representation of linear measurements of irregular-shaped bodies (i.e. plankton) is to consider the volume displaced by that body and to represent its dimension as the radius of a sphere having an equivalent volume. This is illustrated in Fig. 4 where the equivalent volume (V_1, V_2, V_3, V_4, etc.) of irregular particles have diameters (d_1, d_2, d_3, d_4, etc.) which follow a grade scale based on $2^1/_3$. The biomass in each size category is then ($n_i \times v_i$) and peaks in the size spectrum are seen when a particular plankton bloom occurs. Such measurements can be made with electronic counts (e.g. the Coulter Counter®). The total biomass of material measured with the Coulter Counter® is statistically related to such parameters as the weight of particles, chlorophyll *a* concentration and particulate carbon (e.g. Zeitzschel, 1970). The advantages of using a continuous size spectrum for particle distributions in the sea are (i) the size group of plankters contributing most to the total standing stock of plankton can be readily identified as peaks in the spectrum, (ii) biomass diversity indices (Wilhm, 1968) can be calculated from the spectrum, and (iii) the growth increment, or grazing loss, of different size categories can be determined independently of the total biomass of phytoplankton, zooplankton, and other particles (Parsons, 1969; Parsons and LeBrasseur, 1970). However, particle size spectra *per se* do not relate to taxonomic groups and microscopic identification of the principal components in a plankton crop is recommended when using this technique. Also the results include all detrital particulate material, and special methods are sometimes necessary to differentiate between detritus and growing cellular material (Cushing and Nicholson, 1966).

Example illustrations of common phytoplankton and zooplankton are shown in Figs. 5 A, B and C.

1.2 DIVERSITY

The diversity of a plankton community may be expressed using data on the number of species present, the distribution of biomass, the pigment

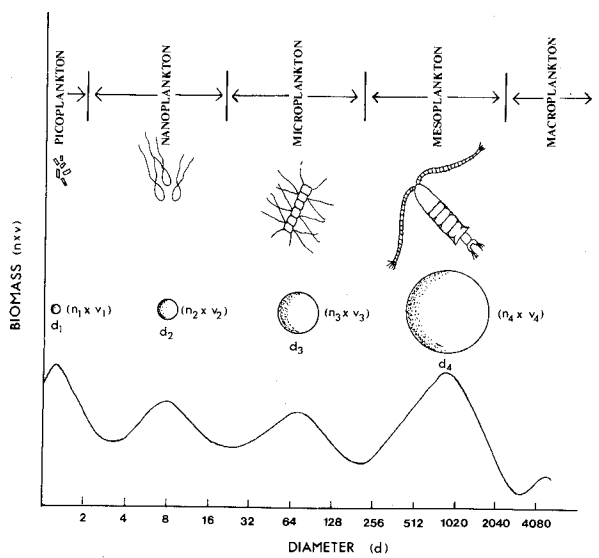

FIG. 4. Particle spectrum representing biomass ($n \times v$) of material in different size categories determined by the diameter (d) of a sphere equivalent in volume (v) to the original particle, times the number of particles (n).

composition, or a number of other parameters which are easily measured properties of plankton. From a heuristic approach, an index of diversity may be used in the same way as other environmental parameters, such as temperature and salinity, to characterize the environment. There are both theoretical and empirical bases for the use of specific diversity indices, but as Lloyd *et al.* (1968) have stated, "which one is 'best' depends upon which one proves in practice to give the most reliable, surprising ecological predictions and the greatest insight".

The simplest expression of diversity is to determine the percentage composition of species in a sample; the more species making up the total, the greater is the diversity of the organisms. However, this value is almost wholly dependent on the total number of individuals (N) and is therefore unsatisfactory as a diversity index. From some of the earliest quantitative studies in ecology it was recognized, however, that a relationship existed between the number of species in a population (S) and the logarithm of the total number of individuals (N), so that the simplest diversity index (d) can be expressed as:

$$d = \frac{S}{\log_{10} N}. \tag{1}$$

This value will be very small under conditions of a plankton bloom and generally high in tropical plankton communities. A better expression which reduces to 0 when all the individuals are from the same population was given by Margalef (1951):

$$d = \frac{S-1}{\ln N}. \tag{2}$$

Margalef (1957) introduced the idea that the 'information content' could be used as a measure of diversity in a plankton sample. Thus the diversity of a collection containing a total of N individuals and $n_1, n_2, \ldots n_i$ individuals of each species can be written as:

$$\frac{N!}{n_1!n_2! \ldots n_i!},$$

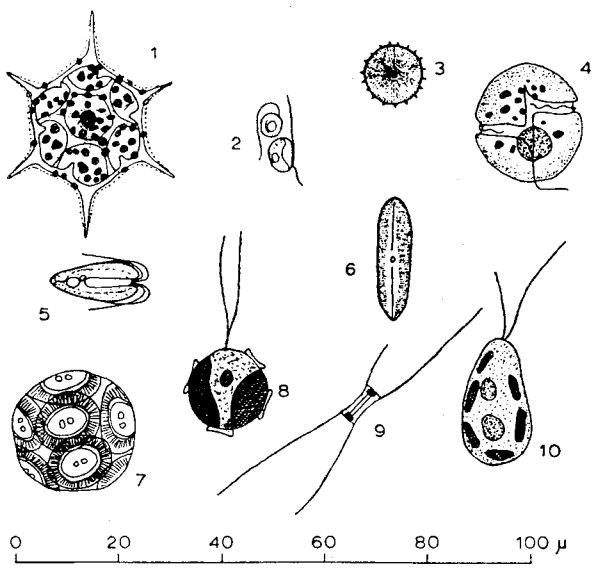

FIG. 5A. Examples of nanoplankton flagellates [*Distephanus* (1), *Thalassomonas* (2), *Gymnodinium* (4), *Tetraselmis* (5), *Coccolithus* (7), *Pontosphaera* (8), *Cryptochrysis* (10)], diatoms [centrate (3), pennate (6), *Chaetoceros* (9)] (redrawn from Wailes, 1939, Cupp, 1943, Fritsch, 1956 and Newell and Newell, 1963).

and information (H in 'bits')* per individual as:

$$H = \frac{1}{N}\log_2 \frac{N!}{n_1!n_2!\ldots n_i!}. \quad (3)$$

The information content as expressed above, eqn. (3), can be interpreted as the degree of uncertainty involved in predicting the species identity of a randomly selected individual. If N is large and none of the n_i fraction are too small, information content per individual (H' in bits) can be approximated from the expression:

$$H' = -\Sigma\, p_i \log_2 p_i \quad (4)$$

where $p_i = n_i/N$ and is the proportion of the collection belonging to the ith species (Shannon and Weaver, 1963). Under some circumstances eqn. (4) will be more easily determined than eqn. (3) but Lloyd *et al.* (1968) have provided examples and tables for the solution of both equations for values of N from 1 to 1050. Margalef (1961) made a statistical comparison between the diversity of plankton samples calculated from the diversity index [eqn. (2)] and the theoretical diversity [eqn. (3)]. There was a highly significant correlation between the two although there was a difference in the regression line depending on whether diversity was determined for a diatom or dinoflagellate population. Using eqn. (4) Lloyd and Ghelardi (1964) related diversity to the maximum possible value for a given number of species if they were all equally abundant. This term was called the 'equitability'(ϵ) and was expressed as the ratio of H to a theoretical maximum (M) for the same number of species, where $n_1 + n_2 + \ldots n_i$. A table of M values for 1 to 1000 species is given by the authors. The value of ϵ in describing a collection may be more useful if units of biomass rather than number are employed to determine diversity (e.g. Wilhm, 1968).

'Equitability', as defined by Lloyd and Ghelardi (1964), is the opposite of 'dominance' which expresses the most abundant species in a population. Hulburt *et al.* (1960) expressed the dominance of a plankton community as the ratio of

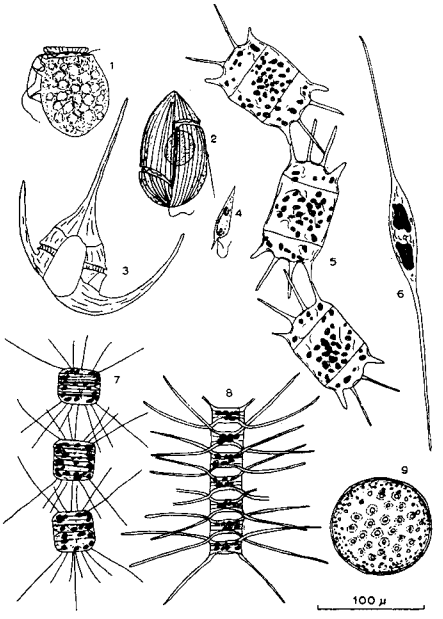

FIG. 5B. Examples of microphytoplankton: dinoflagellates [*Dinophysis* (1), *Gyrodinium* (2), *Ceratium* (3), *Prorocentrum* (4)], diatoms [*Biddulphia* (5), *Nitzschia* (6), *Thalassiosira* (7), *Chaetoceros* (8), *Coscinodiscus* (9)] (redrawn from Wailes, 1939, and Cupp, 1943).

*Information is commonly expressed in 'bits' when using $\log_2$, or 'nats' when using $\log_e$. The following conversion may be useful: $\log_{10} = \log_e \times 2{\cdot}303$ and $\log_2 = \log_e \times 1{\cdot}443$.

the concentration of the most abundant species to the total cell concentration. Also if the presence of one species in a population is nearly always accompanied by another species, the amount of information gained is small. This can be expressed as the 'redundancy' (R) in terms of the equation (Patten, 1962a):

$$R = \frac{H_{max} - H}{H_{max} - H_{min}}, \qquad (5)$$

where H_{max} is the diversity when the species are equally distributed and H_{min} is the diversity when all the individuals belong to one species. The value R varies between O and 1 and is also partially an index of 'dominance'.

The general use of diversity of the type shown in eqns. (3) and (4) above has been discussed by Pielou (1966) who points out that the diversity of a sample should not be regarded as the diversity of a larger population from which it was obtained; the sample itself may, however, be treated as a population and defined. Patten (1959) discusses the absolute diversity of an aquatic community in terms of its information content. As an approximation he calculated that in a Florida lake, the community could be described in terms of 3×10^{24} bits/cm^2/year. If the average information content of a printed page is 10^4 bits, it is apparent that the amount of information required annually to describe the Florida lake community is many orders of magnitude larger than the information contained in the largest libraries! Thus diversity, as discussed in this section, is a property of the entity from which

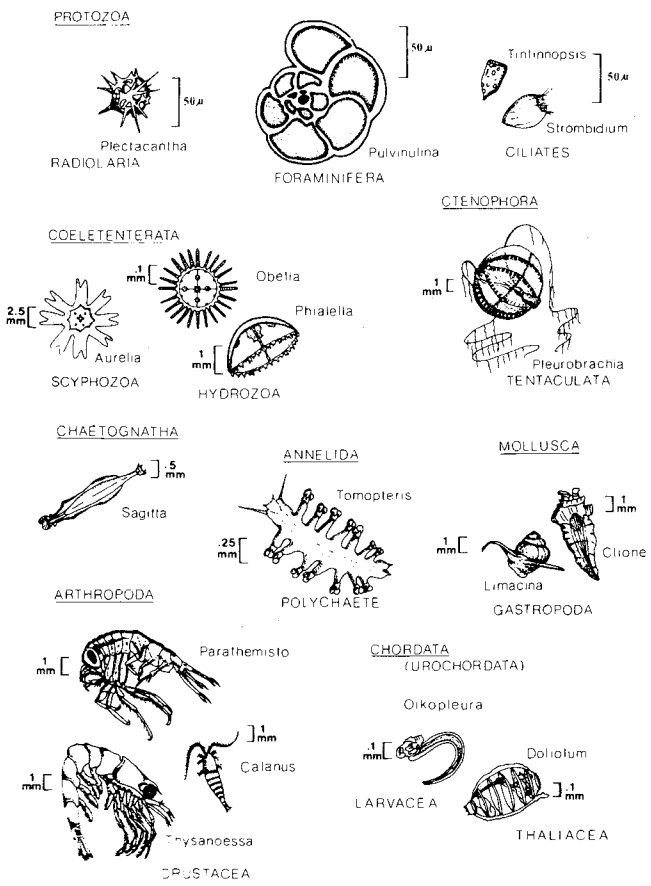

FIG. 5C. Illustrations of the major phyla of zooplankton (redrawn from Lebrasseur and Fulton, 1967; Wailes, 1937 and 1943; Cushman 1931).

the data are collected and not of the whole environment.

The species diversity indices discussed above [e.g. eqn. (2)] are dependent to some extent on the size of the sample, especially for small numbers ($N < 100$). In a method used by Sanders (1968), however, samples of benthic fauna from the same environment, ranging in size from 35 to 2514 individuals, showed no tendency for smaller samples to be less diverse. The technique is described as the 'rarefaction' method and it depends on determining the shape of the species abundance curve rather than obtaining an expression for the absolute number of species per sample.

Changes in the diversity index of samples from a plankton community are shown in Fig. 6. From these data Margalef (1958) recognized three stages of succession. Stage 1 was typical of turbulent waters in which a few species survived and in which there was an occasional bloom of diatoms; stage 3 was characteristic of highly stratified waters in which there was a mature phytoplankton crop and a high diversity following nutrient depletion. Stage 2 was characteristic of inflowing waters which may have transported allochthonous species into the area of study, thus increasing the diversity of organisms present in any sample. Hulburt *et al.* (1960) studied changes in species diversity in the Sargasso Sea and recognized a succession of three species groups. These consisted of a sparse population with a normal distribution of abundant and rare species, a winter period in which a single species was dominant over all other species, and a period of thermal stratification in which dominance was shared by several species. The most extensive field tests of various diversity indices have been carried out by Travers (1971) in the Mediterranean. From this study the author concluded that the degree of maturation and of organization of an ecosystem can be appreciated by means of several diversity indices. From the use of different indices he concluded that a diversity index based on plankton pigments (Margalef, 1965) was a poor method, especially where plankton levels were low; diversity indices based on information theory were considered the best measure of structure although less laborious calculations of diversity can often be used [e.g. eqn. (2)]. Heip and Engels (1974) have compared diversity indices from the point of view of the statistical significance of observed differences or similarities. They conclude by recommending use of the Shannon–Weaver function [eqn. (4)] together with a new index of 'evenness' or 'equitability'.

1.3 SPATIAL DISTRIBUTIONS

1.3.1 Statistical Considerations

In carrying out a series of replicate analyses on a single, well-mixed sample of sea water, small

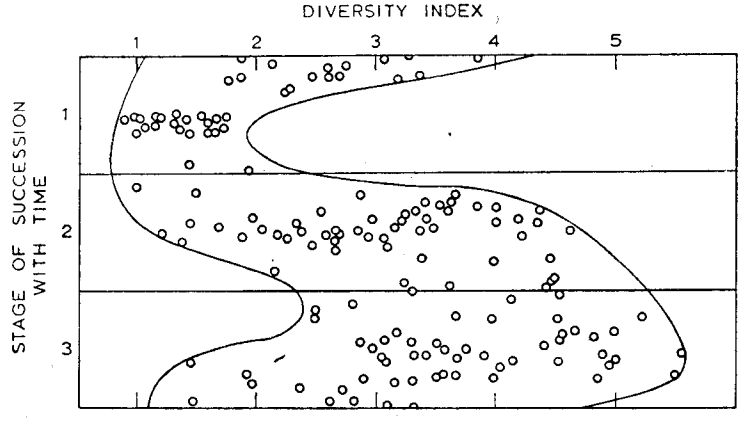

FIG. 6. Stage of succession dependence of diversity index [eqn. (2)] in a number of samples from the surface water at the bay of Vigo (redrawn from Margalef, 1958).

differences in the values obtained may be attributed to analytical technique. Such errors are caused by a lack of instrument reliability, sub-sampling, and slight variations in the way an individual analyst repeats each analysis. It may be assumed that these errors are randomly distributed and that if a large number of replicate analyses are made on one sample, the mean and standard deviation (s) of the analysis can be determined. The precision of the method can then be expressed with a 95% confidence limit for n determinations, as

$$m \pm 2s/\sqrt{n}\ , \qquad (6)$$

where m is the mean of the replicate samples. The principal exception to the use of these statistics for analytical techniques is in the counting of plankton from a settled volume of sea water. In this case the distribution of plankton cells may not be random and special methods may have to be used in order to determine the degree of contagion (Holmes and Widrig, 1956).

The collection of samples of sea water, or plankton from the ocean, introduces much larger differences between replicate samples than can be ascribed to analytical errors alone. Thus Cushing (1962) has summarized a number of reports and showed that in calm weather the % variability (expressed as the coefficient of variation $s/m \times 100$) of the number of three species of plankton in individual hauls varied from 15 to 70%; under conditions of rough weather this variability was increased up to 300%. Cassie (1963) estimated that the coefficient of variation for large samples is most often in the range of 22 to 44%, with obvious exceptions being made for rough weather, or highly stratified environments. Wiebe and Holland (1968) have summarized data on the 95% confidence limits for *single* observations of zooplankton abundance; the range for most data was between *ca.* 40 and 250%.

While the use of sampling gear itself may contribute a small amount of variability to ocean sampling (Cushing, 1962, assigns *ca.* 5% variability to gear operation), the principal cause of variability in replicate samples is due to the non-random or patchy distribution of plankton, and other non-conservative properties, such as the concentration of nutrients. The mechanisms leading to these differences in spatial abundance are many and diverse. They include the physical accumulation of particles by the vertical and horizontal movement of water masses (e.g. divergence and convergence), differences in growth rates of individual plankters, and nutrient uptake and predation patterns of the food chain. These processes are discussed at other points in the text (see Section 1.3.5) and the following discussion (primarily from Cassie, 1962a) deals only with the extent and not the cause of distributions.

In random distributions, two or more samples of sea water of a given volume are equally likely to contain the same organism. The expected distribution of samples with n_1, n_2, n_3, etc., individuals is given by successive terms of the binomial expansion

$$(q+p)^k,$$

where k is the maximum number of individuals a sample could contain, p is the probability of an organism's occurrence and $q = 1-p$. The population mean (μ) and variance (σ^2) of a binomial distribution are

$$\mu = kp \text{ and } \sigma^2 = kpq$$

from which

$$\sigma^2 = \mu - u^2/k. \qquad (7)$$

Since for plankton in a sea water sample $k \rightarrow \infty$, the variance becomes equal to the mean,

$$\sigma^2 = \mu \qquad (8)$$

The above relationship expresses a special case of the binomial distribution in which the probability of an organism occurring ($p = \mu/k$) is small; this is known as the Poisson distribution and the experimental value of the variance (s^2) and mean (m) for replicate plankton collections can be expressed as s^2/m and used to determine if the plankton are randomly or 'over-dispersed'. Theoretically if the value σ^2/μ is greater than 1, the population will be over-dispersed. However, in

practice if s^2/m is calculated for a series of samples their distribution can be represented as $\chi^2/N-1$; thus with twenty samples (19 degrees of freedom), s^2/m should be less than $30{\cdot}14/19 = 1{\cdot}6$ for a 95% probability that the organisms are distributed randomly (Holmes and Widrig, 1956). However, in most cases involving the collection of plankton over an area, the value s^2/m will be significantly greater than 1; thus the ratio can be used as a dispersion coefficient (Ricker, 1937) which along with other parameters (e.g. diversity indices) may be useful in characterizing a body of water.

When populations are over-dispersed the presence of one organism in a sample increases the probability of additional organisms of the same species occurring in the same sample. This is the opposite of a binomial distribution and it can be expressed theoretically as the negative binomial distribution which is given by an expansion of the expression

$$(q-p)^{-k}$$

where $q = 1 + p$. The variance (σ^2) is

$$\sigma^2 = \mu + \mu^2/k. \tag{9}$$

As Cassie (1962b) has pointed out, since p and k are negative, they cannot have the same meaning as they did in the binomial distribution. In particular, however, k appears as a useful parameter for expressing the degree of patchiness, or contagion, in a population. Cassie (1962a) has given an estimate of $1/k$ as $\hat{c}$, where

$$\hat{c} = \frac{s^2 - m}{m^2}, \tag{10}$$

s^2 and m being the sample variance and mean, respectively. The expression [eqn. (10)] was used by Cassie (1959) as a coefficient of dispersion and he concluded that $\hat{c}$ was better than s^2/m, since $\hat{c}$ was not strongly correlated with the mean. This allows for a comparison of dispersion to be made between samples with different means.

In practice it may be found easier to establish an empirical relationship than to fit raw data to a theoretical distribution. Barnes (1952) and Cassie (1962a) have discussed transformations which may be suitable for marine biological data. The most convenient transformation is to convert the raw data to logarithms and the transformed frequencies may then have a log-normal distribution; an example of transformed data is shown in Fig. 7. The mean (m') of the transformed data is the geometric mean and after taking antilogarithms, the value m' will be less than the arithmetic mean, m. Variability about the mean can be expressed as the 'logarithmic coefficient of variation' (Winsor and Clarke, 1940):

$$V' \text{ per cent} + 100(10^{s'} - 1), \tag{11}$$

where s' is the standard deviation calculated from the logarithms of the raw data and V' is the

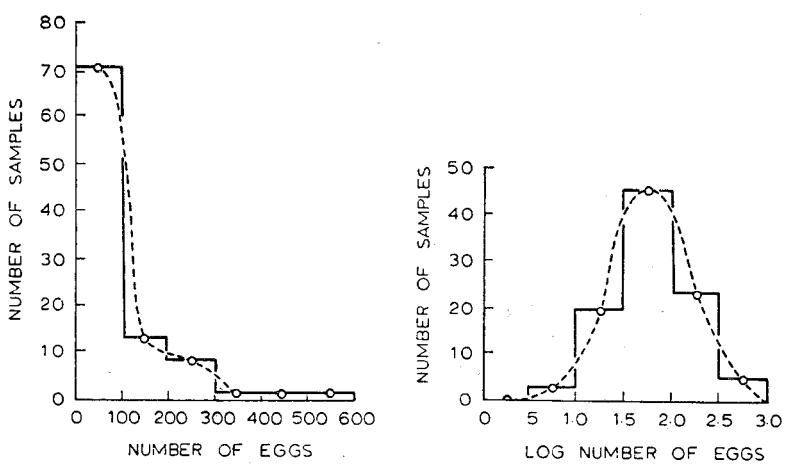

FIG. 7. Frequency distribution of pilchard egg counts in arithmetic and logarithmic forms (redrawn from Barnes, 1952).

logarithmic coefficient of variation. The advantage of using V' has been illustrated by Cassie (1968) who considered two samples with means of 100 and coefficients of variation V (normal distribution) and V' (log-normal distribution) both of 110%. The mean with one standard deviation for the normal distribution was,

$$100 \pm (1{\cdot}10 \times 100) = -10 \text{ to } 210$$

and for log-normal

$$100 \overset{\times}{\div} 2{\cdot}1 = 48 \text{ to } 210.$$

The negative lower limit in the arithmetic range above is meaningless in the context of a normal distribution.

In a detailed study of spatial heterogeneity, Platt *et al.* (1970) separated the sources of variation in a single analysis as follows:

$$\sigma_T^2 = \sigma_0^2 + \sigma_1^2 + \sigma_2^2, \qquad (12)$$

where σ_T^2 was the total variance, σ_2^2 was the variance due to real differences between stations, σ_1^2 was the variance between repeated samples taken at the same station and σ_0^2 included sub-sampling and other analytical errors. The authors found that σ_0^2 and σ_1^2 were about the same size and accounted for *ca.* 10% of the variance each. Real differences between stations were generally much larger, both in time and space. Thus the log-coefficient of variation for a single chlorophyll *a* observation in a near-shore community increased rapidly from 14% at 0·625 sq. mile, to 70% at 1 sq. mile, thereafter remaining relatively constant out to 4 sq. miles. During a study of temporal variations over a period of 5 weeks, the log-coefficient of variation varied from 11 to 111% (mean 42%) at nine stations covering 13 sq. miles in the same location. During this period phosphate varied from 10 to 60%. Rapid temporal variations in V' sometimes occurred over a few days and ranged from 21 to 45% in the case of chlorophyll and from 32 to 64% for phosphate. Since this study was conducted under relatively ideal weather conditions, the values quoted may be considered to be representative of maximum σ_2^2 values, but minimal σ_0^2 and σ_1^2 values. Thus Cassie (1962b) showed that patchiness was greatest in calm seas and least at times of turbulent mixing, such as during storms; conversely the operation of gear over the side at a single point, as well as laboratory analyses on board vessels, becomes much more difficult during rough weather and consequently the terms σ_0^2 and σ_1^2 may be expected to increase under such conditions.

Most of the discussion above pertains to overall descriptions of the patchiness of plankton communities in terms of plankton numbers, chlorophyll *a* or nutrients. Quite a different distributional problem arises when a description is required of the total number of species that might define the fauna of a particular area. The question is then a matter of how large a sample must be filtered in order to include all the species. In experiments conducted while following a current drogue, McGowan (1971) showed that for three groups of plankters (fish larvae, molluscs and euphausiids) the amount of water to be filtered varied with the group. In the case of euphausiids there was no increase in the number of species with the volume of water filtered over the range 128 to 1510 m^3, but for fish larvae and molluscs the amount of water to be filtered in order to include all species was in excess of 10,000 m^3. However, the relationship between the number of species and the volume filtered was logarithmic; for example, *ca.* 80% of the fish larvae species were found in *ca.* 1000 m^3 of water. The amount of water filtered by a plankton net can be increased either by increasing the size of the net or the length of the tow. Wiebe (1971) studied the precision of replicate tows with different nets and towing distances and his conclusion was that the length of the towing distance was considerably more important in determining precision than the size of the net.

While the concept of obtaining statistically reliable results from field observations follows a classical pattern common to many biological observations, it is important to note that purely statistical evaluations may often hide the true nature of a biological event. The simplest example of this would be the statistical fitting of a linear relationship to a non-linear function. The introduction of time series data collections can lead to further statistical misrepresentation if a biasing of data occurs (i.e. when the sampling frequency is

greater than the actual frequency of an event: e.g. a 36-hr sampling strategy of a 24-hr event generates a 72-hr frequency in the data). However, the most important event which is masked by purely distributional statistics is the patchiness of distributions and the temporal spatial scales on which it varies. Platt (1972) was the first person to consider this problem in respect to plankton communities and the technique of spectral analysis which he employed has become widely used; a theoretical discussion of the technique has been given by Fasham (1977) and some practical results of the analyses are discussed below.

1.3.2 Areal Distributions

A large amount of data has been collected on the areal distribution of plankton and nutrients. These data are generally the result of observations carried out at points along the cruise track of a research vessel; consequently while the data are useful for surveys of very large areas (e.g. seas, oceans and the hydrosphere) they are of very little use in trophic studies. The latter subject is discussed later in the text, but for the present it must be apparent that plankton distributions mapped from samples collected miles apart are probably not representative of the food supply for a larval or juvenile fish, which may travel less than 100 m in a day. Thus small-scale plankton distributions are particularly important in assessing the food supply and hence, in part, the survival of very young fish.

It has been recognized from the time of the earliest explorers of the hydrosphere that plankton may sometimes occur in dense swarms or blooms (see Bainbridge, 1957, for historical references). Scientific observations (e.g. Barnes, 1949; Barnes and Marshall, 1951) showed that in general planktonic organisms were more often clumped or aggregated than randomly distributed. For example, Cassie (1959) showed in a study on the occurrence of plankton over a distance of 1 m that the distribution of the diatom *(Coscinodiscus gigas)* was non-random. The problem of collecting detailed samples over appreciable distances was solved in 1936 for larger plankters with the invention of apparatus which could be towed behind ships and continuously collect plankton on a slowly moving fine-mesh belt (Hardy, 1936). An adaptation of this apparatus (Longhurst *et al.*, 1966) for studying micro-distributions of plankton has been particularly important for trophodynamic studies. Using this apparatus Wiebe (1970) was able to show areal patchiness in the distribution of zooplankton species over distances of less than 20 m. Some of the results obtained by Wiebe are shown in Fig. 8. From these data it is apparent that there is both a small-scale and a larger-scale patchiness in the distribution of species reported. Due to the mechanical ability of the apparatus, the minimum distance over which the plankton patches could be detected with a Longhurst–Hardy recorder was *ca.* 14 m.

The most extensive descriptions of large-scale plankton species distributions are contained in reports from the Oceanography Laboratory, Edinburgh (published in *Bulletins of Marine Ecology*). Zooplankton data are obtained from samples collected with Hardy plankton recorders towed behind commercial vessels (Hardy, 1936); an example of the descriptive data is given in Fig. 9. The numbers of zooplankton are reported as averages by rectangular sub-divisions for the North Sea and the Atlantic approaches to the British Isles. Similar data are collected for the larger phytoplankton species which are reported as a percentage incidence for each species.

Some data on regional differences in the plankton on an oceanic scale have been reported on for all of the world's oceans. For example, Omori (1965) has defined three oceanic regions in the north Pacific based on the distribution of three species-groups of copepods. These are (1) a cold off-shore water region characterized by *Calanus plumchrus–C. cristatus,* (2) a warm offshore region associated with *Calanus pacificus* and, (3) a neritic water mass region represented by *Pseudocalanus minutus–Acartia longiremis.* The latter region is oceanographically very complex and large differences in plankton concentrations are encountered on oceanic approaches to neritic environments. Additional information on the oceanic distribution of certain

plankton species can be obtained from a study of sediments. For example, in the case of coccolithophores, the calcium carbonate coccoliths are often preserved both in the surface sediments, and in fossil remains. McIntyre and Bé (1967) have used this technique to describe species-specific zones of coccolithophore production in the Atlantic Ocean and similar maps have been drawn to show the distribution of diatoms and planktonic foraminifera.

Various attempts have been made to summarize productivity data on a global scale. Koblentz-Mishke *et al.* (1970) have reported primary productivity data for the world's oceans, based on a review of a large number of reports, and a modified version of their original figure has been redrawn in Fig. 10. From these results it is apparent that over large areas of the Pacific and Atlantic Oceans, primary production is relatively low but that higher primary productivities are generally found in the proximity of land masses. There are some exceptions to this, such as where the South Equatorial current in the Pacific Ocean causes a band of relatively high primary productivity to occur along the equator. Platt and Subba Rao (1975) have provided a detailed summary of primary productivity estimates in different oceans and seas of the world. Their summary indicates that the total primary productivity of the world's oceans is *ca.* 31×10^9 tons carbon per year. Although the Pacific Ocean accounted for approximately one-third of this value because of its area, the Atlantic Ocean was considered to be more productive per unit area, while continental shelf areas were two to three times more productive than the open ocean, as generally indicated by Fig. 10.

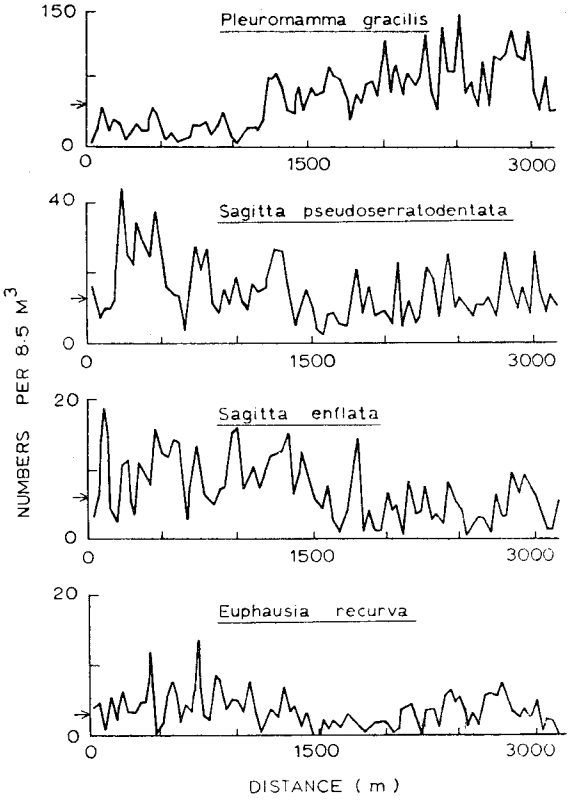

FIG. 8. Plots of abundance versus distance illustrating the presence of large-scale patchiness on which is superimposed smaller-scale patchiness (redrawn from Wiebe, 1970).

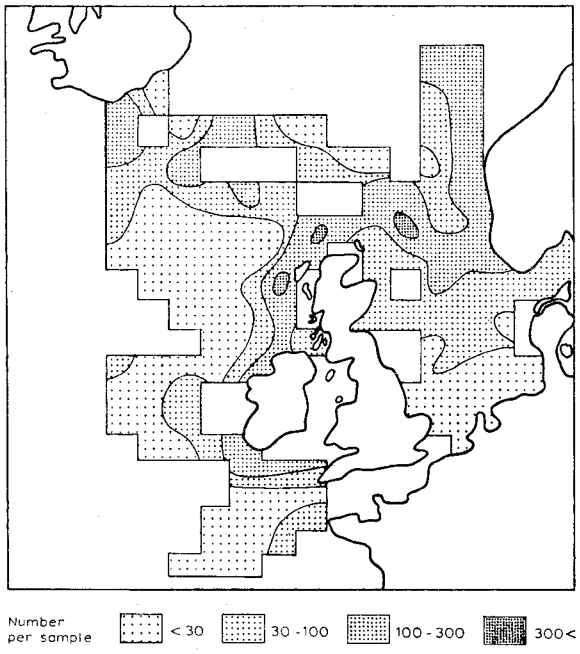

FIG. 9. The distribution of *Calanus finmarchicus,* stages V and VI, from data obtained with a Hardy plankton recorder. Data show the number of animals per sample; blank rectangles indicate insufficient data (redrawn from Colebrook *et al.,* 1961).

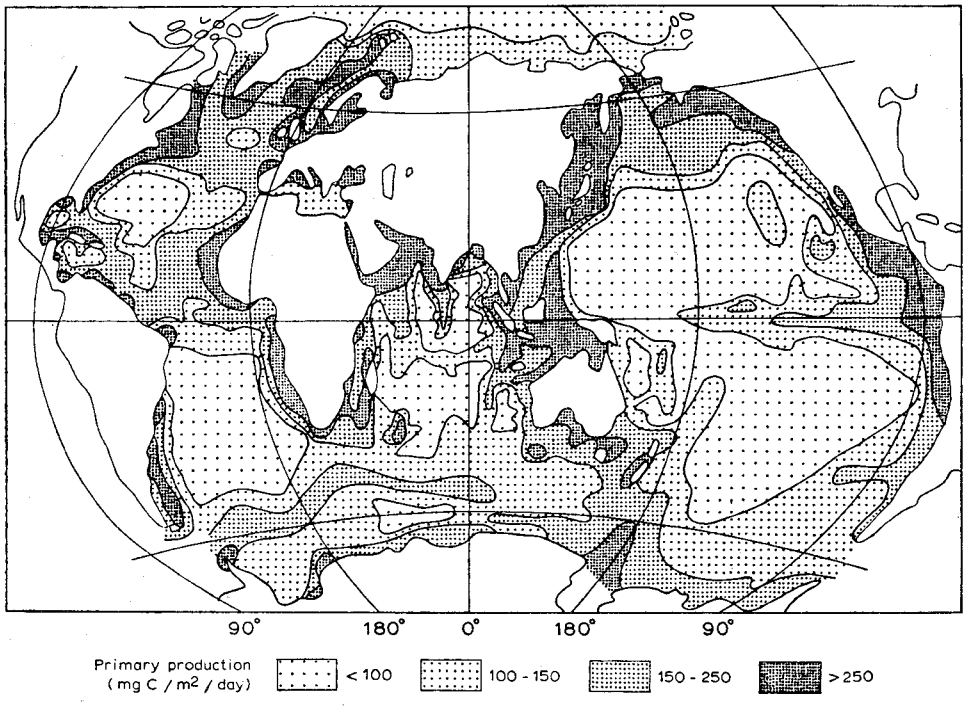

FIG. 10. Distribution of primary production in the World Ocean (redrawn from Koblentz-Mishke *et al.,* 1970).

Differences in biological production associated with near-shore processes will generally give rise to greater patchiness of plankton in neritic compared with oceanic environments. This is true both for large-scale difference in productivity, such as the influence of an estuary on biological production (e.g. Ketchum, 1967) and for small-scale patchiness (e.g. Venrick, 1972). In the latter reference it is shown, for example, that over a 10-mile distance, a lack of aggregation was observed in some species of oceanic phytoplankton; this is interpreted to mean that the randomizing of phytoplankton by turbulent processes is generally greater, relative to biological factors causing differences in productivity, in oceanic compared with neritic environments. Differences in coastal productivity may be associated with several factors — including tides (e.g. Kamykowski, 1973), local morphogeography (e.g. LaFond and LaFond, 1971), and offshore physical processes (e.g. Platt *et al.*, 1972). A special case of higher biological production associated with islands is sometimes referred to as the 'island mass effect'. Gilmartin and Revelante (1974 and references cited therein) generally attribute increased oceanic production in the vicinity of islands to nutrient enrichment caused by local turbulent upwelling in the island passages as well as to the effects of possible nutrient additions from local runoff.

The development of automated analysers has greatly assisted in the description of nutrient distributions in the ocean. An illustration of nitrate distribution obtained with an Autoanalyser® during eight transects of an approximate 10-sq.-mile area is shown in Fig. 11. The illustration has been chosen to show changes in nutrient concentration in an area where nutrient depletion was general but in which there was some upwelling. Over larger areas of ocean, trends in nutrient concentration can be seen which are generally larger than the small-scale differences shown in Fig. 11. This is illustrated in Fig. 12 for nutrient observations carried out with an Autoanalyser® on two cruise tracks across the Pacific Ocean. The greater variability in the results in the western Pacific compared with the Gulf of Alaska reflects

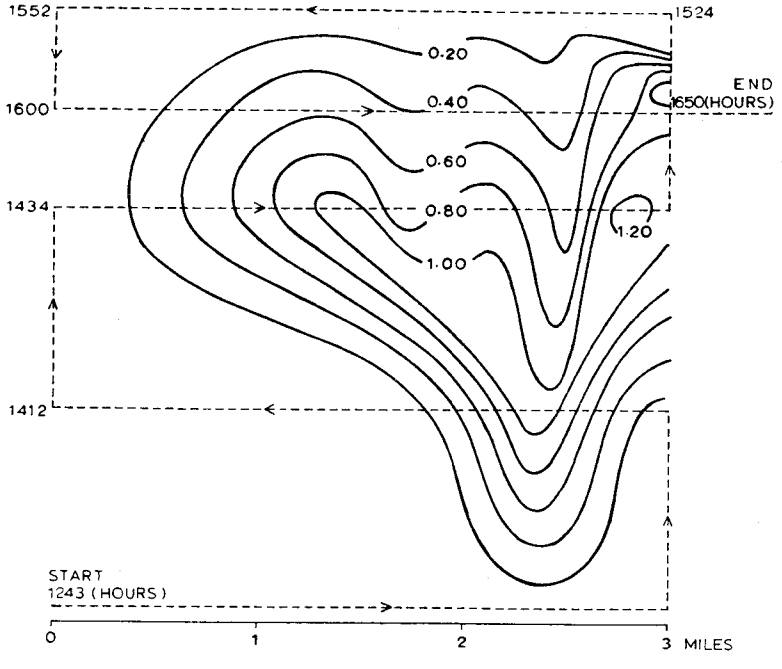

FIG. 11. Nitrate (μg at/l) at the surface off Punta Colnett, Baja California (29° 57'N, 116° 20'W), 9 July 1965. ——— nitrate concentration; — — — cruise track (redrawn from Armstrong *et al.*, 1967).

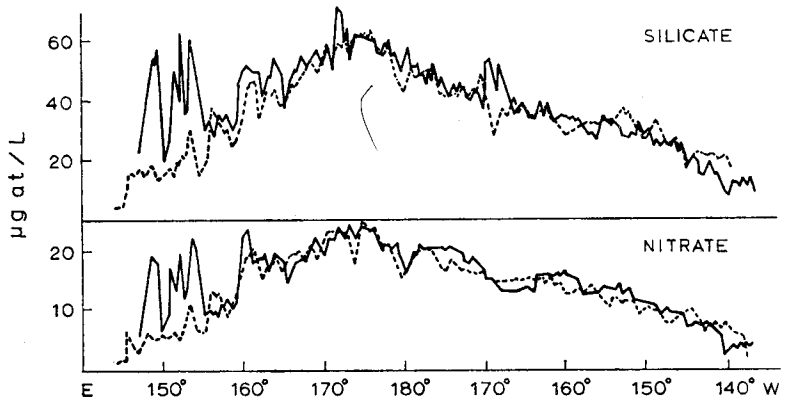

FIG. 12. Silicate and nitrate at 3 m as measured along an eastward and westward cruise track in the subarctic Pacific Ocean during April 1969 (——— west-bound, — — — east-bound, Victoria, B.C., to Tokyo (redrawn from Stephens, 1970).

the mixture of the two very different water masses (the Oyashio and the Kuroshio Currents) off the coast of Asia.

1.3.3 Vertical Distributions

Until quite recently, most vertical profiles of biological parameters were made either with water bottles, which collected samples from discrete depths, or with plankton nets designed to open over some depth interval. The use of automated sampling gear, as well as recent advances in echo-sounding equipment, have greatly improved the data which are now being collected on vertical distributions. Strickland (1968) made direct comparisons between nutrients and chlorophyll *a* as measured in samples pumped from 0 to 75 m and the same data represented by a standard hydrographic cast. Differences between profiles integrated from standard casts and continuously recorded data were particularly marked in the case of chlorophyll *a*; for example the chlorophyll *a* peak at *ca.* 20 m in Fig. 13 measured 2·9 mg/m^3 when detected in pumped samples using a fluorometer but was only 1·3 mg/m^3 according to an integrated curve based on bottle casts at standard depths. Thus the total amount of chlorophyll *a* per m^2 integrated from a bottle cast or a continuous profile also tends to be different; to some extent, however, these errors are smoothed out and variations in chlorophyll *a* per m^2 were found by Strickland (1968) to be less than 25%. Nutrient analyses carried out at the same time showed less variability than the chlorophyll *a* data; nutrient data for integrated bottle and pump samples (i.e. per m^2) generally differed by less than 10%.

The vertical distribution of chlorophyll in the sea generally shows a maximum which may sometimes be found near or at the surface and at other times, at or below the apparent euphotic depth (Steele and Yentsch, 1960). A deep chlorophyll maximum appears to be a seasonal feature of summer vertical profiles as far north as 45° to 50° in both the Atlantic and Pacific Oceans. Anderson (1969) found the chlorophyll maximum off the Oregon coast at *ca.* 60 m was formed by photosynthetically active cells which were apparently adapted to very low light intensity. South of 40°N Venrick *et al.* (1973) have described a deep chlorophyll maximum at 100–150 m. This appears to be a more or less permanent feature of oceanic latitudes as far south as the region of tropical upwelling at 10°, north and south of the equator. In the southern hemisphere the deep chlorophyll maximum starts again south of 10°S and is sometimes found below 200 m.

Large differences in the concentration of zooplankton at specific depths have been encoun-