On the Relationship between Primary Production and Standing Stock of Phytoplankton

By

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Introduction

LOHMANN (1908) was the first investigator to realize the inadequacy of data on total cell concentration for the estimation of the standing stock of phytoplankton. In order to arrive at a true picture of the amounts of plankton present in sea water, he converted his counting results to plasma volumes. LOHMANN's methods involved complicated calculations, and have in general been abandoned in favour of the much simpler process of determining total cell volume. Several workers dealing with marine plankton (e.g., RILEY, 1941, 1957; CUSHING, 1955) or fresh-water plankton (e.g., VERDUIN, 1956; RODHE, VOLLENWEIDER and NAUWERCK, 1958; WRIGHT, 1959) have considered estimates of total cell volume satisfactory for their particular purposes.

It is anticipated (BRAARUD, 1958) that there will be an increasing demand for phytoplankton studies involving counting techniques in conjunction with investigations on primary production according to the ^{14}C method of STEEMANN NIELSEN. Recently, the conversion of counting results to total cell volume values has been recommended (HOLMES, *et al.*, 1958), the implication being that this would facilitate comparisons between the size of the standing stock and the corresponding production values.

There are, however, certain indications that if total cell volume is used as a basis for determinations of standing stock, too much stress will be placed on the large phytoplankton algae in relation to their importance as producers, just as the use of total cell number is likely to cause an over-estimation of small-celled species occurring in large concentrations. RODHE *et al.* (1958) were able to show, with freshwater plankton, that the share in production of the larger algae, i.e., those retained by a plankton net, was in general considerably smaller than their corresponding share in the total cell volume of the populations. These authors apparently used colony size rather than the size of individual cells as a basis for distinguishing the different size categories; it might be

expected that the discrepancy which was noted would have been even larger if this had not been so.

In marine phytoplankton, diatoms frequently constitute the bulk of algae in the large and medium cell size fractions. One conspicuous feature of many planktonic diatoms is the vacuole which, at least in large forms, may occupy a major part of the cell. LOHMANN (1908), in his calculations of plasma volume of diatoms, took particular care to correct his values for the presumably very low content of organic matter in the cell sap. Hence the plasma volumes computed by him mainly represented the thin layer of cytoplasm adhering to the inner cell wall with which the chromatophores are usually associated, in addition to the plasmatic strands traversing the vacuole and supporting the nucleus.

Undoubtedly, in cases where large diatoms form a prominent component of the plankton, only a minor part of the total cell volume of the populations represents photosynthetically active cell substance. In such cases, the relative importance in production of the various species would be represented more closely by their respective plasma volumes than by their cell volumes. An even better solution would be to include in the calculations only those parts of the cytoplasm where the chromatophores are located. The amount of such cytoplasm present in the phytoplankton populations should to some extent depend upon the total cell surface area of the latter. Actually, LOHMANN (1908) observed that the parietal layer of cytoplasm in diatoms usually has a thickness of 1–2 μ. If this is so, total cell surface area, the calculation of which does not offer any greater difficulties than that of total cell volume, may serve as a fairly good estimate of the volume occupied by the chromatophores and the cytoplasm which surrounds them, even when the plankton contains a variety of diatom species.

The present study forms part of a survey of the phytoplankton of the Norwegian Sea in June, 1954. Ecological and biogeographical aspects are being dealt with in a separate paper (PAASCHE, 1960), which also includes a regional comparison between the vegetation and the primary production rates as determined by BERGE (1958). In the following sections are presented some of the quantitative relationships which could be established between cell surface area, cell number, cell volume, and primary production, the purpose of the investigation being an evaluation of the different methods of estimating standing stock size.

Material and Methods

The primary production data were obtained by BERGE as *production capacities* according to a modification of STEEMANN NIELSEN's ^{14}C method (see BERGE, 1958). The production capacity values, expressed as mg C $\times$ 10^{-7} per litre per lux-hour, were determined on surface samples at a light intensity of 4,800 lux, which was considered sufficiently low to justify the assumption that light was the limiting factor for photosynthesis in most or all algae present (see BERGE, 1958). The relationship between production capacity and standing stock could therefore be considered a relatively simple one, mainly determined by the pigment content of the plankton communities. The final production capacity values were corrected so as to represent gross photosynthesis (BERGE, personal communication).

Table 1

Average cell surface areas and cell volumes of some plankton algae

	Number of cells measured	Surface area (μ^2)	Volume (μ^3)
Diatoms			
Chaetoceros borealis	42	9,000	19,000
Chaetoceros debilis	84	730	1,400
Chaetoceros decipiens	54	2,600	9,700
Chaetoceros densus	58	5,000	7,600
Coscinodiscus centralis	25	103,000	2,400,000
Coscinodiscus excentricus	12	8,600	60,000
Fragilariopsis atlantica	14	650	700
Fragilariopsis nana	20	25	15
Nitzschia delicatissima	50	180	70
Nitzschia seriata	40	2,000	2,500
Rhizosolenia alata	13	14,000	37,000
Rhizosolenia hebetata f. *semispina*	40	10,000	18,000
Rhizosolenia styliformis	60	33,700	210,000
Thalassiosira bioculata var. *raripora*	50	400	600
Thalassiosira gravida	43	1,900	5,500
Thalassiothrix longissima	23	17,400	87,500
Others			
Coccolithus huxleyi	31	125	130
Exuviaella baltica	100	450	700
Gyrodinium grenlandicum	20	700	1,000
Phaeocystis pouchetii	10	25	10

The data on standing stock size were obtained by means of the sedimentation technique. The details of the counting procedure have been reviewed elsewhere (PAASCHE, 1960), but possible sources of error will be mentioned briefly below. Estimates of total cell number per litre were arrived at by adding up the concentrations of the different autotrophic plankton species occurring in each sample. For practical reasons, the corresponding values of total cell surface area and total cell volume per litre had to be calculated on the basis of average specific cell surface areas and cell volumes. These were determined using stereometrical formulae in conjunction with cell dimensions which were established for each species in a combined sediment representing a number of selected samples. In Table 1 are summarized specific cell surface areas and cell volumes for the more common algae. Spines were included only in those species where they are known to contain chromatophores.

There was reason to believe that the standing stock estimates could be considered representative only within rather wide limits of the actual populations present in the sea at the time of sampling. Some sources of error, such as those arising from the procedure of sampling and subsampling (see HOLMES and WIDRIG, 1956; LUND, KIPLING, and LE CREN, 1958) evidently affected the cell volume and cell surface area estimates more strongly than the cell number values. The statistical uncertainties relating to sampling concern primarily those species which occur at relatively low frequencies, but which may still form an important component of the plankton because of their large size. Furthermore, it became evident in the course of the plankton counting that the cell counts obtained for this category of algae were influenced by other sources of error as well. It could be shown that especially some of the *Chaetoceros*

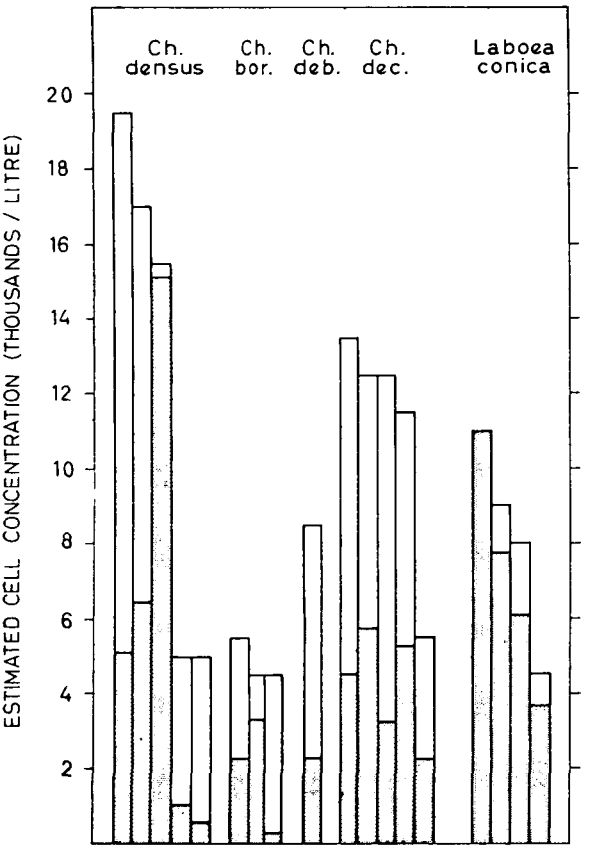

Figure 1. Estimated cell concentrations of *Chaetoceros densus*, *Ch. borealis*, *Ch. debilis*, *Ch. decipiens*, and *Laboea conica* (ciliate) in a number of samples. Estimates based on parallel cell counts in 2 cc cylinders (whole columns) and in 50 cc cylinders (stippled parts).

species did not always sediment completely in the tall 50 cc cylinders in which they were usually counted (Figure 1). Finally, the calculations of specific cell surface areas and cell volumes were clearly subject to considerable error due to the inadequacy of the stereometrical models which were used. Even greater errors probably arose from the application of these average values to populations of atypically small or large cells. In one extreme case it was found that the use of the average cell volume of *Chaetoceros debilis* resulted in an overestimation of the total cell volume of the whole plankton population by as much as 100 per cent.

The total cell number estimates were probably affected little, if at all, by the sources of error just mentioned. In most cases they depended primarily on the concentrations of *Phaeocystis pouchetii* and of small, unidentified flagellates. The difficulties in arriving at correct cell counts for these organisms were enhanced by the circumstance that formalin had been used as a preservative. This reagent is known to destroy some naked flagellates completely, while others are disfigured to such an extent as to make identification very difficult.

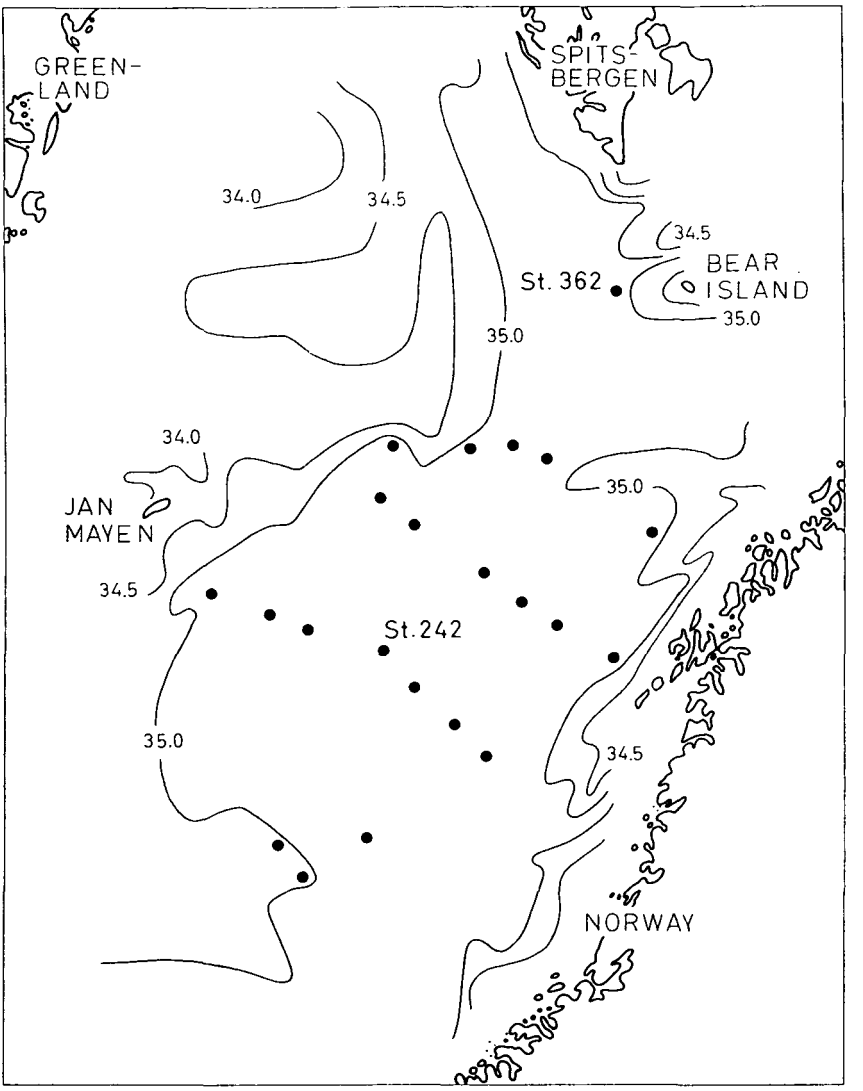

Figure 2. Positions of sampling localities, and isohalines at 20 metres depth according to EGGVIN (see BERGE, 1958).

The sampling programme included localities in all the main types of water occurring in the Norwegian Sea, and provided a large number of simultaneous observations on production capacity and standing stock. The material at hand therefore permitted correlation and regression calculations using four variables, viz. production capacity, cell number, cell surface area, and cell volume. However, before statistical methods could be applied, it was necessary to subdivide the material according to the gross hydrographical features of the sampling localities, in order to reduce the effect of variations in environmental factors upon the relationship between primary production and size of standing stock. Since it was essential that the plankton populations should comprise the

Table 2

Concentrations of the more important species at two localities

(number of cells per litre of sea water)

	Station 242, 0 metres	Station 362, 0 metres
Diatoms		
Chaetoceros borealis	3,180	260
Chaetoceros debilis	67,500	1,455,000
Chaetoceros decipiens	1,000	320
Chaetoceros densus	10,720	720
Coscinodiscus centralis	320	–
Eucampia zoodiacus	–	14,500
Nitzschia delicatissima	105,000	11,500
Nitzschia seriata	20,000	8,500
Rhizosolenia styliformis	1,580	360
Thalassiosira gravida	2,500	20
Others		
Gyrodinium grenlandicum	46,000	6,500
Phaeocystis pouchetii (including small flagellates)	8,744,000	292,000

whole size range of algae, with both small and large species occurring in significant concentrations, only those relationships which were derived for Atlantic water are presented; in the remaining parts of the Norwegian Sea, the vegetation was predominantly small-celled.

The data used in the present study were obtained from surface samples collected at twenty-two stations, the positions of which are shown in Figure 2. All the stations were located in water with a salinity of 34·95 $^{0}/_{00}$ or above, and with surface temperatures ranging from 5°C to 9°C. There was very little stratification in the euphotic zone, and nutrient salt concentrations were probably not so low that they formed a serious limiting factor in photosynthesis (see PAASCHE, 1960). The phytoplankton in these waters was fairly uniform as far as the qualitative specific composition was concerned, but the size of the populations and the relative and absolute concentrations of the different species varied widely. This is demonstrated in Table 2 showing the composition of the communities at two stations.

BARNES (1952) has offered several reasons why biological data obtained during field surveys of marine environments should be transformed in some way or other before statistical methods are applied. In the present case a logarithmical transformation was used. This mode of transformation has been employed in investigations of a similar type by TUCKER (1949) and HOLMES (1958).

Results

The scatter diagrams presented in Figures 3–5 are based on log-transformed values of production capacity and standing stock size. Regression lines are included in the diagrams, and the corresponding regression equations are presented in Table 3. The application of a *t* test showed that while the regressions based on cell surface area and cell volume were clearly significant, the significance of the cell number regression was questionable (Table 3).

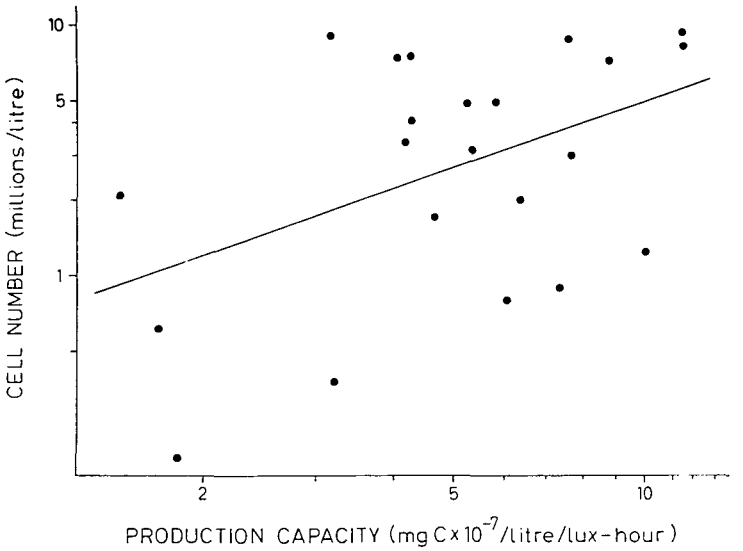

Figure 3. The relationship between cell number and production capacity.

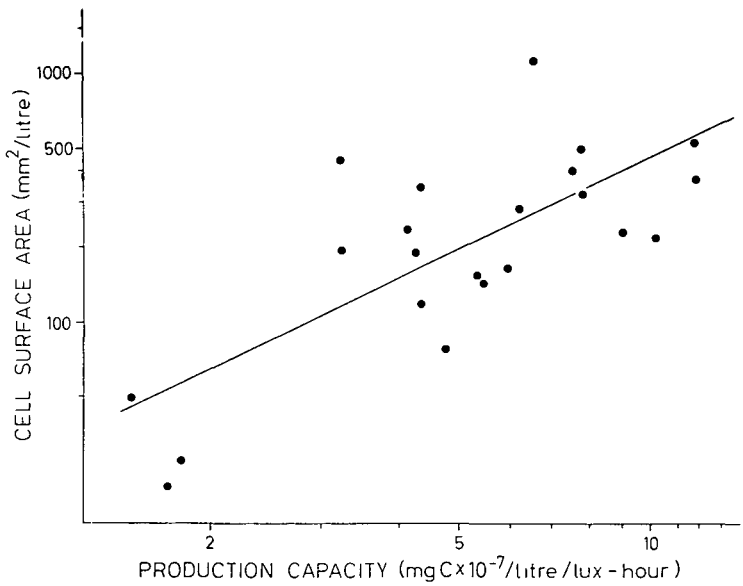

Figure 4. The relationship between cell surface area and production capacity.

Theoretically, a linear relationship is to be expected between non-transformed data on production capacity and standing stock. In the logarithmic scale used, this would mean that the regression coefficients b should not differ from unity. The item $b \pm s_b$ in Table 3 represents the values assumed by b on addition or

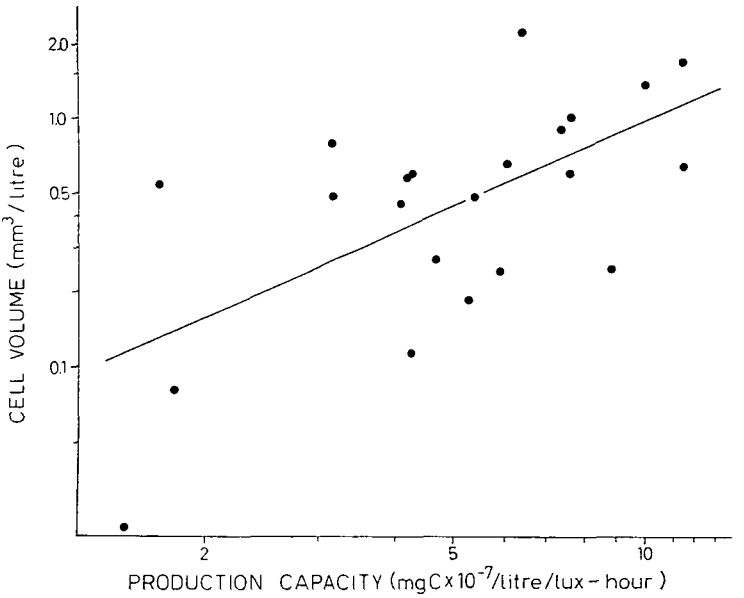

Figure 5. The relationship between cell volume and production capacity.

Table 3

Regression equations for twenty-two surface samples

	Total standing stock estimated as:		
	Cell number	Cell surface area	Cell volume
Units: x =	log production capacity, mg C · 10^{-7} per litre per lux-hour		
y =	log million cells per litre	log mm² per litre	log mm³ · 10^{-3} per litre
Regression equation $y = a + b(x - \bar{x})$....	$y = 0{\cdot}420 + 0{\cdot}865$ $(x - 0{\cdot}699)$	$y = 2{\cdot}299 + 1{\cdot}212$ $(x - 0{\cdot}699)$	$y = 2{\cdot}641 + 1{\cdot}117$ $(x - 0{\cdot}699)$
Probability	0·05–0·02	<0·001	0·01–0·001
$b \pm s_b$	1·250	1·461	1·437
	0·480	0·963	0·797
Standard error of estimate of y.....	0·445	0·288	0·366
Same, re-transformed as % of estimate	+179%	+94%	+132%
	− 64%	−48%	− 57%

subtraction of its standard deviation. An inspection of these values suffices to show that the deviations from unity which do occur are not significant.

The scatter around the regression lines is very considerable, causing large standard errors of estimate (Table 3). An attempt to predict standing stock size from single production capacity values would at most yield an approximate indication of the order of magnitude involved. The question arises whether the present results are at all comparable with those obtained by other investigators using somewhat different methods.

JENKIN (1937) calculated the percentage utilization of incident radiation energy available for photosynthesis in *Coscinodiscus excentricus*. At low light intensities, about 7% of the light falling on exposed cell surface was used. If in the surface area regression (Table 3) the deviation of b from unity is disregarded, the ratio between production capacity and cell surface area is given by the antilogarithm of the difference $(\bar{x} - a)$, which is $2{\cdot}5 \times 10^{-9}$ mg C per lux-hour per mm^2. However, only a fraction of the total cell surface of the populations is simultaneously exposed to light. If all cells were of spherical shape, this fraction would be 0·25 of the total; this value is probably not far removed from the average in any mixed phytoplankton population. Hence, converting to larger units of surface area and light intensity, assimilation in the populations investigated was on the average 1×10^{-3} mg C per kilolux-hour per cm^2 of exposed cell surface. Using the equivalents 1 kilolux = 0·006 g cal per cm^2 per minute (HARVEY, 1957), and 1 mg C = 9·4 g cal, it is found that if the incident energy were to be completely utilized in photosynthesis, the amount of carbon assimilated would be $38{\cdot}3 \times 10^{-3}$ mg C per kilolux-hour per cm^2. Hence the degree of utilization in the populations under investigation was 1/38·3, which is 2·6%. Considering that the methods used are rather different from those employed by JENKIN, the agreement with the value obtained by her seems quite good. At any rate, since the percentage utilization is lower, rather than higher, than the standard set by JENKIN's value, it would seem that the possible failure to recover some of the primary producers in the quantitative samples did not on the whole seriously affect the established relationship between cell surface area and production capacity.

A similar check could be applied in the case of the cell volume regression. STEEMANN NIELSEN and HANSEN (1959) have shown that in temperate surface plankton, the rate of assimilation at low light intensities is about 0·36 mg C per kilolux-hour per mg chlorophyll. In the same way as above for cell surface area, the equation relating cell volume to production capacity (Table 3) is found to correspond to a value of $1{\cdot}14 \times 10^{-3}$ mg C per kilolux-hour per mm^3. According to GILLBRICHT (1952), 1 μg of chlorophyll is contained in 0·139 mm^3 of diatom plankton, which means that 1 mm^3 of such plankton has a chlorophyll content of $7{\cdot}2 \times 10^{-3}$ mg. Therefore, the rate of assimilation per unit of chlorophyll which according to the regression equation was the most likely one at the low light intensities used, was 1·14/7·2, or 0·16 mg C per kilolux-hour per mg chlorophyll. Again, the agreement with the value given by the earlier investigators must be considered quite satisfactory.

The various correlation coefficients which could be derived are presented in Table 4. The probabilities of the coefficients according to a t test are included in the table.

The three coefficients in the first half of the table indicate the degree of mutual dependence present between values of standing stock size obtained by means of the different methods. Actually, bearing in mind the limited number of observations, too much stress should not be placed on the numerical values of the coefficients and the differences between them. But there can be no doubt that the tendency brought out by the coefficients is real. Those small-celled organisms which form the major fraction of a population in terms of cell number contribute very little to its total cell volume, the latter being instead determined primarily by the larger species present. Apparently, in the type of plankton investigated, there was a very low degree of correlation between cell

Table 4

Correlation coefficients for twenty-two surface samples

	Correlation coefficient	Probability
Cell number / Cell surface area	0·50	0·02–0·01
Cell number / Cell volume	0·16	...
Cell surface area / Cell volume	0·72	<0·001
Cell number / Production capacity	0·45	0·05–0·02
Cell surface area / Production capacity	0·74	<0·001
Cell volume / Production capacity	0·62	0·01–0·001

number and cell volume. This result was to be expected in view of the fact that the numerical proportion between large and small algae was by no means constant at the different sampling localities. Cell surface, on the other hand, showed a fair degree of correlation with cell number as well as with cell volume. This agrees with the very reasonable assumption that values of total cell surface area rest more evenly on all size categories of plankton algae.

These considerations may be illustrated more specifically using data from one station (242) where the composition of the phytoplankton was in several respects rather close to the average for all the localities investigated. The diagrams in Figure 6 show the relative proportions of the more important species in

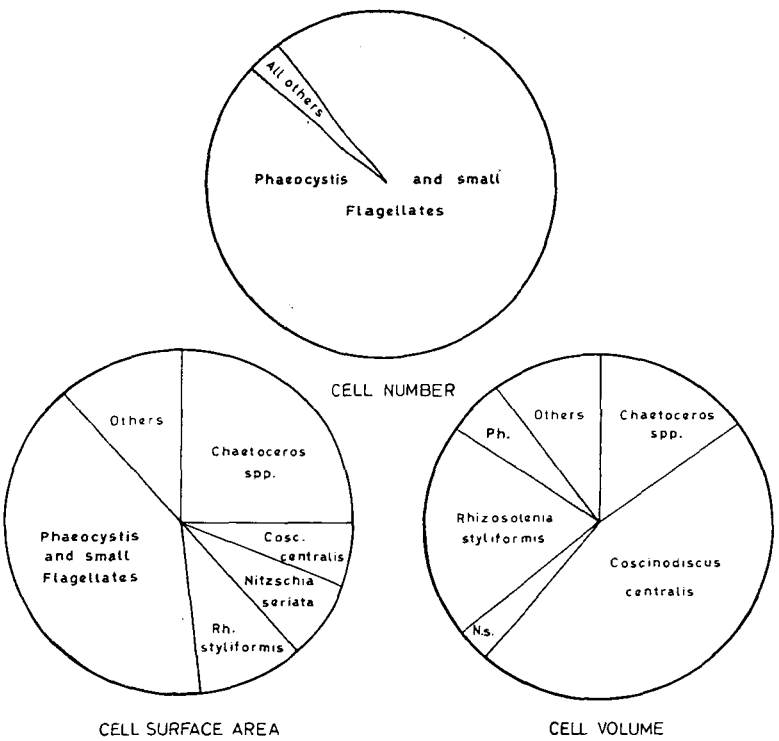

Figure 6. Relative proportion of various species in total cell number, total cell surface area, and total cell volume at station 242.

the total standing stock present, estimated on the basis of cell number, cell surface area, and cell volume, respectively. Numerically, *Phaeocystis pouchetii* and unidentified naked flagellates formed by far the most important fraction of the population. If cell surface was used, various diatoms of medium or large size were about as prominent as *Phaeocystis* and small flagellates. Finally, in terms of cell volume, a major fraction of the total standing stock was accounted for by large diatoms of the genera *Rhizosolenia* and *Coscinodiscus*.

The remaining three correlation coefficients in Table 4 relate production capacity to standing stock estimated according to the respective methods. The highest correlation was present when cell surface area was used as a unit, while the use of cell volume and especially of cell number led to lower correlation values. A result of this kind was to be expected, provided that the reasons presented above for adopting cell surface area as a measure of standing stock of producers are valid. It should be pointed out however, that from a statistical point of view, the differences between the three coefficients may probably just as well be fortuitous. If a larger number of data had been available, and care had been taken to avoid some of the more obvious errors such as those arising from the use of an inadequate preservative, or the use of average specific cell dimensions, it might have been worthwhile to carry the statistical investigation further. By employing statistical methods for testing the possible significance of differences between correlation coefficients, or by applying analogous tests to the corresponding regressions (see WILLIAMS, 1959), it might have been possible to obtain more conclusive evidence in favour of one or the other method of determining size of standing stock.

Discussion

It appears that photosynthesis in phytoplankton shows a high degree of correlation with the chlorophyll content, at least when light intensities are low (RYTHER, 1956b), although a strict proportionality is not to be expected (STEEMANN NIELSEN and HANSEN, 1959). Therefore, if it is assumed that the use of cell surface area is the most adequate method for the estimation of standing stock of primary producers, it follows that the chlorophyll content per unit of cell surface area should be more nearly constant in the different algal species than either chlorophyll per unit of cell volume or per cell.

Starting from data on number of cells per μg chlorophyll in various phytoplankton species, presented by HARVEY (1934), KREY (1939), GRAHAM (1943), and ATKINS and PARKE (1951), and using available information on cell dimensions, calculations were made of cell surface area per μg chlorophyll. The results of these calculations are presented in Table 5. For the sake of comparison, values of cell volume per μg chlorophyll, computed from the same set of data, are included in the table.

The selection of species used requires some comment. Of diatoms on which relevant information is accessible, *Coscinodiscus centralis* and *Nitzschia seriata* are not included in the table. A possible misprint in the original table by ATKINS and PARKE (1951) precludes the use of the data supplied by these authors on *C. centralis*. The form of *N. seriata* studied by GRAHAM (1943) was by him described as "minute", and it seems doubtful whether the average cell dimensions of this species can be used in connexion with the data presented by

Table 5

Number of cells, cell surface area, and cell volume per unit of chlorophyll in some phytoplankton species

Species	Number of cells per μg chlorophyll	Source	Specific cell surface area μ^2	Specific cell volume μ^3	Source for cell dimensions used	Cell surface area (mm^2) per chlorophyll (μg)	Cell volume ($\mu^3 \cdot 10^6$) per chlorophyll (μg)
Diatoms							
Biddulphia regia . .	745 *)	HARVEY (1934)	107,000	2·2 mill.	HUSTEDT (1930)	80	1,640
Rhizosolenia alata	23,500 *)	HARVEY (1934)	14,000	37,000	present invest.	330	870
Thalassiosira gravida	123,000	ATKINS & PARKE (1951)	1,600	4,500	ATKINS & PARKE (1951)	195	550
Chaetoceros vanheurckii . . .	170,000	GRAHAM (1943)	1,800	5,430	CUPP (1943)	305	920
Chaetoceros gracilis	286,000	KREY (1939)	220	230	CUPP (1943)	63	66
"*Nitzschia closterium* f. *minutissima*" . .	743,000	ATKINS & PARKE (1951)	35	18	ATKINS & PARKE (1951)	26	13
Others							
Gymnodinium sp.	58,000	ATKINS & PARKE (1951)	700	1,700	ATKINS & PARKE (1951)	40	100
Dicrateria inornata	563,000	ATKINS & PARKE (1951)	50	33	ATKINS & PARKE (1951)	28	19

*) Converted from cells per HPU, using the factor 0·3 HPU per μg chlorophyll (BANSE, 1956).

that author. One dinoflagellate and one chrysophycean are included as a supplement to the more complete set of diatoms listed.

Calculations of the present kind are necessarily subject to considerable error. Nevertheless, the data in Table 5 seem to indicate that there is less variation between species with respect to the ratio between cell surface area and chlorophyll content, than is the case with either of the two other ratios. This is seen most clearly from the range of single values in the respective columns. For cell surface area/chlorophyll, the difference between the highest and the lowest value is about 13-fold, while it is 125-fold for cell volume/chlorophyll and 1000-fold for cell number/chlorophyll. A comparison with the data on cell dimensions shows that, as expected, small species have more cells per unit of chlorophyll than large ones, while conversely large species have more cell volume per unit chlorophyll than small ones. With cell surface area, however, there is no such marked tendency. Clearly, this fact may be interpreted as a confirmation of the assumption that the measurement of plankton populations

in terms of cell number or cell volume leads to over-emphasis of the role played in production by small or large plankton algae, respectively. It is especially noteworthy that in the case of very large diatoms such as *Biddulphia regia*, where the great vacuoles cause very high values of cell volume per unit chlorophyll, the ratio cell surface area/chlorophyll differs but little from that of the smallest phytoplankton species.

Still, judging from Table 5, there seem to exist considerable variations between species with respect to the amount of cell surface area per unit of chlorophyll. Such variations are of course to be expected, since the structural factors which govern the chlorophyll content in the highly differentiated plankton algae presumably are very complex and only in part correlated with the extent of cell surface.

Inter-specific variations in chlorophyll content obviously contributed to the residual variation around all the regression lines, though they may have been of less importance in the surface area regression (Figure 4) than in the volume and cell number regressions (Figures 3 and 5). There are other factors as well which, although they are of a less fundamental order, may have had a similar effect. The chlorophyll content of plankton algae is known to vary intra-specifically within quite wide limits, depending upon environmental conditions such as light intensity (RYTHER, 1956a; STEEMANN NIELSEN and HANSEN, 1959), nutrient salt concentrations (HARVEY, 1953; YENTSCH and VACCARO, 1958), or temperature (MARGALEF, 1954). The importance of these factors in regulating the general interrelationship between photosynthesis and standing stock has on the whole received much attention (e.g., RILEY, STOMMEL, and BUMPUS, 1949). Especially noteworthy are the diurnal variations in photosynthetic capacity which have been shown to result from high light intensities during the day (DOTY and OGURI, 1957); they may be accompanied by short-term variations in chlorophyll content (YENTSCH and RYTHER, 1957). Although little specific information is available, it seems probable that the different species in a plankton community are not influenced in the same way by changes in the environmental conditions, and the effect of the latter on the relationship between the community as a whole and its production capacity is therefore presumably of quite a complex nature.

It is not likely that the data used in the present study were seriously influenced by local or diurnal variations in environmental factors. According to BERGE (1958), light intensities just below the surface in the Norwegian Sea in June 1954 were 7,000 lux or lower, which is very little compared with the intensities needed to produce marked short-term variations in photosynthetic capacity. Although the samples were collected at all hours, the possibility of such variations can be disregarded. As was stated in an earlier section, temperature was rather uniform throughout the sampling area, and nutrient limitation was probably not serious.

The possible proportionality between photosynthesis and cell surface area in large diatoms has several implications which however, with the present state of knowledge, can be the subject of theoretical consideration only. It has been assumed (MUNK and RILEY, 1952), that the degree to which a given nutrient salt concentration of the medium affects the rate of assimilation in diatoms, as measured by the time required for cell division, is primarily determined by the ratio between cell surface area and cell volume. However, in the large and strongly vacuolized diatoms, that part of the cytoplasm in which

photosynthesis is going on might have just as much cell surface at its disposal for the absorption of nutrient salts as would be the case in smaller forms lacking vacuoles. Consequently, they would have the same possibilities as the latter for satisfying those nutritional needs which are immediately linked with the assimilation processes, even when nutrient salt concentrations in the medium are so low as to be generally limiting to photosynthesis. Nor should the nutrient salt concentration of the sea water be more strongly limiting to cell division in the large diatoms, unless there is a specific need for keeping the nitrate and phosphate concentrations in the cell sap on a level more or less corresponding to the nitrogen and phosphorus content of the cytoplasm itself. Whether this is so is still an open question which can only be answered by future investigations.

The fact remains however, that on the whole large diatoms probably have a lower rate of cell division than smaller ones. This is brought out by field observations made by numerous investigators, showing that even during the spring outburst, the larger diatom species always occur in lower cell concentrations than at least some of the smaller algae. The few existing data on division rates under culture conditions (BRAARUD, 1945; LANSKAIA and SIVKOV, 1950) or in nature (MARGALEF, DURAN, and SAIZ, 1955) might possibly be taken to indicate the same phenomenon.

The most likely explanation might be that in large diatoms, a relatively smaller fraction of the energy ultimately deriving from photosynthesis is available for the reproduction of the cytoplasm including the photosynthetic apparatus. GROSS and ZEUTHEN (1948) found that the ionic composition of the cell sap in *Ditylum brightwellii* is probably different from that of sea water. Cyanide, which is known to inhibit respiration, was found to cause plasmolysis in the *Ditylum* cell. If the findings of GROSS and ZEUTHEN are representative, it would seem that in large diatoms, part of the respiratory energy is continually being used for the maintenance and reproduction of the vacuole.

Acknowledgements

The author wishes to express his gratitude to the members of the Research Division of the Fisheries Directorate, Bergen, who collected the phytoplankton samples during a cruise with the research vessel "G. O. Sars". Thanks are due especially to Mr. Grim BERGE, who placed the primary production data obtained by him at the author's disposal.

Summary

1. Phytoplankton samples collected in Atlantic water in the Norwegian Sea in June 1954, were worked up according to the sedimentation method. Standing stock size was expressed in terms of cell surface area as well as of cell number and cell volume. Production capacities had been determined by BERGE, using his modification of the ^{14}C method.

2. Using log-transformed data on standing stock and production capacity, regressions and correlations were calculated for surface samples.

3. The observed relationships between standing stock size and production capacity agreed well with similar observations by earlier authors.

4. The results supported the hypothesis that the total cell surface area of

plankton communities rests more evenly on all size categories of plankton algae than do either total cell volume or total cell number. However, it was not possible to produce conclusive statistical evidence that cell surface area is the most adequate measure of standing stock of primary producers.

5. On the basis of data presented by various investigators, it was demonstrated that the chlorophyll content per unit of cell surface area in a number of phytoplankton species is more nearly constant than chlorophyll per volume unit or per cell.

6. The low division rate of large diatoms was tentatively explained as resulting from a continual expenditure of energy in the maintenance and reproduction of the vacuole.

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